Inventory and monitoring of biodiversity : an assessment of methods and a case study of Glacier National Park, MT

by Diane Marie Debinski

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Biological Sciences
Montana State University

Abstract:
Biodiversity is currently threatened around the world, yet humankind knows little about its distribution or rates of loss. Because biodiversity can be defined at the level of species, habitats, or genes, temporal changes can be assessed at several different levels. These changes may indicate responses to natural disturbances, human-induced changes, or long-term environmental trends. However, no standard analysis techniques for biodiversity assessment have yet been developed. In order to protect biodiversity or to use it as an indicator of environmental change, baseline data must be collected and analysis techniques must be developed.

This research applies and evaluates sampling and analysis techniques for inventory and monitoring of biodiversity. Glacier National Park is used as a case study. Birds and butterflies were chosen to demonstrate species diversity inventory. The butterfly, Euphydryas gillettii, was used to demonstrate genetic diversity assessment.

Biodiversity assessment sites were established throughout a range of habitats and monitored during the summers of 1987, 1988 and 1989. Thirty-three sites were monitored for birds and twenty-four sites were monitored for butterflies. Presence/absence sampling was used to classify species commonness and rarity. Goals accomplished included 1) describing the current species composition, 2) identifying diversity hotspots and sites supporting rare species, and 3) creating a baseline for assessing change.

A discourse on biodiversity assessment would not be complete, however, without addressing the problems inherent in biodiversity assessment and management. Replication in both time and space is necessary to distinguish natural background variation in species distribution from true changes and sampling artifact. It is often difficult to reconcile the need for sampling replication within a habitat type with the need to survey a large, highly diverse ecosystem. Further, it is extremely difficult to use biodiversity as an environmental indicator unless relationships between species and environmental changes are specific and well-understood. Finally, management for biodiversity requires a large-scale perspective on ecosystem management and a modest understanding of the natural history of the species examined. Unless biodiversity assessments are done thoroughly and carefully, they will have limited descriptive or predictive value.

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A thesis submitted in partial fulfillment
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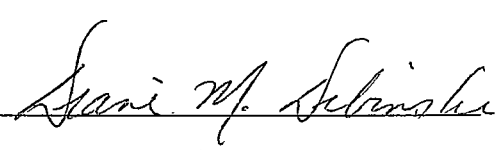
Signature 

Date 1 June 1991

"For someone studying natural history,
life can never be long enough"

Miriam Rothschild, British Entomologist,
television interview on Nova, 1986

VITA

Diane Debinski was born in Baltimore, Maryland on October 26, 1962. She became fascinated by natural history at the age of nine on her first trip to the mountains of western Maryland. She earned a dual B.A degree in Biology and Environmental Studies in 1984 from the University of Maryland at Baltimore County. She went on to find her fundamental niche at the University of Michigan's School of Natural Resources. There she studied Natural Resource Policy, Economics, and Management, hoping to gain a broader perspective on conservation issues. Her thesis was entitled "Using Decision Analysis to Improve Recovery Planning for Endangered Species", and she obtained her M.S. in 1986. She took a year's sabbatical from academia after the M.S., spending time studying crested auklets in the Aleutian Islands, AK, then studying politics in Washington, D.C. Next stop was Bozeman, MT for a degree in Conservation Biology. The Bozeman program led her into this research project at Glacier National Park, three years of incredible field work which included a few grizzly encounters. But the bears didn't put too much of a damper on data collection; they simply added some spice to the backcountry camping. If given the option, she'd do it all over again in an instant.

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TABLE OF CONTENTS

TABLE OF CONTENTS--Continued

TABLE OF CONTENTS--Continued

TABLE OF CONTENTS--Continued

Page

LIST OF TABLES

LIST OF TABLES--Continued

LIST OF TABLES--Continued

LIST OF FIGURES

LIST OF FIGURES--Continued

ABSTRACT

Biodiversity is currently threatened around the world, yet humankind knows little about its distribution or rates of loss. Because biodiversity can be defined at the level of species, habitats, or genes, temporal changes can be assessed at several different levels. These changes may indicate responses to natural disturbances, human-induced changes, or long-term environmental trends. However, no standard analysis techniques for biodiversity assessment have yet been developed. In order to protect biodiversity or to use it as an indicator of environmental change, baseline data must be collected and analysis techniques must be developed.

This research applies and evaluates sampling and analysis techniques for inventory and monitoring of biodiversity. Glacier National Park is used as a case study. Birds and butterflies were chosen to demonstrate species diversity inventory. The butterfly, *Euphydryas gillettii*, was used to demonstrate genetic diversity assessment.

Biodiversity assessment sites were established throughout a range of habitats and monitored during the summers of 1987, 1988 and 1989. Thirty-three sites were monitored for birds and twenty-four sites were monitored for butterflies. Presence/absence sampling was used to classify species commonness and rarity. Goals accomplished included 1) describing the current species composition, 2) identifying diversity hotspots and sites supporting rare species, and 3) creating a baseline for assessing change.

A discourse on biodiversity assessment would not be complete, however, without addressing the problems inherent in biodiversity assessment and management. Replication in both time and space is necessary to distinguish natural background variation in species distribution from true changes and sampling artifact. It is often difficult to reconcile the need for sampling replication within a habitat type with the need to survey a large, highly diverse ecosystem. Further, it is extremely difficult to use biodiversity as an environmental indicator unless relationships between species and environmental changes are specific and well-understood. Finally, management for biodiversity requires a large-scale perspective on ecosystem management and a modest understanding of the natural history of the species examined. Unless biodiversity assessments are done thoroughly and carefully, they will have limited descriptive or predictive value.

CHAPTER 1

INTRODUCTION

Biodiversity is the variety among living things: variety in ecosystems, habitats, species, and genes. Biodiversity is currently threatened around the world, yet humankind knows little about its distribution or rates of loss. In most cases, we don't even understand ways in which biodiversity is important to the human race. The lack of a comprehensive data base to document biological diversity is a major problem. In order to protect biodiversity or to use it as an environmental indicator, baseline data must be collected and analysis techniques must be developed. The goal of the research presented here is to begin to develop techniques for inventorying and monitoring biodiversity.

Threats to Biodiversity

Biodiversity is threatened both in the tropics and in temperate climes. For example, Montana's natural heritage program of the Nature Conservancy is specifically concerned with several globally imperiled species such as the whooping crane, Coeur d'Alene salamander, black footed ferret, piping plover, arctic grayling, and pallid sturgeon (Genter, pers.

comm.).

As Huntley (1989) summarizes the problem, "Neither Darwin nor Wallace could have envisaged that the biological wealth they were revealing to the world at the start of the Industrial Revolution would be heading for destruction within the next century."

Only a few years ago, biologists believed that the earth supported 3 to 5 million species of all living organisms. However, current research in the tropics suggests that there may be 30 million species of insects alone. Many species at risk of extinction are not even known to science, and their ecological roles and potential values to humans are also mysteries (Wolf 1987). The earth is currently losing species at a rate 1,000 to 10,000 times faster than the normal evolutionary rates (Huntley 1989). Not since the Cretaceous Period, about 65 million years ago, has the earth experienced such a high rate of extinction. During mass extinctions the fittest are not necessarily the ones that survive. Survivors tend to be the ecological opportunists, weedy species that reproduce quickly, eat indiscriminantly, and tolerate a wide range of conditions (Wolf 1987).

The threats to biological diversity in any forest, preserve, or park can be separated into two types, exogenous and endogenous. Exogenous threats manifest themselves as acid rain, pesticide drift, exotics, or loss of migratory

habitat, and they are initiated from outside the protected area. Endogenous effects occur within the protected area, and include fragmentation and insularization, decreased immigration or elimination of vital resources inside a reserve.

Humans can be regarded as diversity generators through the use of laboratory and agricultural research. The type of diversity generated in this case is genetic diversity. However, the amount of genetic diversity we generate in no way compensates for the amount of species and habitat diversity which is being lost. Indeed, humans do not create genes; we simply re-arrange existing genes. As such, our ability to generate biodiversity should not be overestimated.

The Value of Biodiversity

The Office of Technology Assessment's (OTA) report, "Technologies to Maintain Biological Diversity", sums up the value of biodiversity as follows: "Human welfare is inextricably linked to, and dependent upon, biological diversity". Diversity is necessary to 1) sustain and improve agriculture, 2) provide opportunities for medical discoveries and industrial innovations, and 3) preserve choices for addressing unpredictable problems and opportunities for future generations. Biological diversity is the basis of adaptation and evolution and is intrinsic to

all ecological processes. It contributes to research, education, cultural heritage, recreation and tourism, the development of plant and animal domesticates, and the supply of harvested resources (OTA 1987).

Hotspots of Biodiversity

Before we can create management strategies and political policies to protect biodiversity, we must understand its spatial and temporal distribution. Our distribution knowledge gap is evident both in tropical and temperate forests. For example, a recent survey of 19 trees in a Panamanian tropical forest produced 950 species of beetles, 80% of which were previously unknown to science (Reid and Miller 1989). Terrestrial species richness is often correlated with elevation and precipitation. However, regions rich in one taxonomic group are not necessarily rich in other taxonomic groups.

Aspects of rarity can be separated into two categories: endemism and scarcity. Endemic species are found only within a limited geographic area, whereas scarce species may have a wide distribution, but are abundant nowhere. Endemism is commonly associated with areas of high species diversity. Endemic species are particularly vulnerable to extinction as their ranges are often restricted to small areas, and if a population goes extinct, there is a lower probability of recolonization from other areas. Endemic

species-are often found on mountains, islands, peninsulas, and other areas where dispersal is restricted by geography or where unique conditions lead to the evolution of specialized characteristics. There are more endemic plant species relative to animal species, probably because of the dispersal limitations of plant species (Reid and Miller 1989).

Scarcity is best exemplified by animals at the top of the food chain, e.g. bears, eagles, sharks, or large cats. The size of their home range limits the density of their populations. Habitat fragmentation can have serious consequences for such organisms, making them much more vulnerable to extinction than more densely populated species.

Preserving Biodiversity

The major reservoirs of biodiversity in the U.S. are in public lands, and the vast majority of protected areas in these lands are the national parks. Indeed, creating parks and nature reserves has been the traditional method of preserving biological diversity worldwide. But setting aside or reserving these land areas is not a complete solution to the problem. Often these reserves are not large enough, and in many developing countries it is extremely difficult to protect them from poachers. Even if establishment of parks and reserves were sufficient, Wolf

(1987) estimates that 1.3 billion hectares would have to be set aside to conserve representative samples of all the earth's ecosystems. Currently 425 million hectares in 3,500 areas worldwide are "protected."

Newmark (1987) conducted a survey of national parks in the Rocky Mountains of the U.S. to analyze species extinction as a function of park area. Parks less than 4000 square km had lost from 23% to 43% of their mammal species since their establishment. Only the largest parks which contained 4000 to 21,000 sq. km had retained a high percentage of their native inhabitants. The loss of species evidently occurred so slowly that it went unnoticed. These results have been criticized, however, due to the disagreements regarding the data (Quinn et al., in press)

MacArthur and Wilson's island biogeography study (1967) demonstrated a direct relationship between the area of an island and the number of species it can sustain. Refuges can be viewed as islands in a sea of inhospitable terrain. Reducing habitat size increases the risk of extinction, while increasing the distance of the island from the nearest source of colonists reduces the chances of recolonization after local extinction. "Faunal collapse" occurs as refuges become more and more isolated by development (timber harvest, housing projects, oil drilling, etc.).

Biodiversity and Ecosystem Stability

No agreement exists among ecologists regarding the relationship between biological diversity and ecosystem function. Three hypotheses have been proposed that underscore this lack of agreement: (1) diversity and function are intimately linked on a one-to one basis, (2) considerable loss of diversity may occur without impairing ecosystem function, or (3) the functional capacity of an ecosystem is likely to be impaired long before diversity declines (Cairns and Pratt 1986).

Species diversity has no consistent relationship with ecosystem productivity. Species-rich tropical rainforests are extremely productive, but so are coastal wetlands that have relatively low diversity. For example, in *Spartina* salt marshes one species provides almost all of the primary productivity. The loss of species can either increase or decrease primary productivity. For example, a loss of mycorrhizal fungi decreases the growth rate of plants on which they depend. Conversely, extirpation of sea urchins and limpets allows an increase of algal productivity in the intertidal zone (Reid & Miller 1989).

Advances in ecology have provided us with some specific relationships, however, that will aid our understanding of how environmental changes affect species diversity and how changes in species diversity affect certain ecosystem

processes and function. For example Reid & Miller (1989) outline the following relationships:

(1) Species composition is continually changing in most communities, and species-specific responses to environmental changes do not necessarily occur in congress. Thus, in preserving biodiversity our goal should not always be preservation of the exact present community, but rather maintenance of the species and the ecosystem processes.

(2) Species richness can sometimes be increased by increasing the diversity of habitats within an ecosystem, but this intervention can be a "double-edged sword." Such intervention may result in preserving those species less vulnerable to extinction (i.e., those that thrive in early successional habitats and benefit from disturbance) rather than those at greatest risk (i.e., those that require large tracts of late successional habitats).

(3) Habitat patchiness influences both the composition of species in a ecosystem and the interactions among species. For example, heterogeneous environments tend to have more stable predator-prey or host-parasite interactions, as there are escape patches that prevent total extinction.

(4) Periodic disturbances such as fires, hurricanes, and floods are important in creating patchy environments that foster high species richness and influence the interactions among species. Consequently, preservation of species diversity may require management of the environment so as to preserve natural patterns of succession.

(5) Species richness is influenced by size and isolation of habitat patches, as well as the transition zones between habitats. Such "ecotones" often support species that would not occur in continuous habitats (Lovejoy et al. 1986).

(6) Some communities have "keystone" species which exhibit a disproportionate influence on the characteristics of an ecosystem. In worst case scenarios, local extinction of a keystone species may cause a "cascade effect" whereby other species within the community dwindle in number or are extirpated themselves.

Methods of Biodiversity Assessment

If biodiversity is to be protected, it must be inventoried and monitored. Establishment of an inventory

and monitoring program is not an easy task, regardless of the ecosystem. In order to conduct such an assessment, the researcher should be familiar with the landscape and topography of the area, competent in using a suitable and efficient sampling method, have reasonable taxonomic ability, and a realization of the kinds and approximate numbers of samples to be taken in the study (Gauch, 1982).

There have been several attempts to set up biodiversity inventory and monitoring programs, both at the level of a national park survey and at the level of a nationwide survey. Sequoia National Park has a program to sample biodiversity at 3400 Universal Transverse Mercator (UTM) intersections within the park. UTMs are geographic marker lines similar to longitude and latitude lines that are separated by 1 km. The survey concentrates on vegetation analysis, but any bird, mammal, reptile, or amphibians identifiable by sight or sound from within the plot (regardless of distance) are noted. Sampling radius from the UTM intersection varies according to the scale and mobility of each class of organisms. Systematically, each of these sites is being monitored over time, and the information is being integrated into a Geographic Information System (GIS). The most expensive and time-consuming element of this project, as in most biodiversity assessments, is the field inventory. Approximately 500 of the 3400 sites were sampled during the first six years of

the project (1985-1991). The budget for this work was approximately $40,000 per year, and there were five employees involved in the sampling (Esperanza, pers. comm.)

A well-established nationwide inventory and monitoring program for species diversity is the breeding bird survey. This standardized survey is conducted throughout the U.S. at various sites twice a year. Volunteers travel designated roads, stopping every 1/2 mile to conduct an audio and visual census for 3 minutes. The resulting databases are invaluable for detecting large-scale regional trends. These surveys, however, do not provide the level of sampling intensity necessary to monitor bird populations in a reserve such as Glacier National Park. For example, there are only three regions within this park that are surveyed in the breeding bird survey (Babb, Polebridge, and a portion of the Going to the Sun highway), and all of these sites are along roads. Wilderness areas are neglected, and a large portion of the park is ignored. Further, based upon the results of this research, three minutes twice a year does not approach the amount of time necessary to conduct a thorough census.

Noss (1990b) proposes a heirarchical framework for choosing biodiversity indicators on a nationwide scale. Proceeding from top down, inventories should start at the regional landscape scale and progress down to the levels of community-ecosystem, population-species and genetics. A GIS system would be used to integrate existing data and

establish baseline conditions. For example, ecosystem and species distribution maps would be overlain with maps of distribution and intensity of stressors (road density, grazing, habitat fragmentation). Hot spots and ecosystems of high risk would be identified based upon their species richness, endemism, and risk to impoverishment due to anthropogenic stressors. Noss notes that selection of indicators would be based upon the question to be answered, but provides no specifics. He also suggests that a rigorous sampling scheme should be developed using controls (e.g., wilderness areas) and treatments (national forests). This is a good starting point, but the details of implementation are still quite vague. Details of current databases and information availability are left undiscussed.

Gap analysis (Davis et al. 1990, Scott 1987) is an approach that has been implemented in Idaho and California, and offers a more tangible solution to biodiversity inventory and monitoring on a state or national scale. The technique of gap analysis focuses on identifying centers of endemism, species richness, and vegetation diversity, and then identifying gaps in the distribution of protected areas. The analysis can be conducted at several scales, including biogeographic, regional, and local. A GIS is used to compare the locations of species richness with the locations of existing reserves to show where biodiversity is already well protected and where additional reserves will do

the most good. Species distribution is predicted from a knowledge of habitat associations and distribution of vegetation types or based upon published literature. Gap analysis can be used to calculate the proportion of threatened or endangered species in existing reserves, to identify the species or habitat types that are not protected by reserves, or to determine whether adequate corridors exist between areas of high species richness. Scott et al. (1989) estimated that a gap analysis of vegetation, vertebrates and butterflies could be completed nationwide within four years at a total cost of $20 to $25 million The Nature Conservancy uses a two-pronged approach for their land management and acquisition programs. A "coarse filter" is used to conduct a community-level assessment of preservation status to identify communities that need to be preserved. Then a "fine filter" is used to identify habitats for threatened, endangered, and rare species. In this way, both habitats and species are considered.

The newest proposal to solve the biodiversity assessment problem is that of "rapid assessment." Rapid assessment is a technique for quickly surveying an ecosystem's complement of plants and animals and recommmending steps for their protection. It focuses on identifying hotspots of biodiversity as conservation priorities. The advantage of this technique is that it brings the challenge of biodiversity preservation down to

manageable proportions. The disadvantages are that it may distract policymakers from the need for better management on all wildland areas or the need to support long-term ecological studies (Wolf 1991). However, rapid assessment may be the the best available for the present time in tropical forests which are quickly being destroyed.

The problems associated with these large-scale techniques are numerous. Data quality in terms of low spatial resolution, uneven spatial coverage, currency of dynamic features and map accuracy is of utmost importance. Besides this cartographic uncertainty, the ecological relationships used to estimate species presence are not always rigorous. Even if the habitat is perfectly suitable, the species may not be present. Finally, locating and consolidating the data can be quite costly and time consuming (Davis et al. 1990).

In summary, although the level of detail differs, each of the aforementioned techniques has the same goal: to acquire a detailed description of the species composition, and habitat zones in the area under consideration. By documenting changes in biodiversity over time, scientists will be able to assess the status of an ecosystem. In doing so, some of the questions regarding diversity and stability may be answered, and we may learn to distinguish biodiversity changes induced by natural effects relative to those induced by humans.

An inventory and monitoring program must meet several criteria in order to accomplish these goals. It must track a wide variety of taxonomic groups and representatives of different guilds. It necessarily should be conducted on a large spatial scale so that a full array of habitat types are described. Information on species distribution and abundance should be collected so that clear-cut levels of commonness and rarity can be assessed. The program must be carried out over the course of several decades or more so that background noise (i.e, fluctuations due to variations between years) can be distinguished from variation caused by human-induced events.

Logistical considerations in biodiversity assessment include scale, intensity, precision, and scope. Higher costs are obviously associated with more thorough assessments. Taxonomic groups should be prioritized, as it would be impossible to monitor every single species or taxon around the globe. Finally, regional or nationwide biodiversity assessments should involve major database integration and should be incorporated into a GIS. It may be easier to begin at a small-scale level prior to establishing a nationwide biodiversity database. For this reason, this research focuses on a small-scale level, specifically in one park in Montana, Glacier National Park.

The Case Study

Glacier National Park

Glacier National Park is one of the most pristine parks in the United States. Its 4000 square km encompass elevation ranges from 1097 m to 3048 m. The west side of the park is a temperate rainforest with cedar/hemlock (*Thuja plicata / Tsuga heterophylla*), spruce/fir (*Picea englemanii / Pseudotsuga menzeisii*) and lodgepole pine (*Pinus contorta*) stands, while the east side is drier and windier, with aspen (*Populus tremuloides*) parklands and sagebrush (*Artemesia tridentata*) meadows. Habitat types include alpine meadows, bogs, and rocky ridges, riparian corridors, low elevation meadows, ponderosa pine stands, lodgepole pine, spruce/fir, and cedar/hemlock dominated forests.

Ecologically diverse areas such as those found in Glacier are prime for monitoring environmental changes. The total community can be partitioned into trophic groups, guilds, residency status groups and individual species. Each of these groups may serve as a different type of indicator because of their varying susceptibility to changes. For example, changes in the relative contribution of guilds of species to the total community may isolate one portion of the community that serves as an indicator of a specific change (Steele et al. 1984).

Accessibility to the park is limited to two types of roads: those that skirt the perimeter of the park, and a single road that winds through the middle of the park up to Logan Pass (Going to the Sun Highway). Given these constraints, hiking is required to access many of the habitats. However, the wilderness character of Glacier makes it a prime candidate for monitoring biodiversity in an undisturbed state.

Previous inventory and monitoring programs in Glacier, as in most of the national parks, occured primarily on a species-specific basis, targeting those species of special interest. For example, grizzly bears (*Ursus arctos*), elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), cutthroat trout (*Salmo clarki*), and bald eagles (*Haliaeetus leucocephalus*) have been studied intensively since the inception of Glacier's science research program in 1967. Genetic analysis has been conducted on the cutthroat trout in alpine lakes. Very few taxonomic groups have been fully documented. The only exception has been through vegetation monitoring. In cooperation with the GIS, a vegetation database was created which includes geographic and topographic elements (Carl Key, pers. comm.). Further, a recent fire study incorporated the inventory of various types of beetles in its assessment (Michael Ivie, pers. comm.).

Research Goals

The goal of this research was to develop methods for replicative sampling and analysis of biodiversity in Glacier National Park, Montana. This biodiversity assessment concentrates on species diversity, but a case study of genetic diversity assessment is also included.

Some of the reasons for developing methods to inventory and monitor biodiversity in Glacier were 1) to assist in describing the current species composition, 2) to provide a method to identify diversity hotspots and rare species, and 3) to establish a technique to assess change. Ideally, these types of data will be useful in understanding the relationships between diversity and ecosystem status. However, before these relationships can be understood, one must first obtain a thorough description of the current community and the variation in baseline species distributions.

CHAPTER 2

SPECIES DIVERSITY ASSESSMENT IN GLACIER NATIONAL PARK

Introduction

One way in which the status of an ecosystem may be assessed is to document changes in its biodiversity over time. Because biodiversity can be defined at the level of species, habitats, or genes, temporal changes can be assessed at several different levels. These changes may indicate responses to natural disturbances, human-induced changes, or long-term environmental trends.

In addition to serving as a "miner's canary" for ecosystem integrity, biodiversity has important intrinsic values; thus, its protection is an appropriate endpoint in itself (Noss, 1990b). As other public lands are developed or managed for multiple-use goals, the U.S. National Park system is becoming increasingly important as a major reservoir of biodiversity in this country.

The first step in assessing the role of national parks as biodiversity reserves is development of an appropriate inventory and monitoring system for biodiversity in these parks. This chapter describes the initial steps in the

development of such a system for Glacier National Park (GNP), Montana, U.S.A.

Ideally, a comprehensive inventory of biological diversity for a large, diverse ecosystem should consist of the following components: 1) accurate maps or a computerized Geographic Information System (GIS) showing all vegetation zones and habitat types, 2) accurate and up-to date species lists, distributional maps, and abundance data for all vertebrate taxa, major invertebrate taxa and plants, and 3) an assessment of genetic diversity in its rare species and species of special interest. Additionally, information on land uses (past, present, and future) and exogenous influences (e.g. acid deposition) with potential impacts on biological diversity is highly desirable. Currently, GNP has collected very little of these data.

Recognizing the importance of biodiversity to the park, Dr. Cliff Martinka, GNP's Chief Scientist, was interested in developing an inventory and monitoring program that would provide an empirically sound basis for the area's biodiversity protection. However, budgetary constraints were severe; the money available for the project was sufficient only to keep two people in the field for three summers. Could a worthwhile project be launched from such a limited resource base? Several decisions were made at the outset. First, it was clear that a comprehensive survey of habitat, species, and genetic diversity in GNP was well

beyond the scope of the budget. Because a GIS-based vegetation survey with data on topographic elements, spectral classes, and fire history was already underway, and because a survey of genetic variation had recently been conducted on cutthroat trout populations, concentrating further efforts on species diversity seemed to be a logical choice. Second, it was also clear that a most useful study would have to focus on one or two taxonomic groups rather than trying to inventory the park's entire biota. Check lists of the birds, mammals, butterflies, vascular plants, carabid beetles, and spiders present in GNP already existed, so one or more of these groups was a logical possibility. The focus of this project was terrestrial, with the idea that aquatic organisms could be added at a later date. Third, a proper biodiversity assessment would necessarily be conducted on a large spatial scale--park-wide, and it would also entail obtaining information on species distribution and abundance so that clear-cut levels of commonness and rarity could be assessed. Thus, an appropriate sampling plan would be intermediate between a faunal (or floral) survey and a detailed ecological investigation. Finally, species distributions needed to be assessed because they are far easier to quantify than is abundance. Because the frequency of ocurrence of many species is correlated with their average local density (Brown, 1984; Bock, 1987), spatial and temporal trends in abundance could be estimated

from distributional data--provided they were obtained in a systematic manner.

Thus, the ultimate goal was to be able to track patterns of changing distribution and abundance in several indicator taxa into the future. The immediate goals of this project were to (1) choose representative taxa that could be inventoried and monitored and serve as indices of the state of overall biological diversity in GNP, (2) establish an appropriate sampling regime and methodology, and (3) evaluate various analytical techniques for dealing with the database. Specific questions and issues regarding species diversity that were addressed in this study are noted below:

1) Describing the Data

a) What criteria should be used to select taxa for survey?

b) What is the distribution of species, communities, and ecosystems in Glacier National Park?

c) How adequate are current park species lists as historical species presence/absence documentation?

2) Species/Habitat Assemblages

a) Are predictable species assemblages routinely found in close association within a refuge? Can a given species assemblage be used to predict habitat type?

b) Is there a spatial correlation between sites of high

species diversity and sites that support rare species?

c) Is there a correlation between habitat diversity and species diversity?

3) Sampling Efficiency Analysis

a) Should census sites be homogenous or heterogeneous in habitat type given a goal of identifying a maximum number of species within the limitations of personnel and time.

b) How is the cost/benefit of replication within habitat types reconciled with the need to survey a large, highly diverse ecosystem?

c) What is the most efficient use of resources? How much difference should one expect in results if the sampling effort were cut in half? If it were doubled?

d) How many samples are needed, and how intensive a sampling effort is necessary to detect rare species? How many species should one expect to miss given the effort invested?

e) How reliable are the new data collected via biodiversity inventory? What level of confidence can/should managers have in their species lists?

f) How many years of censusing are necessary to distinguish background noise from real population fluctuations? What differences should be perceived as biologically significant?

4) Management Implications

What areas of the reserve merit special protection, intervention, or efforts to manage biodiversity?

Methods

Criteria for Choice of Indicator Taxa

Diamond (1986) recommends that vertebrates should be chosen as indices of biological diversity as a whole because they tend to be the best-known taxonomically, and are politically the most easily salable. Scott et al. (1987) concur, but include butterflies as well. Because plants, fungi, and invertebrates are vastly more abundant and potentially are ecologically more significant than vertebrates, an adequate inventory and monitoring system for biological diversity should include a reasonable selection of these groups, in addition to vertebrates.

Birds are suitable because they are ecologically diverse and use a wide variety of food and other resources. Therefore, they reflect the condition of many aspects of the ecosystem. They also represent several trophic groups or guilds, and by having a short generation time, they exhibit quick responses to environmental change (Steele et al. 1984). Finally, they are good indicators because they are conspicuous, ubiquitous, intensively studied, and often appear to be more sensitive than other vertebrates (Morrison 1986).

Indicator groups need not represent any particular level of the taxonomic hierarchy; they could range from the genus level (*Drosophila*) to that of a subkingdom (vascular plants). Nor did they necessarily need to be monophyletic (e.g. "small mammals"). With this in mind, the following guidelines were used in evaluating potential indicator groups for a terrestrial environment.

1. The group must be appropriate for the park in terms of numbers of species and levels of abundance. For example, salamanders would be inappropriate because only one or two species occur in GNP in very restricted habitats. Clearly, it is much easier to establish clear-cut levels of commonness and rarity in more speciose and widely-distributed groups.

2. The group should be found throughout the park.

3. The group should be politically salable (e.g., butterflies are more appealing to the public than spiders).

4. The group must be amenable to sampling and identification to the species level by non-specialists.

5. The group should not contain species that are directly exploited by humans. The distribution and abundance of such species are likely to be influenced strongly by management practices.

6. The group should contain at least some taxa with short generation times. Such species monitored over several generations of the taxa should show rapid responses to environmental changes.

7. The group should contain species in different trophic or habitat guilds, and some of its species should respond to different aspects of the environmental matrix.

8. The group should be relatively well-known in terms of its ecology and life-history information.

Once several potential groups had been identified, the

following considerations were used in assembling the overall set of groups to be included:

1) Does the set include a representative spectrum of the overall biological diversity present in the park?

2) Does it include a number of trophic levels and guilds (e.g. producers, decomposers, and various consumer guilds such as herbivores, granivores, insectivores, detritivores, etc.)?

3) Does it include groups that respond to different aspects of the environmental matrix (e.g., the diversity of bird species in most temperate zone communities is more related to the structure of the vegetation (Willson 1974), while butterfly diversity is more related to its chemical composition. Not surprisingly, Murphy and Wilcox (1986) and Wilcox et al. (1986) found that habitat components important to butterfly diversity are very different from those for bird diversity).

Groups such as (1) vascular plants, (2) macro-fungi (mushrooms, bracket fungi, etc.), (3) birds, (4) small mammals, (5) butterflies, (6) carabid beetles, (7) bumblebees, (8) drosophilids, (9) dragonflies, and (10) terrestrial molluscs satisfied most of the above criteria. Of these 10, two groups, small land birds (generally passerines plus woodpeckers and hummingbirds) and butterflies seemed particularly appropriate for the initial efforts. Both groups are tractable in the field, are taxonomically and ecologically well-known, and popular amoung amateur naturalists. Birds and butterflies also have their peak activity periods at different times of the day (early morning and mid-day, respectively) which would facilitate sampling.

Census Sites

During 1987, 84 sites were sampled. My objective in this first year was to census extensively throughout the park. Some sites were sampled for birds, some for butterflies, a few for both. These sites were selected primarily on the basis of their position in the topographic/elevational gradients in GNP instead of by habitat types. This was done for two reasons. First, temperature and moisture gradients, quite independent of habitat types defined by vegetation, are often of primary importance in determining the distribution and local abundance of most terrestrial plant and animal taxa (e.g. Whittaker 1952; Terborgh 1970; Brussard 1985). Temperature correlates with elevation, and moisture is correlated with both elevation and topography (i.e. slope, aspect, and exposure); both factors affect the metabolic functions of animals either directly or indirectly. Second, vegetation is often distributed as a continuum, so it is very difficult to divide into discreet packets, particularly at a scale that is biologically meaningful to each species in groups as diverse as birds and butterflies. Although several methods of habitat categorization were considered (Elton and Miller 1954; Southwood et al. 1979; Bunce and Shaw 1973), the technique eventually employed involved marking each site's location on a 7.5 minute United States Geological Survey (USGS) topographic map, recording its elevation, slope, and

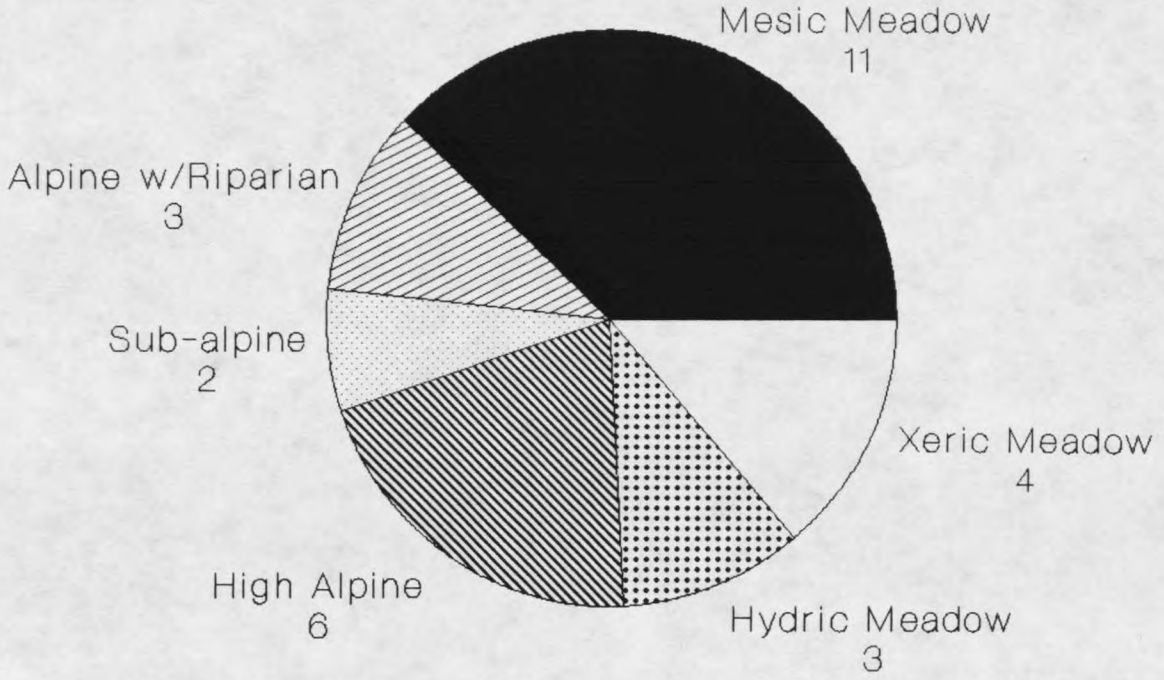
exposure, and making a brief and very general categorization of its habitat type (e.g. xeric meadow, riparian, lodgepole pine forest).

This procedure each site to be located on two-dimensional graphs representing the available "ecological space" in GNP using elevation as the ordinate and moisture conditions (ranging from hydric to xeric on the flats and based on aspect, corrected for slope and exposure, on mountainsides) as the abscissa. Additional sites were then chosen to maximize the full range of topographic/elevational conditions in the Park. Coverage by habitat type is illustrated for butterflies (Fig. 1) and for birds (Fig. 2).

The 1987 sites varied in both size and shape. Because many of them were inaccessible by road, most could be visited only once. Although this was probably not quite as serious for surveying birds due to their longer lifespan, phenological differences among butterflies (i.e., early- versus late-summer emerging species) created a potential problem for adequate coverage of this group.

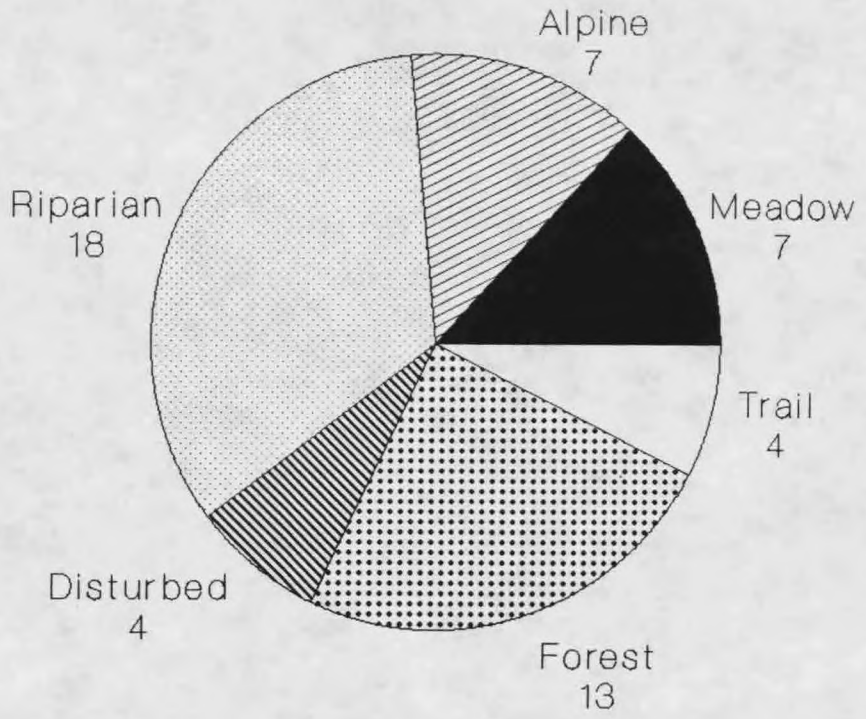
In order to address the temporal replication problem, the number of sites sampled was reduced in 1988 and 1989 to 33, the maximum number that could be visited at least twice during the summer by two people. In this way, each site was surveyed more intensively, rather than surveying GNP extensively. These sites were still fairly representative of the range of geographic and environmental variation

Figure 1. Habitat Types
Butterfly Biodiversity Sites - 1987



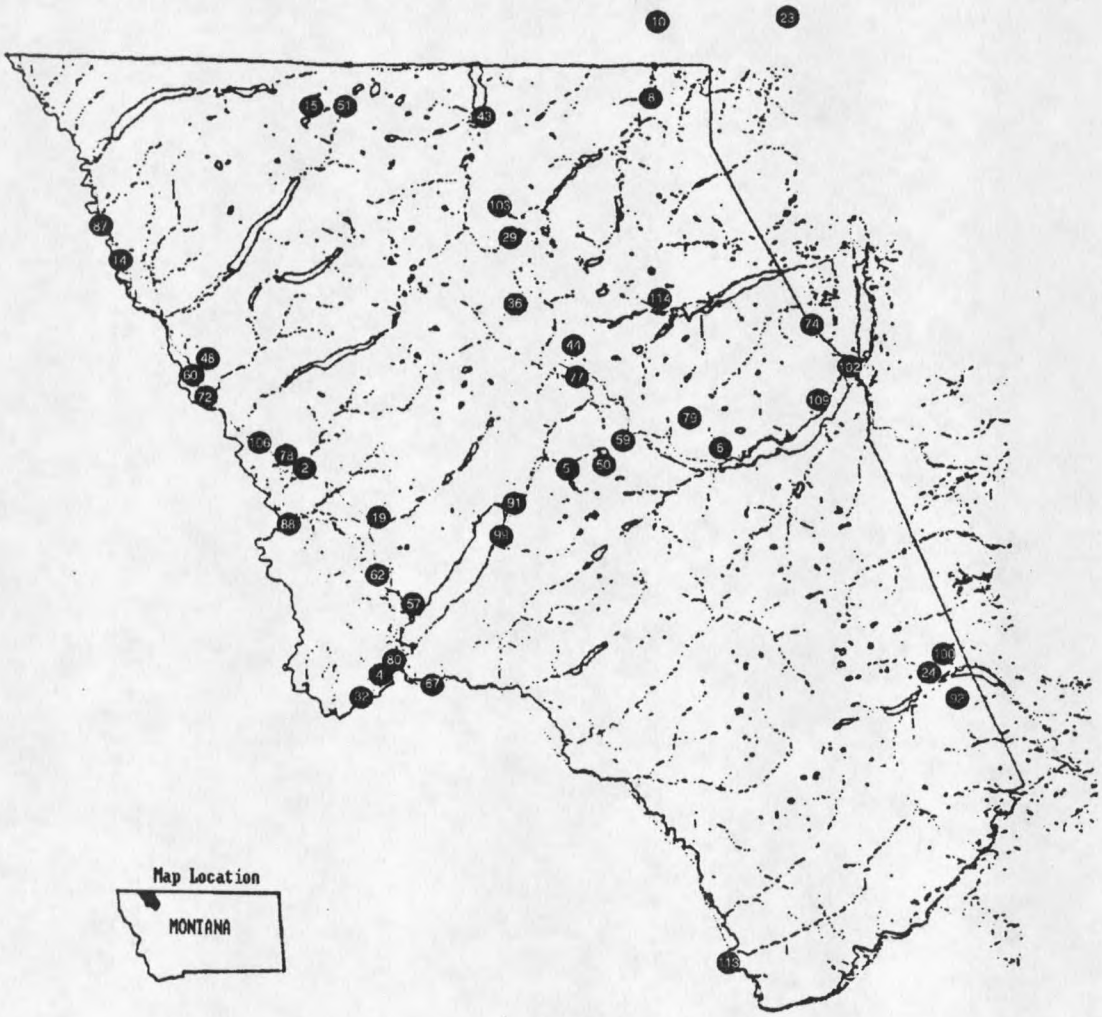
 # Sites within each habitat type

Figure 2. Habitat Types
Bird Biodiversity Sites - 1987



 # Sites within each habitat type

Fig. 3. Glacier Nat. Pk. Biodiversity Sites



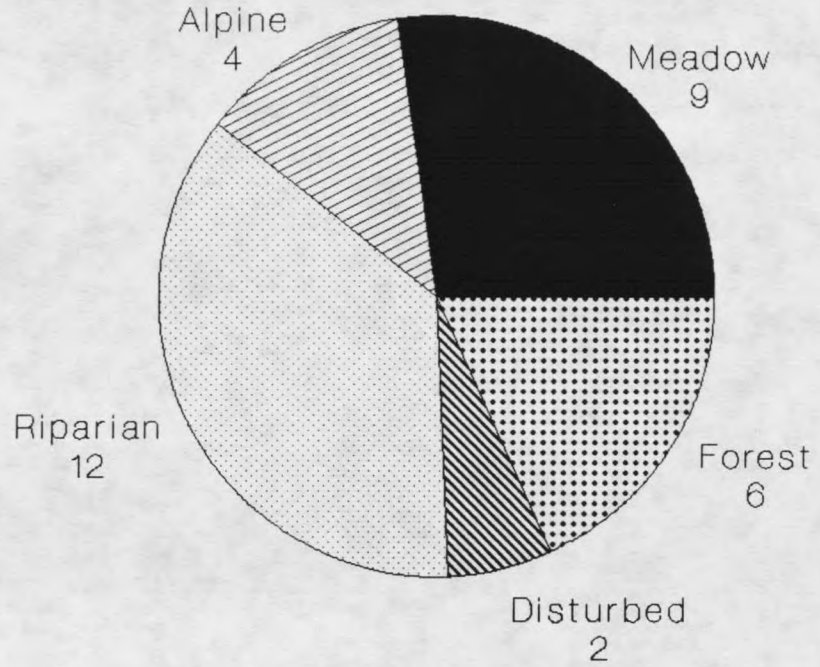
See Appendix A for site descriptions

within the park (Figure 3). Each of the 1988-89 sampling sites was one square km in size and defined by UTM coordinates on USGS topographic maps. Sample plots this large were chosen on the basis of field experiences in 1987. Smaller sampling areas did not capture enough small-scale patchiness to be biologically meaningful to most of the birds and to some of the large, active butterflies (e.g. swallowtails).

Although community ecology stresses sampling sites that are homogeneous in structure and composition (Gauch, 1982), this methodology maximized habitat diversity within the 1988-89 sites. This was done for two reasons. First, this study was designed to inventory species occurrences across a very large area, so site homogeneity was forgone to maximize broadscale coverage. Second, it was observed in 1987 that species diversity tended to be much higher along ecotones, so a number of ecotones was included in many of the sites. Nevertheless, broad habitat-type characterizations were still possible at each site (Figures 4 and 5).

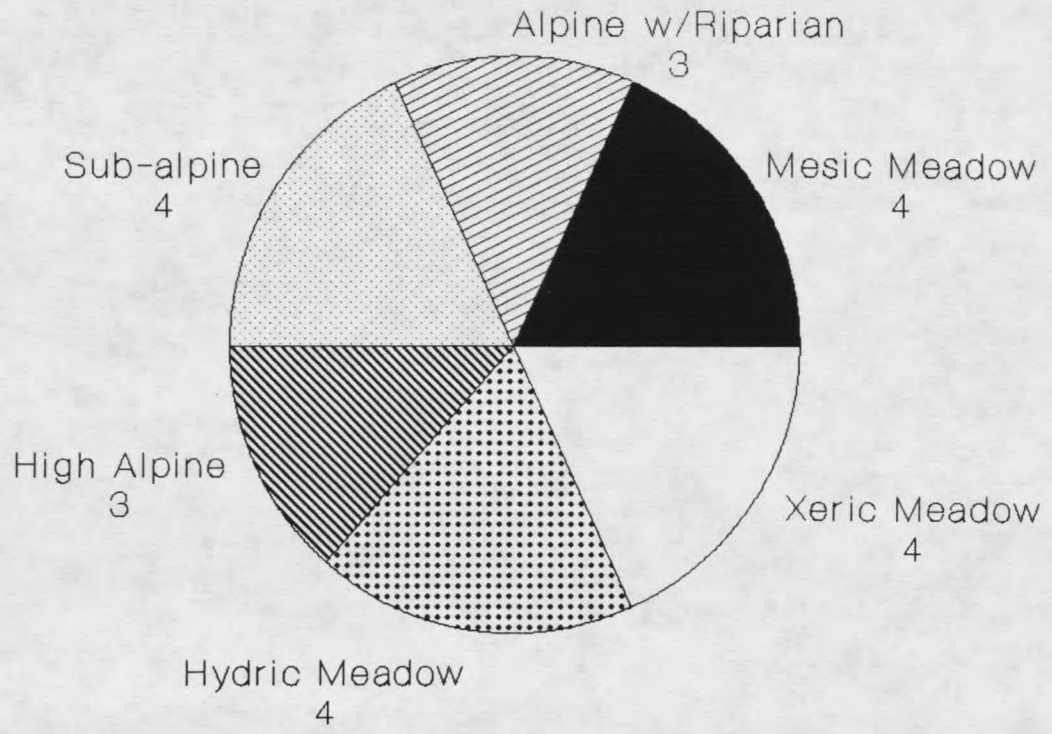
This particular design results in a certain type of bias. Vegetation types or "ecological space" defined by position on the topo/elevational gradient are not sampled in direct proportion to their frequency of occurrence in GNP. Instead, some of the less-frequent habitats were overrepresented in attempting to maximize the opportunity to sample rare species and to increase coverage of "ecological

Figure 4. Habitat Types
Bird Biodiversity Sites - 1988,89



 # Sites within each habitat type

Figure 5. Habitat Types
Butterfly Biodiversity Sites - 1988-89



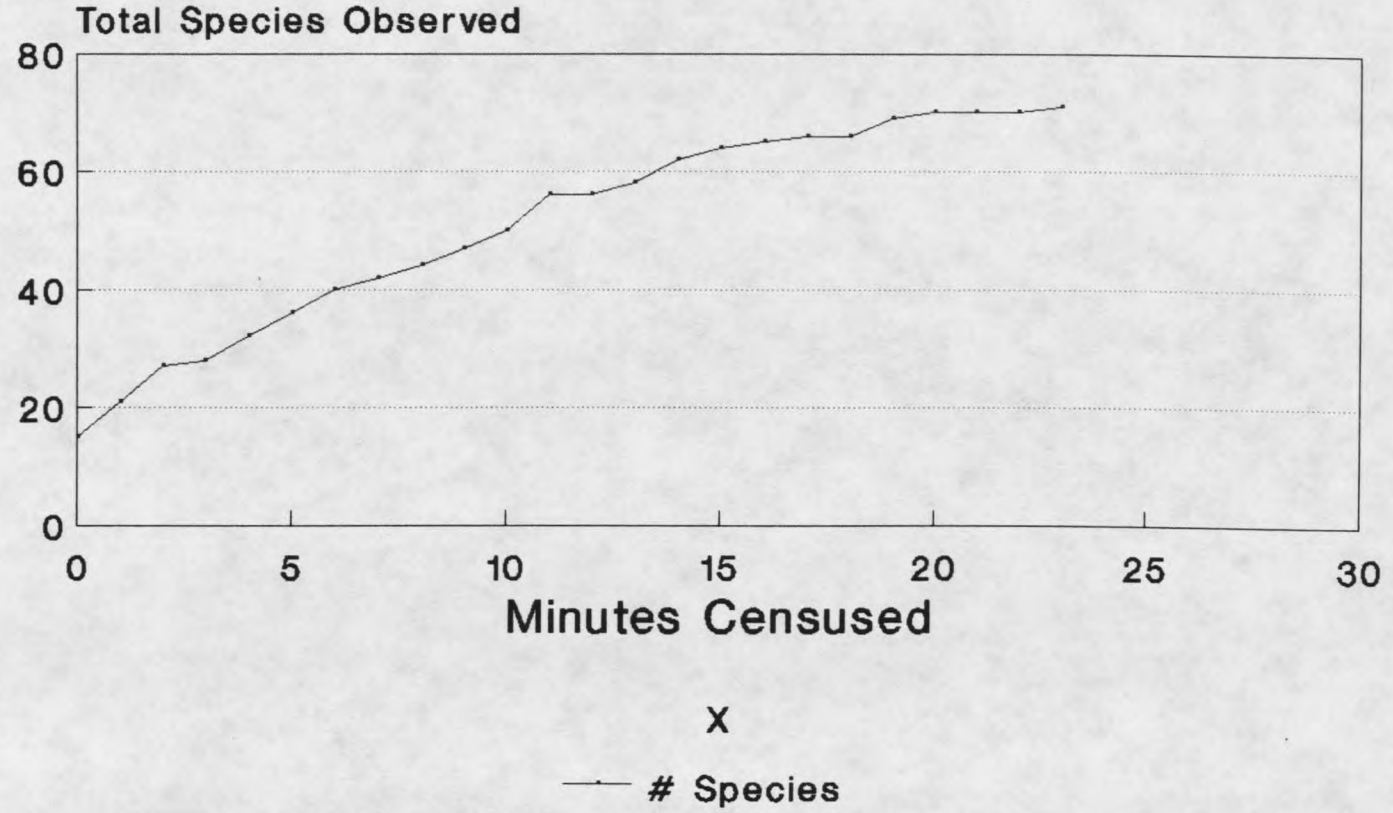
#Sites within each habitat type

space" along temperature and moisture gradients. The primary disadvantage of this approach is in statistical analysis of the data; the perceived rarity of a species may or may not be indicative of its true level of rarity in GNP.

Birds were censused aurally and visually at a given sample site during a two-hour period, while butterflies were censused by netting for 20 minutes and releasing in three separate 50 x 50 meter subplots. These sample periods were established empirically by plotting the number of species recorded against time (Figure 6). The average time at which the species/effort curve flattened out (no more species added) was considered to be the optimal sampling time. A summary of the intensive sampling procedure is shown in Table 1.

Qualitative Sampling Trail transects were often sampled while hiking to quantitative plots. Statistical analysis of these data is limited due to the lack of standardization; however the database provides additional descriptive information on species commonness and rarity throughout the park.

Fig. 6: Species Effort Curve
Butterflies 1988



Cumulative #species over all sites

Table 1. Summary of Intensive Sampling Procedure and Database. Existing Presence/Absence Species Diversity Database for Glacier National Park 1988-1989.

Sample Sites:
1 sq. km. biodiversity plots throughout the park, representative of a wide range of elevation and moisture gradients and habitat types
Methodology:
Butterflies sampled in 3 - 50 X 50 m. subplots within the sq. km. for 15-20 minutes/subplot.
Birds sampled in full 1 sq. km. for 2 hours.
Sites Surveyed:
24 sites for butterflies (2-3 reps.) 35 sites for birds (1 -2 reps.)

Habitat Characterization in Sample Sites Terrestrial habitats usually are defined by vegetation, and vegetation can be classified either by structure (the horizontal and vertical occupation of space by plants) or by taxonomic composition. Because the structural complexity of vegetation has been associated with species diversity in several vertebrate taxa (e.g. birds (Karr and Roth 1971; Willson 1974; Cody 1986)), it is important to incorporate some measure of structure in a habitat classification. On the other hand, plant associations defined by the species that dominate them are traditionally the fundamental unit of habitat classification (e.g., Pfister et al. 1977), and

certain groups that eventually should be included in the biodiversity assessment probably are influenced less by the structure of the vegetation than by its taxonomic composition. Thus, although species composition needed to be incorporated into the habitat classification plan as well, detailed habitat analysis involving both vegetation structure and taxonomic composition would have been inordinately time-consuming.

A second problem, typical of diversity studies is that the degree of resolution for habitat analysis. Because sampling for species diversity in the various indicator groups was done on different spatial scales within the sites, the degree of resolution required for detailed habitat analysis was different for each group. For these reasons, the initial habitat classifications at each site were very general, including only gross structural categories (e.g. forest, scrub, grassland) and consist of the dominant plant species (e.g. mixed ponderosa/lodgepole pine forest) at each vegetation layer (e.g. upper canopy, lower canopy, shrub, and groundcover). More detailed habitat descriptions can be developed as needed at a level of detail appropriate for each indicator group. For example, the traditional measure of vegetation structure in studies of bird diversity is done by collecting foliage height profiles and estimating foliage cover (e.g. MacArthur and MacArthur 1961; Willson 1974). Species composition of

woody plants may be important as well (James and Wamer 1982). Thus, if it is deemed desirable to do a detailed study of bird/habitat relations at some time in the future, measurements of these parameters on the appropriate scale can be undertaken on the sites.

The moisture gradient classification was as follows; meadows with standing water or water flowing through them throughout most of the summer were classified as hydric (most of these are early successional meadows, previously ponds or lakes), mesic meadows had no standing water after spring snow melt, and usually had a diverse group of flowering plants and grasses, dry, open meadows, characterized by open ground and sagebrush as the primary vegetation, were classified as xeric.

Presence/Absence Sampling

Species diversity in a given area consists of two components: richness (the number of species present), and equitability (the evenness of their relative abundances). In taxonomically well-known groups richness is relatively easy to estimate by a direct count of the species encountered, provided that the sampling effort is sufficient. However, most taxa are very difficult to sample in such a way that the proportions of individuals per species in a sample are representative of their true abundances in the community (e.g. Shapiro 1975; Verner

1983), making an accurate estimation of equitability difficult to obtain. This is particularly true in extensive surveys where habitat differences exacerbate differences in detectability. For these reasons only species occurrences were recorded at a sampling site. Thus, the diversity index was "S", the observed number of species.

Presence-absence data has many advantages for extensive surveys. First, the bulk of the information on this scale of inquiry lies in qualitative differences in species composition (Greig-Smith, 1971). Second, sampling for absolute, or even relative species abundances requires so much time that the number of samples obtainable drops drastically (Poore 1962). Finally, there seems to be general agreement that the observed number of species is the simplest, most practical, and most objective measure of species diversity (Hurlburt 1971; Peet 1974; Whittaker 1972).

For some indicator groups the sites have to be searched on several different occasions during the year because of phenological differences among species. For others, one or two temporal replicates is sufficient. Some rare species that actually are present in the park will almost certainly not show up in the samples. These species, once identified, must be searched for separately, by targeting appropriate habitats. When a population has been located, a biodiversity plot can be established on site.

Evaluating Biodiversity Data

A variety of techniques were used to analyzed the GNP biodiversity data. They are outlined here and a detailed analysis and discussion follows:

Describing the Data

(1) A data base was constructed detailing baseline distributional data on all species in topographic and ecological space.

(2) Historic species lists were compared to current biodiversity census results to target potential changes in community composition.

(3) A modified rank occurrence analysis was used to determine what type of community structure is suggested by the distribution of common and rare species (see Magurran, 1988).

(4) Frequency of occurrence data was analyzed to identify species that are restricted to specialized habitats or isolated populations (rare species, fragmented populations, or species confined to successional habitats). For example:

alpha rarities - species that are rare in a common habitat, i.e. species on the stress ends of environmental gradients or near range edges

beta rarities - species associated with rare or unusual habitats

(5) Sites were compared to identify "hot spots", sites that support the highest species diversity.

Species/Habitat Relationships

(6) Principal components analysis was used to sort out major species assemblages distinguishing sites. Using habitat requirements of major species at the extremes of the principal components and habitat types of site groupings, principal components were interpreted. A cluster analysis of principal component scores was then conducted to construct dendrograms of site assemblages.

(7) ANOVA and discriminant analysis were used to discern species/habitat relationships.

(8) Elevation and moisture gradient analysis was conducted to determine those habitat conditions that support the highest species diversity.

(9) An analysis was conducted to determine the effect of edges on species diversity. Various types of edge and non-edge habitats were compared with respect to species diversity and species composition.

Sampling Efficiency Analysis

(10) Spatial and temporal fluctuations in species diversity and composition were analyzed within sites and between years using the Jaccard's coefficient for biotic similarity and a G-test (Sokal & Rohlf, 1981).

(11) A cost-benefit analysis was conducted to determine the optimum number of samples needed to detect rare species.

Results

Describing the Data

Historic Species Lists Historic species lists were compared to these species lists to determine whether species diversity has changed over time. The historic species lists were *Birds of Glacier National Park*, a checklist compiled by Dave Shay, a ranger who worked in Glacier National Park for 20 years, and *Butterflies of Glacier National Park*, compiled in 1980 by Steve Kohler. Data for Kohler's list came from university collections at Montana State University and University of Montana, private collections, the GNP collection, records from natural history museums, and a review of the published literature. Some of these recorded sightings date back to 1920, but there is also detailed information from collections during the last decade. Kohler's list included

a total of 83 butterfly species.

John S. Garth, a Glacier naturalist in 1935, also compiled a species list of butterflies during the summers of 1935, 1949, and 1950. Many of the species on Garth's list concurred with Kohler's list after standardization using Scott (1986), but seven species were additions to the Kohler list. Thus, according to the Kohler and Garth records, the total number of butterfly species ever recorded in the park between 1920 and 1980 was 90.

All but two of the species on Kohler's list have been sighted within the last decade, and most have been seen within the past few years. *Colias pelidne* and *Everes comyntas* have not been sighted since 1935. *Papilio bairdii* has not been sighted since 1950.

Fifty-seven of the 90 butterfly species were found during the July 1 -Sept. 9, 1987 censusing (Tables 2 & 3). Because of a late field season (starting 30 June), several of the early species were missed in 1987. By starting the censusing earlier during the 1988 season (1 June), the total species sighted increased to 69. Two species (*Lyceana hyllus* and *Nymphalis californica*) new to both the Kohler and Garth lists were found in 1987, four new species (*Callophyrs sheridanii, Vannessa carye annabella, Satyrium saepium* and *Neophasia menapia*) were found in 1988, and three new species were found in 1989 (*Callophyrs polios, Speyeria aphrodite* and the monarch butterfly, *Danaus plexippus*).

Thus the total number of species observed during the three-year censusing was 86, and the new park species total is 99.

Ninety-two of the 125 bird species were observed in the three years of biodiversity sampling. Eighty-seven of these species were seen in biodiversity sampling sites (Tables 2 & 4).

Table 2. Comparison of Historic Species Assemblages with Species Found in Biodiversity Sampling

Taxonomic group	Historical Species	Cumulative Species	New species
Butterflies			
1987	57	59	2
1988	69	77	4
1989	66	86	3
new total species:	102		
Birds (passerines and woodpeckers only)			
1987	69	69	0
1988	71	82	0
1989	80	87	0
total species:	125		

Note: cumulative species includes new species

Analysis of Commonness and Rarity

Birds: Although the commonness and rarity of most species was comparable between the two lists, eleven species considered common on the GNP checklist were rarely observed in the biodiversity sites (Table 5).

Table 3. Total Annual Species Occurrences - Butterflies

(* Significant changes for G-test between 1988 and 1989 at p<.05)

Species	1987	1988	1989	
# records:	90	161	167	
PARNASSIUS CLODIUS AMERICAN APOLLO	1	1	0	
PARNASSIUS PHOEBUS * SMALL APOLLO	18	33	17	
PAPILIO MACHAON BAIRDII ARTEMISIA SWALLOWTAIL	0	0	0	Garth 1950
PAPILIO ZELICAON * WESTERN SWALLOWTAIL	0	5	22	
PAPILIO GLAUCUS TIGER SWALLOWTAIL	0	1	5	
SSP. RUTULUS *	3	17	53	
PAPILIO MULTICAUDATA TWO-TAILED TIGER SWALLOWTAIL	0	0	0	
PAPILIO EURYMEDON * PALLID TIGER SWALLOWTAIL	0	6	24	
PIERIS PROTODICE CHECKERED WHITE	2	0	0	
PIERIS CALLIDICE				
SSP. OCCIDENTALIS PEAK WHITE	12	38	44	
PIERIS NAPI SHARP-VEINED WHITE	4	15	20	
PIERIS RAPAE CABBAGE BUTTERFLY (SMALL WHITE)	4	12	6	
COLIAS MEADII ALPINE ORANGE	3	5	2	
COLIAS EURYTHEME * ORANGE SULFUR (ALFALFA BUTTERFLY)	27	6	52	
COLIAS PHILODICE * COMMON SULFUR	10	7	46	
COLIAS INTERIOR * PINK-EDGED SULFUR	20	40	27	
COLIAS ALEXANDRA ULTRAVIOLET SULFUR	3	0	0	
COLIAS PELIDNE BLUEBERRY SULFUR	0	0	0	
COLIAS NASTES ARCTIC GREEN SULFUR	1	3	1	
NEOPHASIA MENAPIA PINE WHITE	0	2	0	New 1988
ANTHOCHARIS SARA WESTERN ORANGE TIP	0	3	3	

Table 3. Total Annual Species Occurrences - Butterflies (continued)

EUCHLOE AUSONIA SSP. AUSONIDES DAPPLED MARBLE	0	8	13	
HARKENCLENUS TITUS CORAL HAIRSTREAK	2	1	4	
SATYRIUM SYLVINUS WESTERN WILLOW HAIRSTREAK	0	0	0	
SATYRIUM SAEPIUM BUCKTHORN HAIRSTREAK	0	1	0	New 1988
CALLOPHYRS SHERIDANII LITTLE GREEN HAIRSTREAK	0	4	0	New 1988
CALLOPHYRS POLIOS HOARY ELFIN	0	0	1	New 1989
CALLOPHYRS AUGUSTUS BROWN ELFIN	0	0	1	
CALLOPHYRS FOTIS DESERT ELFIN	0	0	1	
CALLOPHYRS ERYPHON * WESTERN PINE ELFIN	0	6	23	
CALLOPHYRS SPINETORUM BLUE MISTLETOE HAIRSTREAK	0	0	1	
LYCEANA PHLAEAS SMALL COPPER	0	1	1	
LYCEANA CUPREUS LUSTROUS COPPER	2	3	0	
LYCAENA XANTHOIDES GRAY COPPER	0	0	0	
LYCEANA HETERONEA BLUE COPPER	7	12	12	
LYCEANA HELLOIDES PURPLISH COPPER	5	2	1	
LYCEANA DORCAS CINQUEFOIL COPPER	2	0	0	
LYCEANA MARIPOSA * FOREST COPPER	15	16	3	
LYCEANA HYLLUS BRONZE COPPER	2	0	0	New 1987
EPIDEMIA NIVALIS LILAC-EDGED COPPER	6	3	1	
PLEBEJUS IDAS "ARGYROGNOMON" * NORTHERN BLUE	28	46	15	
PLEBJUS SAEPIOLUS GREENISH CLOVER BLUE	16	32	36	
PLEBJUS ICARIODES * LUPINE BLUE	2	2	29	
PLEBJUS ACMON * SILVER-STUDDED BLUE	4	7	0	

Table 3. Total Annual Species Occurrences - Butterflies (continued)

PLEBJUS GLANDON PRIMROSE BLUE	0	11	5	
EVERES AMYNTULA WESTERN TAILED BLUE	3	5	3	
EVERES COMYNTAS TAILED BLUE	0	0	0	Garth 1935
EUPHILOTES ENOPTES SSP. ANCILLA DOTTED BLUE	0	1	0	
GLAUCOPSYCHE LYGDAMUS SILVERY BLUE	0	0	4	
GLAUCOPSYCHE PIASUS ARROWHEAD BLUE	0	1	0	
CELASTRINA ARGIOLUS SSP. LANDON SPRING AZURE	0	3	1	
LIMENITIS ARTHEMIS WHITE ADMIRAL	0	0	3	
LIMENITIS WEIDEMEYERII WESTERN ADMIRAL	2	3	0	
LIMENITIS LORQUINI * ORANGE-TIP ADMIRAL	11	15	2	
VANESSA ATALANTA RED ADMIRAL	2	1	2	
VANESSA CARDUI * PAINTED LADY	0	20	1	
VANNESSA CARYE SSP. ANNABELLA WESTERN PAINTED LADY	0	4	0	New 1988
NYMPHALIS VAU-ALBUM * COMMA TORTOISE SHELL	6	8	1	
NYMPHALIS MILBERTI FIRE-RIM TORTOISE SHELL	23	36	26	
NYMPHALIS ANTIOPA MOURNING CLOAK	8	14	11	
NYMPHALIS CALIFORNICA * WESTERM TORTOISE SHELL	15	7	0	New 1987
POLYGONIA GRACILIS SSP. ZEPHYRUS HOARY COMMA	1	4	3	
POLYGONIA SATYRUS GOLDEN ANGELWING	6	7	3	
POLYGONIA FAUNUS GREEN COMMA	15	19	10	
POLYGONIA COMMA COMMA ANGELWING	2	0	0	
CHLOSYNE GABBII SSP. DAMOETAS PEARLY CHECKERSPOT	0	1	0	

Table 3. Total Annual Species Occurrences - Butterflies (continued)

CHLOSYNE PALLA CREAMY CHECKERSPOT	6	12	16	
PHYCIODES THAROS PEARL CRESCENT	13	24	32	
PHYCIODES CAMPESTRIS * FIELD CRESCENT	4	20	43	
PHYCIODES MYLITTA THISTLE CRESCENT	0	0	0	
EUPHYDRYAS GILLETTII YELLOWSTONE CHECKERSPOT	3	3	9	
EUPHYDRYAS CHALCEDONA				
SSP. COLON	0	0	0	
SSP. ANICIA WESTERN CHECKERSPOT	28	30	26	
EUPHYDRYAS EDITHA RIDGE CHECKERSPOT	3	4	9	
BOLORIA SELENE SILVER MEADOW FRITILLARY	6	6	12	
BOLORIA EPITHORE WESTERN MEADOW FRITILLARY	6	15	18	
BOLORIA ALBERTA ALBERTA ALPINE FRITILLARY	2	0	0	
BOLORIA ASTARTE ARCTIC RIDGE FRITILLARY	0	0	1	
BOLORIA TITANIA * PURPLE BOG FRITILLARY	6	13	4	
SPEYERIA CORONIS CORONIS FRITILLARY	0	0	0	Garth 1935
SPEYERIA EDWARDSII GREEN FRITILLARY	1	0	0	
SPEYERIA ZERENE * ZERENE FRITILLARY	7	15	1	
SPEYERIA CALLIPPE CALLIPPE FRITILLARY	0	0	0	
SPEYERIA EGLEIS GREAT BASIN FRITILLARY	0	2	3	
SPEYERIA ATLANTIS * ATLANTIS FRITILLARY	31	36	20	
SPEYERIA HYDASPE * LAVENDER FRITILLARY	13	12	4	
SPEYERIA MORMONIA * MORMON FRITILLARY	19	64	17	
SPEYERIA CYBELE GREAT SPANGLED FRITILLARY	1	0	1	
SPEYERIA APHRODITE APHRODITE FRITILLARY	0	0	3	New 1989
COENONYMPHA TULLIA				
SSP. AMPELOS RINGLET	0	0	0	

Table 3. Total Annual Species Occurrences - Butterflies (continued)

COENONYMPHA TULLIA SSP. INORNATA	6	25	34	
CERCYONIS PEGALA WOOD NYMPH	8	5	12	
CERCYONIS OETUS SMALL WOOD NYMPH	26	43	38	
OENEUS UHLERI ROCKY MOUNTAIN ARCTIC	0	2	0	
OENEUS CHRYXUS BROWN ARCTIC	0	7	18	
OENEUS ALBERTA PRAIRIE ARCTIC	0	0	0	
OENEUS MELISSA MOTTLED ARCTIC	0	0	0	
EREBIA EPIPSODEA COMMON ALPINE	4	25	40	
DANAUS PLEXIPPUS MONARCH	0	0	0	New 1989

Table 4. Total Annual Species Occurrences: Birds.

(* Significant changes for G-test between 1988 and 1989 at p<.05)

Species	1987	1988	1989
# records	117	59	68
VIREO SOLITARIUS			
SOLITARY VIRIO	3	3	9
VIREO OLIVACEUS			
RED-EYED VIRIO	8	2	1
VIREO GILVUS			
WARBLING VIRIO *	3	9	34
SETOPHAGA RUTICILLA			
AMERICAN REDSTART	6	17	25
VERMIVORA PEREGRINA			
TENNESSEE WARBLER	0	0	3
VERMIVORA CELATA			
ORANGE-CROWNED WARBLER *	1	0	13
VERMIVORA RUFICAPILLA			
NASHVILLE WARBLER	0	0	0
DENDROICA PETECHIA			
YELLOW WARBLER	15	11	17
DENDROICA CORONATA			
YELLOW-RUMPED WARBLER *	7	10	29
DENDROICA TOWNSENDI			
TOWNSEND'S WARBLER	1	12	20
SEIURUS NOVEBORACENSIS			
NORTHERN WATERTHRUSH *	2	3	13
OPORORNIS TOLMIEI			
MACGILLIVRAY'S WARBLER *	13	15	43
GEOTHLYPIS TRICHAS			
COMMON YELLOWTHROAT	5	6	14
WILSONIA PUSILLA			
WILSON'S WARBLER *	2	5	20
REGULUS SATRAPA			
GOLDEN-CROWNED KINGLET	20	25	33
REGULUS CALENDULA			
RUBY-CROWNED KINGLET *	0	7	32
PASSER DOMESTICUS			
HOUSE SPARROW	0	0	0
DOLICHONYX ORYZIVORUS			
BOBOLINK	0	0	0
STURNELLA NEGLECTA			
WESTERN MEADOWLARK	0	0	0
XANTHOCEPHALUS XANTHOCEPHALUS			
YELLOW-HEADED BLACKBIRD	0	3	3
AGELAIUS PHOENICEUS			
RED-WINGED BLACKBIRD	2	6	13

Table 4. Total Annual Species Occurrences: Birds. (continued)

ICTERUS GALBULA			
NORTHERN ORIOLE	1	3	2
EUPHAGUS CAROLINUS			
RUSTY BLACKBIRD	0	0	0
EUPHAGUS CYANOCEPHALUS			
BREWER'S BLACKBIRD	0	5	2
QUISCALUS QUISCULA			
COMMON GRACKLE	0	0	0
MOLOTHRUS ATER			
BROWN-HEADED COWBIRD *	5	7	23
PIRANGA LUDOVICIANA			
WESTERN TANAGER *	2	6	16
PHEUCTICUS MELANOCEPHALUS			
BLACKHEADED GROSBEAK	0	1	4
COCCOTHRAUSTES VESPERTINUS			
EVENING GROSBEAK	0	0	0
PINICOLA ENUCLEATOR			
PINE GROSBEAK	1	0	2
PASSERINA AMOENA			
LAZULI BUNTING	0	0	4
CALAMOSPIZA MELANOCORYS			
LARK BUNTING	0	0	0
PLECTROPHENAX NIVALIS			
SNOW BUNTING	0	0	0
CARPODACUS CASSINII			
CASSIN'S FINCH	2	2	1
LEUCOSTICTE ARCTOA			
ROSY FINCH	3	1	2
CARDUELIS FLAMMEA			
COMMON REDPOLE	0	0	0
CARDUELIS PINUS			
PINE SISKIN *	55	19	41
CARDUELIS TRISTIS			
AMERICAN GOLDFINCH	2	2	2
LOXIA CURVIROSTRA			
RED CROSSBILL	0	0	0
LOXIA LEUCOPTERA			
WHITE-WINGED CROSSBILL	1	0	0
CALCARIUS ORNATUS			
CHESTNUT-COLLARED LONGSPUR	0	0	0
PIPILO ERYTHROPHTHALMUS			
RUFOUS-SIDED TOWHEE	0	0	0
PASSERCULUS SANDWICHENSIS			
SAVANNAH SPARROW	2	3	1
AMMODRAMUS LECONTEII			
LE CONTE'S SPARROW	0	0	0
POOECETES GRAMINEUS			
VESPER SPARROW	2	1	1

Table 4. Total Annual Species Occurrences: Birds. (continued)

CALCARIUS LAPPONICUS			
LAPLAND LONGSPUR	0	0	0
SPIZELLA ARBOREA			
AMERICAN TREE SPARROW	0	0	0
SPIZELLA PASSERINA			
CHIPPING SPARROW *	2	11	26
SPIZELLA BREWERI			
BREWER'S SPARROW	0	0	0
MELOSPIZA MELODIA			
SONG SPARROW	17	16	19
MELOSPIZA LINCOLNII			
LINCOLNS SPARROW *	0	0	7
ZONOTRICHIA LEUCOPHRYS			
WHITE-CROWNED SPARROW *	7	6	15
ZONOTRICHIA ALBICOLLIS			
WHITE-THROATED SPARROW	1	0	0
PASSERELLA ILIACA			
FOX SPARROW *	2	1	20
JUNCO HYEMALIS			
DARK-EYED JUNCO *	44	20	48
TACHYCINETA THALASSINA			
VIOLET-GREEN SWALLOW	4	1	5
TACHYCINETA BICOLOR			
TREE SWALLOW	14	16	14
RIPARIA RIPARIA			
BANK SWALLOW	7	1	4
STELGIDOPTERYX SERRIPENNIS			
NORTHERN ROUGH-WINGED SWALLOW	2	0	1
HIRUNDO RUSTICA			
BARN SWALLOW	9	7	8
HIRUNDO PYRRHONOTA			
CLIFF SWALLOW	3	4	4
PERISOREUS CANADENSIS			
GRAY JAY *	13	2	18
CYANOCITTA STELLERI			
STELLER'S JAY	2	1	3
PICA PICA			
BLACK-BILLED MAGPIE	0	0	0
CORVUS CORAX			
COMMON RAVEN *	18	10	26
CORVUS BRACHYRHYNCHOS			
AMERICAN CROW	0	1	5
NUCIFRAGA COLUMBIANA			
CLARK'S NUTCRACKER	2	5	11
PARUS ATRICAPILLUS			
BLACK-CAPPED CHICKADEE	47	17	24
PARUS GAMBELI			
MOUNTAIN CHICKADEE	0	8	10

Table 4. Total Annual Species Occurrences: Birds. (continued)

PARUS HUDSONICUS			
BOREAL CHICKADEE	0	0	0
PARUS RUFENSCENS			
CHESTNUT-BACKED CHICKADEE	0	1	0
SITTA CAROLINENSIS			
WHITE-BREASTED NUTHATCH	0	0	0
SITTA CANADENSIS			
RED-BREASTED NUTHATCH *	37	23	35
CERTHIA AMERICANA			
BROWN CREEPER	1	0	1
CINCLUS MEXICANUS			
AMERICAN DIPPER	3	1	5
TROGLODYTES AEDON			
HOUSE WREN	2	7	2
TROGLODYTES TROGLODYTES			
WINTER WREN	1	4	10
CISTOTHORUS PALUSTRIS			
MARSH WREN	0	0	0
SALPINCTES OBSOLETUS			
ROCK WREN	0	0	0
DUMETELLA CAROLINENSIS			
GRAY CATBIRD	2	2	2
TURDUS MIGRATORIUS			
AMERICAN ROBIN *	53	27	58
IXOREUS NAEVIUS			
VARIED THRUSH	25	15	15
CATHARUS GUTTATUS			
HERMIT THRUSH	1	3	1
CATHARUS USTULATUS			
SWAINSON'S THRUSH *	44	30	46
CATHARUS FUSCENSCENS			
VEERY	1	3	3
SIALIA MEXICANA			
WESTERN BLUEBIRD	0	0	0
SIALIA CURRUCOIDES			
MOUNTAIN BLUEBIRD	1	3	2
MYADESTES TOWNSENDI			
TOWNSEND'S SOLITAIRE	0	0	3
ANTHUS SPINOLETTA			
WATER PIPIT	2	1	3
ARCHILOCHUS ALEXANDRI			
BLACK-CHINNED HUMMINGBIRD	0	1	0
SELASPHORUS PLATYCERCUS			
BROAD-TAILED HUMMINGBIRD	0	0	0
SELASPHORUS RUFUS			
RUFOUS HUMMINGBIRD	5	3	5
STELLULA CALLIOPE			
CALIOPE HUMMINGBIRD *	5	1	13

Table 4. Total Annual Species Occurrences: Birds. (continued)

CERYLE ALCYON			
BELTED KINGFISHER	2	3	5
COLAPTES AURATUS			
NORTHERN FLICKER *	29	18	34
DRYOCOPUS PILEATUS			
PILIATED WOODPECKER	2	4	11
MELANERPES ERYTHROCEPHALUS			
RED-HEADED WOODPECKER	2	0	0
MELANERPES LEWIS			
LEWIS' WOODPECKER	0	0	0
SPHYRAPICUS VARIUS			
YELLOW-BELLIED SAPSUCKER *	21	13	24
SPHYRAPICUS THYROIDEUS			
WILLIAMSON'S SAPSUCKER	0	0	0
PICOIDES VILLOSUS			
HAIRY WOODPECKER *	2	0	11
PICOIDES PUBESCENS			
DOWNY WOODPECKER	0	1	3
PICOIDES ARCTICUS			
BLACK-BACKED WOODPECKER	0	0	0
PICOIDES TRIDACTYLUS			
THREE-TOED WOODPECKER	0	0	4
TYRANNUS TYRANNUS			
EASTERN KINGBIRD	0	1	2
TYRANNUS VERTICALIS			
WESTERN KINGBIRD	0	0	0
CONTOPUS SORDIDULUS			
WESTERN WOOD-PEWEE	0	4	11
CONTOPUS BOREALIS			
OLIVE-SIDED FLYCATCHER *	1	5	15
SAYORNIS SAYA			
SAY'S PHOEBE	0	0	0
EMPIDONAX TRAILLII			
WILLOW FLYCATCHER *	14	8	20
EMPIDONAX MINIMUS			
LEAST FLYCATCHER	0	16	8
EMPIDONAX HAMMONDII			
HAMMON'S FLYCATCHER *	3	0	21
EMPIDONAX OBERHOLSERI			
DUSKY FLYCATCHER	1	0	2
EMPIDONAX DIFFICILIS			
WESTERN FLYCATCHER	0	1	0
BOMBYCILLA GARRULUS			
BOHEMIAN WAXWING	1	0	0
BOMBYCILLA CEDRORUM			
CEDAR WAXWING *	23	12	26
EREMOPHILA ALPESTRIS			
HORNED LARK	0	0	0

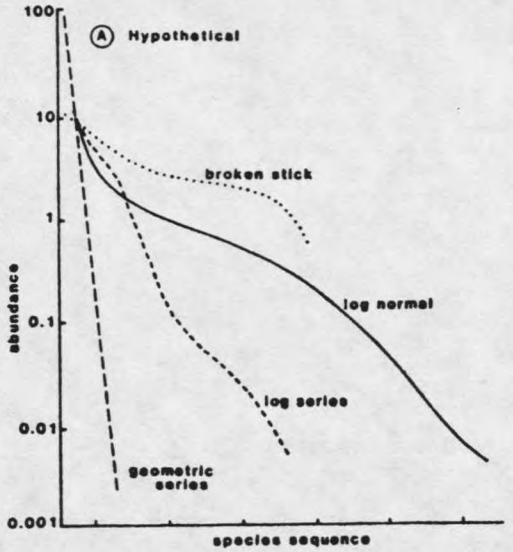
Table 5. Common Birds Under-represented in Glacier National Park Censuses.

Species	Habitat/Characteristic
evening grosbeak	forest/human habitation
pine grosbeak	forest
common redpoll	snow-covered field
red crossbill	forest
savannah sparrow	open grasslands
vesper sparrow	open grasslands
mourning dove	human habitation
horned lark	open grassland
brown creeper	deep forest
townsend's solitaire	mountain slopes
nighthawk	active in evening
lazuli bunting	grasslands
downy woodpecker	forest

Rank Occurrence Analysis A rank occurrence analysis was conducted by plotting a histogram of frequency of occurrence throughout the park for each species. The results are analogous to the standard rank abundance curves shown in Fig. 7, but frequency of occurrence is used in place of abundance. The 1989 bird and butterfly data both show a strikingly similar lognormal distribution (Figs 8-9).

Very few species occur at high frequency. Rather, most species fall into some varying degree of rarity. This distribution is said to be characteristic of birds in a deciduous forest (Magurran 1988). The range of commonness and rarity is not large, but this is partially an artifact of the method used to estimate abundance. Because abundance estimates were based upon number of sites in which a species

Fig. 7. Rank Abundance Curves



Species abundances are plotted from highest to lowest abundance to create a histogram of abundances. The shape of the rank abundance curve is said to be indicative of the type resource partitioning in the community. See text for more details. (after Magurran 1988)

Fig. 8. Rank Occurrence
Birds 1989

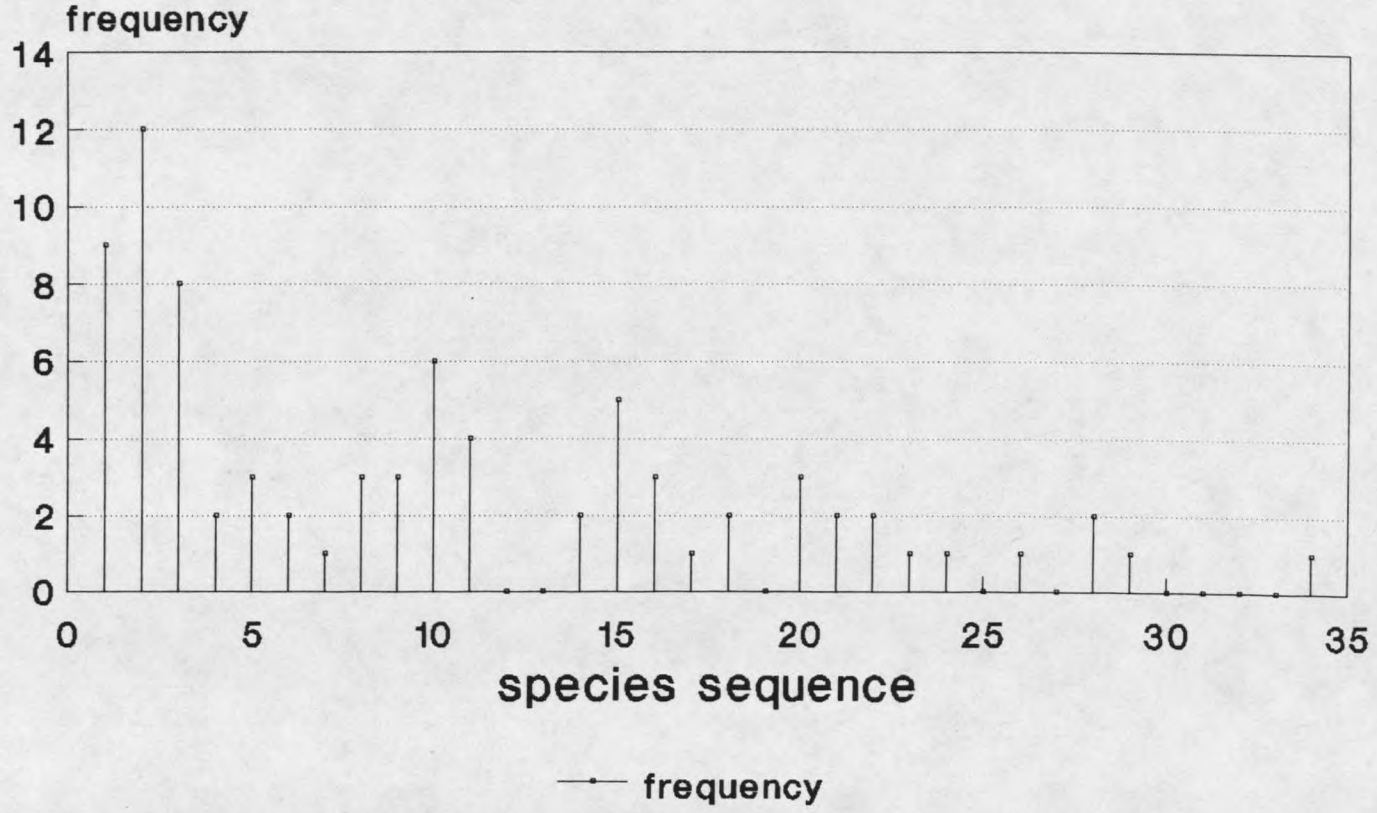
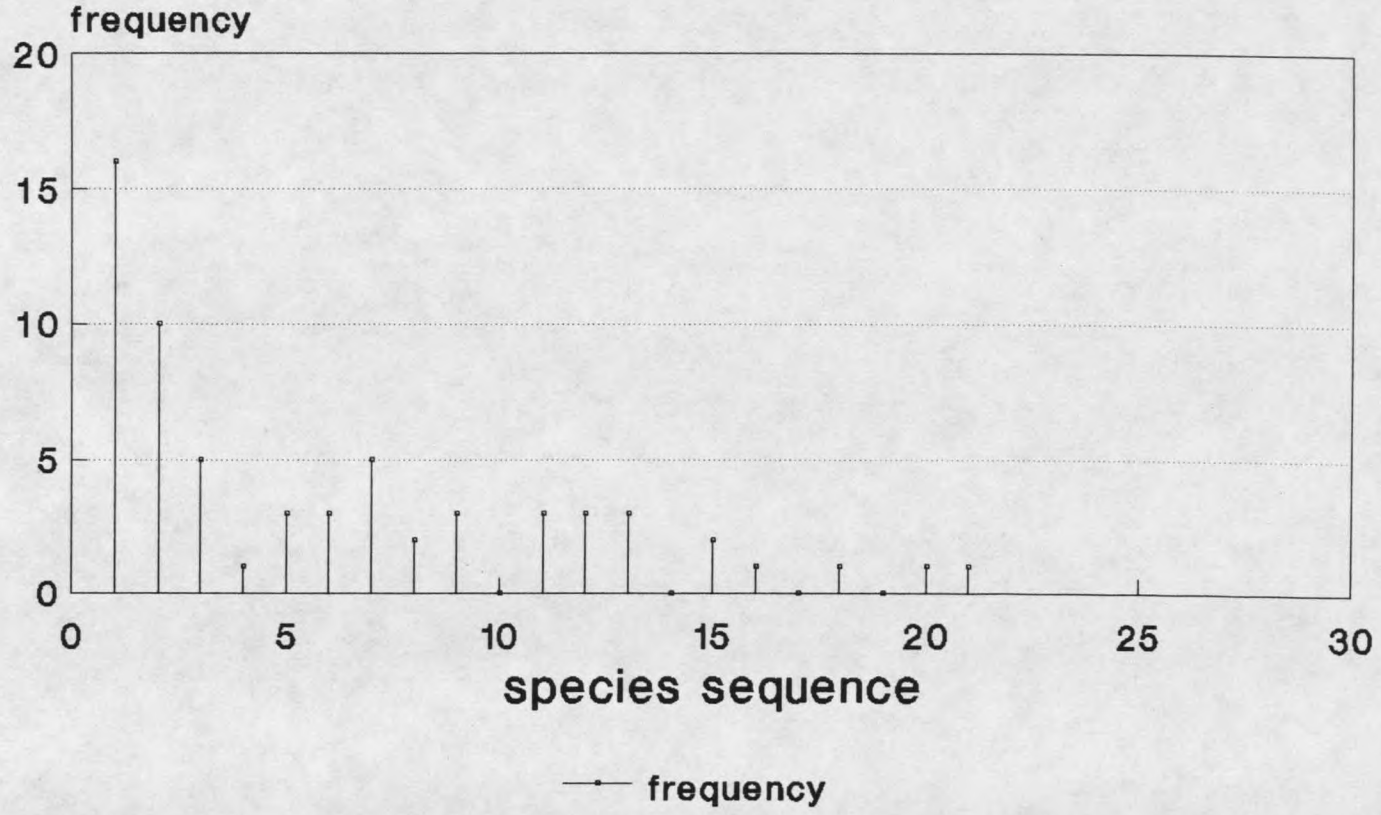


Fig. 9. Rank Occurrence
Butterflies 1989



was observed out of the total, the maximum abundance was the total number of sites (the American robin, the most common bird, received the maximum ranking of 34, as it was seen in all 34 of the bird sites).

Sites Supporting Rare Species Some species are only found in a few habitats within the park. For example, birds such as brown creepers, or northern waterthrushes require specific habitats. Furthermore, butterflies such a *E. gillettii, C. nastes, V. atalanta*, and *L. hyllus* were only noted once in all of the 1987 sampling (Tables 3 & 4). Later seasons revealed a similar level of rarity. *E. gillettii* is habitat specific, while *C. nastes* is on the edge of its range. Both of these species are extremely susceptible to any environmental changes.

Table 6 lists sites supporting rare butterfly species in 1989 (rare defined as occurring in less than three (13%) of the 24 total sites) include Lone Pine Prairie, Sullivan Meadow, Hidden Lake, and Scenic Point (two meadows and two alpine sites). Lone Pine and Sullivan Meadows were also hot spots for species diversity. No rare species were found in sites that had fewer than 14 species total.

Table 7 lists sites supporting rare bird species (defined as above) included Desantos (8), Spot Mt. (3), Lone Pine Prairie (2), Hidden Meadow (2), Two Dog Flats (2),

Table 6. Sites Supporting Rare Species - Butterflies 1989.

Site	# Rare Species
Lone Pine Prairie	4
Sullivan Meadow	4
Hidden Lake	4
Scenic Point	3
Christensen Meadow	2
Spot Mountain	2
Hidden Meadow	2
McGee Meadow	2
Baring Creek	2
Rocky Knob	2
St. Mary Vistor Center	1
Two Dog Flats	1
Belly River	1
Desantos	1
Round Prairie	1
Rt. 8 Burn	1
Wilbur Creek	1
Granite Park	1

Table 7. Sites Supporting Rare Species - Birds 1989.

Site	# Rare Species
Desantos	8
Spot Mt.	3
Lone Pine Prairie	2
Hidden Meadow	2
Two Dog Flats	2
St. Mary Campground	2
Logan Pass	2
Anaconda Meadow	1
Mud Lake	1
Rt. 8 Burn	1
Lake McDonold W.	1
Christensen Meadow	1
Dry Fork	1
Quarter Circle Bridge	1
Packer's Roost	1
Scenic Point	1
Baring Creek	1
Fifty Mountain	1

Logan Pass (2), and St. Mary Campground (2). As in the butterfly data, there was a correlation between presence of rare species and high species richness. Desantos was an outlier with respect to the number of rare species. This may be explained by the fact that it was also an outlier in habitat type. It was the most northern site, and this aspen parkland habitat was not replicated in any of the other sites. Table 8 provides a list of rare species and the corresponding sites supporting them.

Table 8. Sites supporting Rare species.

Butterflies 1987-1989

Species	Sites
Parnassius clodius	Big prairie
Papilio glaucus	St. Mary Visitor Center
Euphilotes anoptes	Baring Creek
Glaucopsyche piasus	Baring Creek
Callophyrs spinetorum	McGee Meadow
Celastrina argolius	Sullivan Meadow, Rocky Knob, Baring Creek
Epidemia nivalis	Hidden Lake, Big Prairie
Everes amyntula	Hidden Meadow, Sullivan Meadow
Lycaena phlaeas	Dutch creek NW, Belly river trail
Neophasia menapia	Kootenai Lakes, Christensen meadow, Hidden Lake
Colias meadii	Rocky Knob, Spot Mt.
Colias alexandra	2 Med./Bison Mt., Siyeh Pass, Christensen Meadow, Rt. 8 Burn
Colias nastes	Siyeh pass, Stoney Ind. Cg., Granite trail
Anthocharus sara	Siyeh pass, Scenic Point, Christensen Meadow
Harkenclenus titus	Baring creek, Spot Mt.
	Two Dog flats, St. Mary R.S.
	Baring Creek, Wilbur Creek

Table 8. Sites supporting Rare species (continued).

Butterflies 1987-1989

Species	Sites
Lyceana helloides	Hidden Lake, Baring Creek, West Glacier
Lyceana cupreus	Siyeh pass, Siyeh Bend Highline Trail 4 mi. from Logan Pass
Lyceana hyllus	Christensen meadow, Kootenai lakes
Lyceana mariposa	Round Prairie, Rt. 8 Burn
Limenitis weidemeyerii	Christensen m., Belly river trail
Limenitis arthemis	Belly river, Desantos
Vannessa atalanta	Mud creek meadow, Bear creek, Lone Pine Prairie
Vannessa cardui	Lone Pine Prairie, Spot Mt., Hidden Meadow
Polygonia gracilis	Granite trail, Lone Pine Prairie, St. Mary Visitor Center
Polygonia satyrus	Lone Pine Prairie, Hidden Meadow
Euphydryas gillettii	Christensen meadow, Belly River, Marias Pass, Red Meadow
Euphydryas editha	Christensen meadow
Boloria alberta	Siyeh pass
Boloria astarte	Scenic Point
Boloria titania	Christensen m., Sullivan m.
Speyeria egleis	McGee Meadow
Speyeria cybele	Christensen meadow, Rocky Knob
Speyeria hydaspe	Hidden Lake, Granite Park
Speyeria zerene	Two Dog Flats
Speyeria aphrodite	McGee Meadow
Callophyrs polios	Spot Mt.
Chlosyne gabbii	Bison Mt.
Oeneus uhleri	Baring Creek, Rt. 8 Burn

Table 8. Sites supporting Rare species (continued).

Birds 1987-1989

Species	Sites
orange-crowned warbler	Packer's Roost
Northern oriole	W. Glacier, Rt. 8 Burn, Dry Fork, Belly River/Cosley Desantos
American goldfinch	Belly River (Canada), Desantos
white-winged crossbill	Mud lake
vesper sparrow	Desantos, Belly R./Cosley
savannah sparrow	Spot Mt., McGee Meadow
white-throated sparrow	Belly River campground (U.S.)
cassin's finch	Lake McDonold West, Fifty Mt.
rough-winged swallow	Quarter Circle bridge, W. Glacier, St. Mary Campground
house wren	Sullivan meadow, Desantos, Belly River Campg., (U.S.)
winter wren	Fish lake
hermit thrush	Packer's roost, Ponderosa P., Rt.7
dusky flycatcher	Lone Pine prairie, Two Dog Flats, Anaconda Meadow, Big Prairie
mountain bluebird	Desantos, Spot Mt.
downy woodpecker	Lone Pine Pr., Hidden Meadow, Anaconda Meadow, Apgar Lookout Tr.
brewers blackbird	Desantos, Mud Lake, Belly/Cosley
Eastern kingbird	Hidden Meadow, Desantos, Belly River/Cosley, Apgar Look Tr.
water pipit	Logan Pass, Spot Mt. McGee Meadow Sullivan Meadow
rosy finch	Logan Pass, Fifty Mt., Sullivan, Walton R.S
Stellar's jay	Dry Fork, Baring Creek, Granite Park, St. Mary Campg.
pine grosbeak	Lone Pine Prairie, Scenic Pt., Anaconda Meadow, Sperry Tr.
black-headed grosbeak	Belly river/Cosley, Big Prairie, Hidden Meadow
red-eyed vireo	Christensen Meadow, Flathead R.S.
brown creeper	Anaconda meadow, Christensen Meadow

Diversity Hotspots Initial analysis of site-specific species diversity was conducted by combining all temporal replicate censuses at each of the sites (Tables 9-10). Thus, if a species was present in any one of the censuses, it was considered present in the summary data set for that site.

Table 9. Diversity Between Census Sites - Butterflies. Annual Butterfly Site Biodiversity Index (total species)

Butterfly Site	# Species			
	1987	1988	1989	1989S
Spot Mt. (10)	N	31	20	20
Christensen M. (9)	27	30	24	23
Hidden Lake (10)	11	20	17	17
Preston Park (12)	4	19	5	5
Belly River Cg. (4)	N	19	19	19
Baring Creek (6)	N	18	17	16
Sullivan Meadow (8)	18	18	20	18
Lone Pine Prarie (5)	13	17	22	18
Stony Indian Pass (6)	7	17	8	8
Granite Park (7)	N	17	14	14
Hidden Meadow (4)	N	16	20	17
Wilbur Creek (5)	N	16	16	16
Two Dog Flats (3)	11	15	20	20
Big Prarie (4)	3	14	15	15
McGee Meadow (6)	3	13	19	14
M.Fork Flathd W.G. (2)	N	13	N	N
Scenic Point (4)	8	12	16	16
Flattop Mountain (3)	7	12	4	4
Rocky Knob (5)	N	12	16	16
Desantos (5)	N	11	18	18
Fifty Mountain (6)	4	10	4	4
Rt. 8 Burnscar (3)	N	10	16	16
St. Mary Lake (3)	4	9	22	14
Round Prarie (4)	5	7	18	16
Mud Creek	N	N	9	9

Note: # in parentheses is the total samples in 1987
N = not sampled

1989S is a species richness standardized by using only 2 temporal replicates of 3 plots each (6 total replicates)

Table 10. Diversity Between Census Sites - Birds. Annual Bird Site Biodiversity Index (total # species)

Bird Site	# Species	1987	1988	1989
Hidden Meadow		N	25	38
Desantos		N	20	32
Rt 8 Burnscar		11	19	30
Flathead Ranger Station		5	17	21
Middle Fork Flathead W. Glac.		23	17	27
Granite Park		N	17	9
Belly River Campg., Canada		21	16	N
Lone Pine Prarie		12	16	39
St Mary's Lake at V.C.		13	16	25
Sullivan Meadow		8	16	33
Lake Mcdonold		5	14	29
Dry Fork		N	14	N
Swan Lake		N	14	N
Quarter Circle Bridge		8	13	27
Logan Pass		6	13	12
Belly River Ranger Station		6	12	N
McGee Meadow		N	12	24
Christensen Meadow		14	12	28
Mud Lake		11	12	30
Apgar Lookout		9	12	19
Sperry Trail		11	11	19
Moose Flat		N	11	N
Ponderosa Pine Rt. 7		N	11	17
Packer's Roost		8	11	20
Sacred Dancing Cascade		15	10	18
Issac Walton Ranger Station		11	10	34
Baring Creek		N	9	14
Rocky knob, Flathead R.S. rd.		N	8	23
Anaconda Meadow		8	8	31
Avalanche Lake		N	8	17
Belly River/Cosley Trail		7	8	21
Mud Creek Meadow		N	7	32
Fish Lake		9	4	N
Two Dog Flats		N	N	32
Scenic Point		3	N	17
Round Prairie		5	N	N

N - not sampled

The 1987-1989 biodiversity sites were ordinated with respect to species richness. Sites that ranked in the top five in any of the three years were included in the summary list (Tables 11 & 12). Three of the low elevation sites were diversity hotspots both for butterflies and for birds (Lone Pine Prairie, Sullivan Meadow, and Hidden Meadow). In some cases, the same site was ranked as first or second for two consecutive years (Christensen Meadow for butterflies, Hidden Meadow for birds).

Table 11. Diversity Hotspots 1989: Butterflies.

Site	Species Richness 1987	1988	1989
Christensen Meadow	27	30	24
Spot Mountain	N	31	20
St. Mary V.C.	4	9	22
Lone Pine Prairie	13	17	22
Hidden Meadow	N	16	20
Sullivan Meadow	18	18	20
Two Dog Flats	11	15	20
Hidden Lake	10	20	17

N = not sampled)

Direct interpretation of the butterfly species richness data is constrained, however, by differential sampling replication between some of the sites. The goal to conduct 3 samples per plot, with three spatial replications at each census was hindered by the inaccessibility of some of the sites. As such, replication within a site was not

consistent. Figure 10 shows a positive correlation between number of census samples and species richness estimates. It appears that two samples are not sufficient for estimating total diversity at a site, but after six samples, the curve begins to remain constant.

Table 12. Diversity Hotspots 1989: Birds.

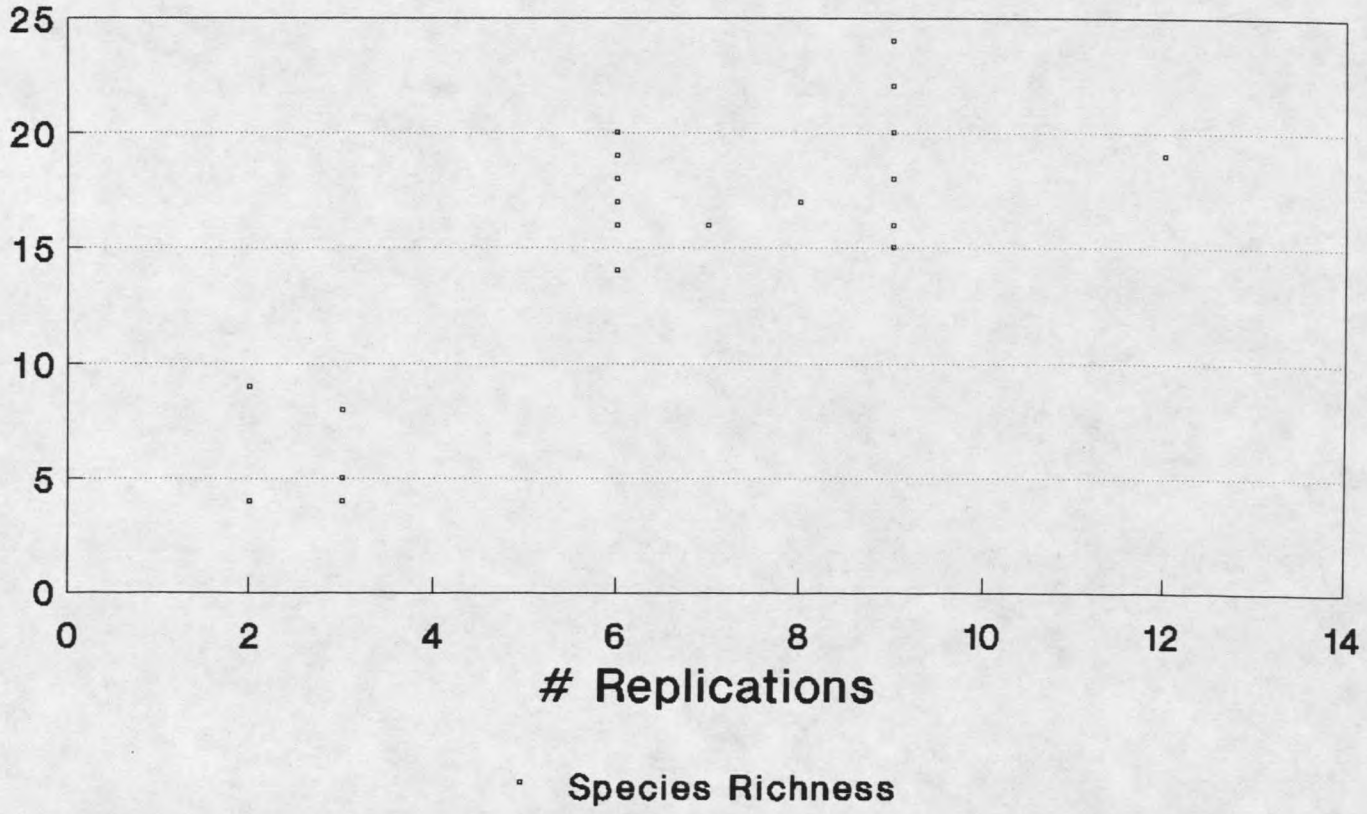
Site	Species Richness 1987	1988	1989
MFF W. Glacier	23	17	19
Belly Cg. CA	21	16	N
Hidden Meadow	N	25	38
Desantos	N	20	32
Lone Pine Prairie	12	16	39
Sullivan Meadow	8	16	33
Mud Creek Meadow	N	7	32

N - not sampled

To test for an effect of differential replication between sites, the butterfly data were re-analyzed, using data from only the first two censuses (Table 9 Column 1989S). In this way, the estimate of species richness was not confounded by the number of sample replicates. Interestingly enough, most of the sites on either extreme of the species richness spectrum maintained their positions. However, as one might expect, a few of the highly-replicated sites (3 to 4 temporal replicates) ranked lower after standardizing the number of replicates used in species

Fig. 10. Replication & Richness

Butterflies 1989



effect of # reps. on species richness

richness estimates. For example, St. Mary V.C. and McGee Meadow, originally in the top ten and with replicates of 3 and 4 respectively, were reduced to rankings of twenty and eighteen after standardization of sample number. Lone Pine Prairie and Hidden Meadow similarly dropped several ranks after standardization. Each had 3 replicates originally. Stony Indian Pass, Rt. 8 Burn, Scenic Point, and Rocky Knob, two of which had more than 2 replicates moved up in rankings. Thus, standardization of sample number is important prior to interpreting species richness. This differential replication problem did not arise in the bird biodiversity data, as two temporal replicates were conducted at each site.

Species/Habitat Relationships

Species Assemblage Analysis - PCA and Cluster Analysis

Principal Components Analysis (PCA) was to determine which environmental variables affect species distribution. Using the presence/absence data of species (all replicates combined for a site) as variables and census sites as observations, a PCA was conducted on both the bird and butterfly data using correlation matrices. The principal component (PC) scores were then plotted as scatter plots and clustered to form dendrograms of site relationships.

PC axes were described by inspecting the site

distribution and the species characterizing extreme values of the PC's. If these subjective axis descriptions represented quantifiable variables, PC values were tested against the true values using a correlation analysis.

Butterfly 1988 PCA When plotting PC scatter plots (Figs. 11 & 12), the following descriptions were applied to PC axes 1-3:

axis 1 = elevation of site
axis 2 = species richness of site
axis 3 = commonness vs. rarity of species in site

Correlation analysis revealed that axis 1 was significantly correlated with elevation ($r = .83$, $p<.01$) and axis 2 was significantly correlated with species richness ($r = .88$, $p<.01$). Axis 3 was a subjective descriptor, so it was not tested for correlation.

Because these PCs were associated with high percent explained variances (17.75, 10.46, 9.42, and 8.30 for PCs 1 through 4 respectively), PC scores 1, 3 & 4 were used in cluster analysis to form dendrograms (Fig. 13). The two major clusters are separated into alpine and low elevation sites. When PC 2 is included, Spot Mt. and Christensen meadow are outliers due to high species richness of the sites. By removing PC 2 from the analysis, these two outliers are incorporated into the two main clusters. McGee Meadow, Rocky Knob, and Rt 8 Burnscar are also outliers in Fig. 13. Extremes of moisture level may be PC 4, which is

Fig. 11. Butterfly PCA 1988

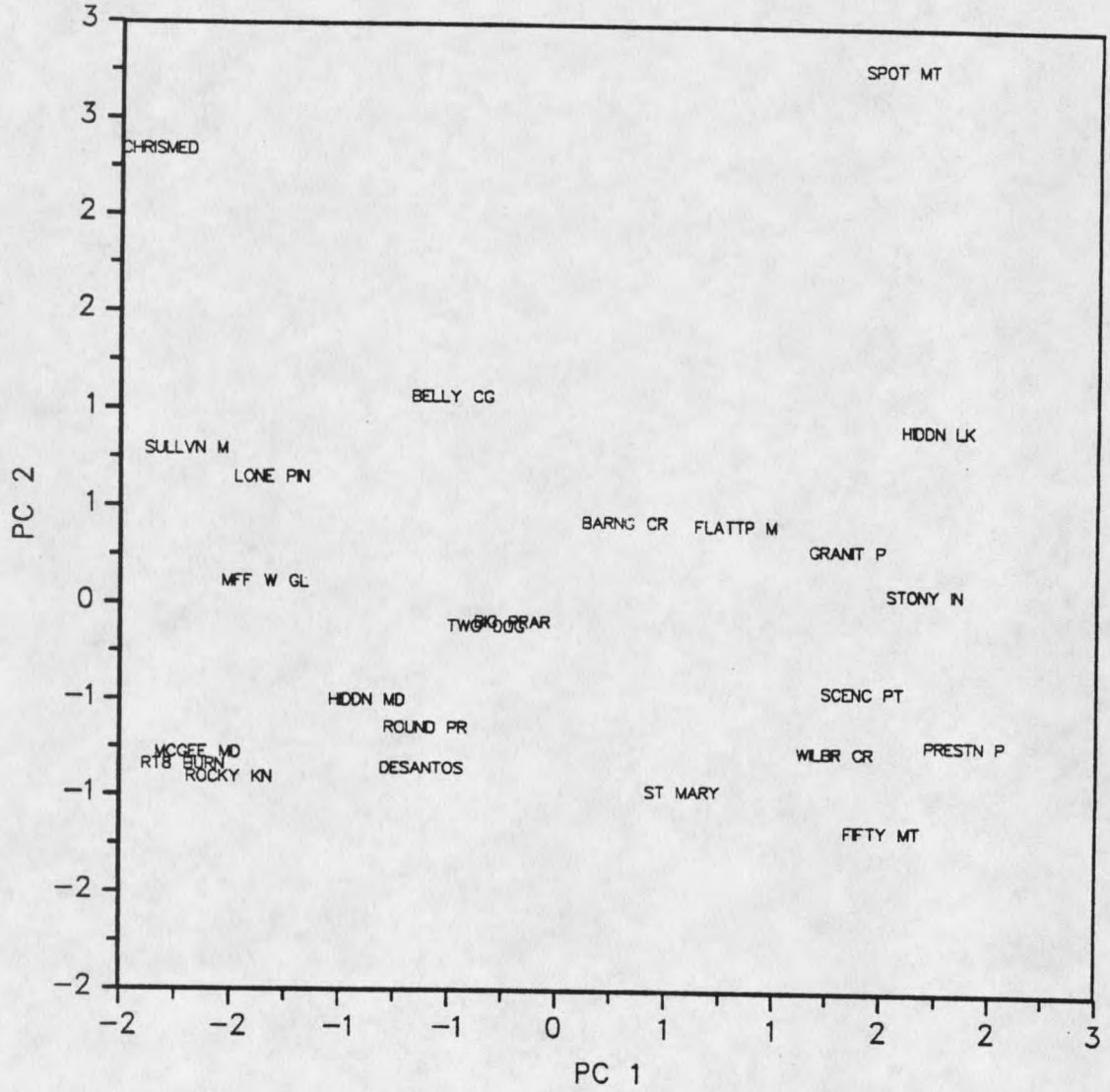


Fig. 12. Butterfly PCA 1988

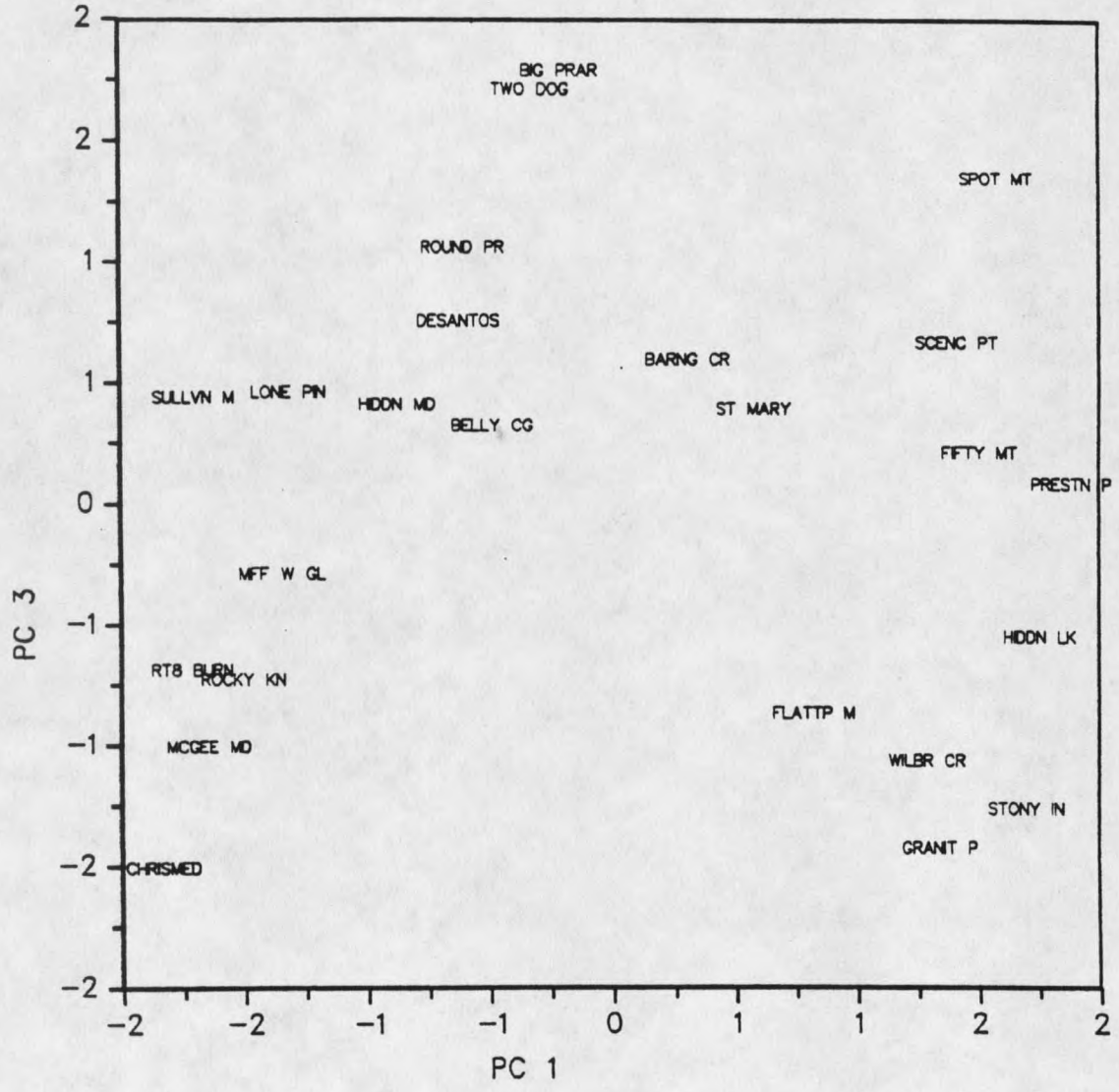
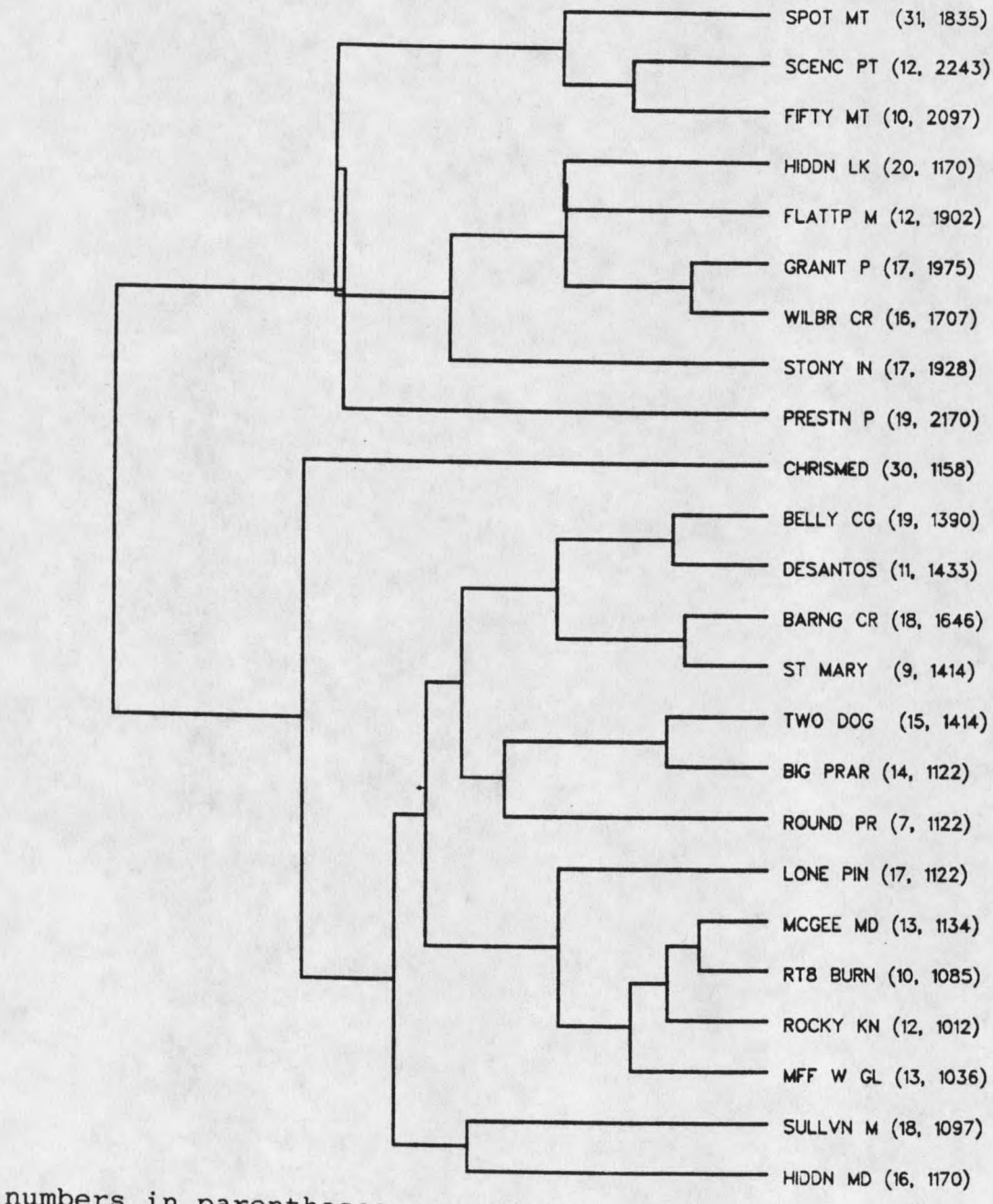


Fig. 13. Butterfly Cluster Analysis - 1988



numbers in parentheses are species richness and elevation (m)

separating them from the low elevation group. Further analyses would have to be conducted to justify this explanation.

Bird 1988 PCA PCA results for the bird data revealed somewhat less obvious PC classifications upon initial inspection. However, the habitat characteristics were revealed by investigating habitat preferrences of prominent species at the extremes of the PC values. The following descriptions were assigned using Figures 14 & 15:

PC 1 = structural diversity of habitat
PC 2 = elevation of site
PC 3 = moisture level of site

Structural diversity of habitat and moisture level of the sites were not estimated in this analysis, so PC axes 1 and 3 could not be tested for correlation. However, PC 2 was tested for correlation with elevation. The correlation was lower that that for butterflies ($r=.39$), but it was still significant ($p<.05$)

The percent explained variance associated with each eigenvalue did not isolate the first few variables as major descriptors for bird data of 1988. Conversely, there was a gradual tapering of explained variance from eigenvalues 1 - 32. This analysis was run using both a covariance and a correlation matrix for comparison. The explained variance did not change, but higher eigenvalues were obtained using

Fig. 14. Bird PCA 1988

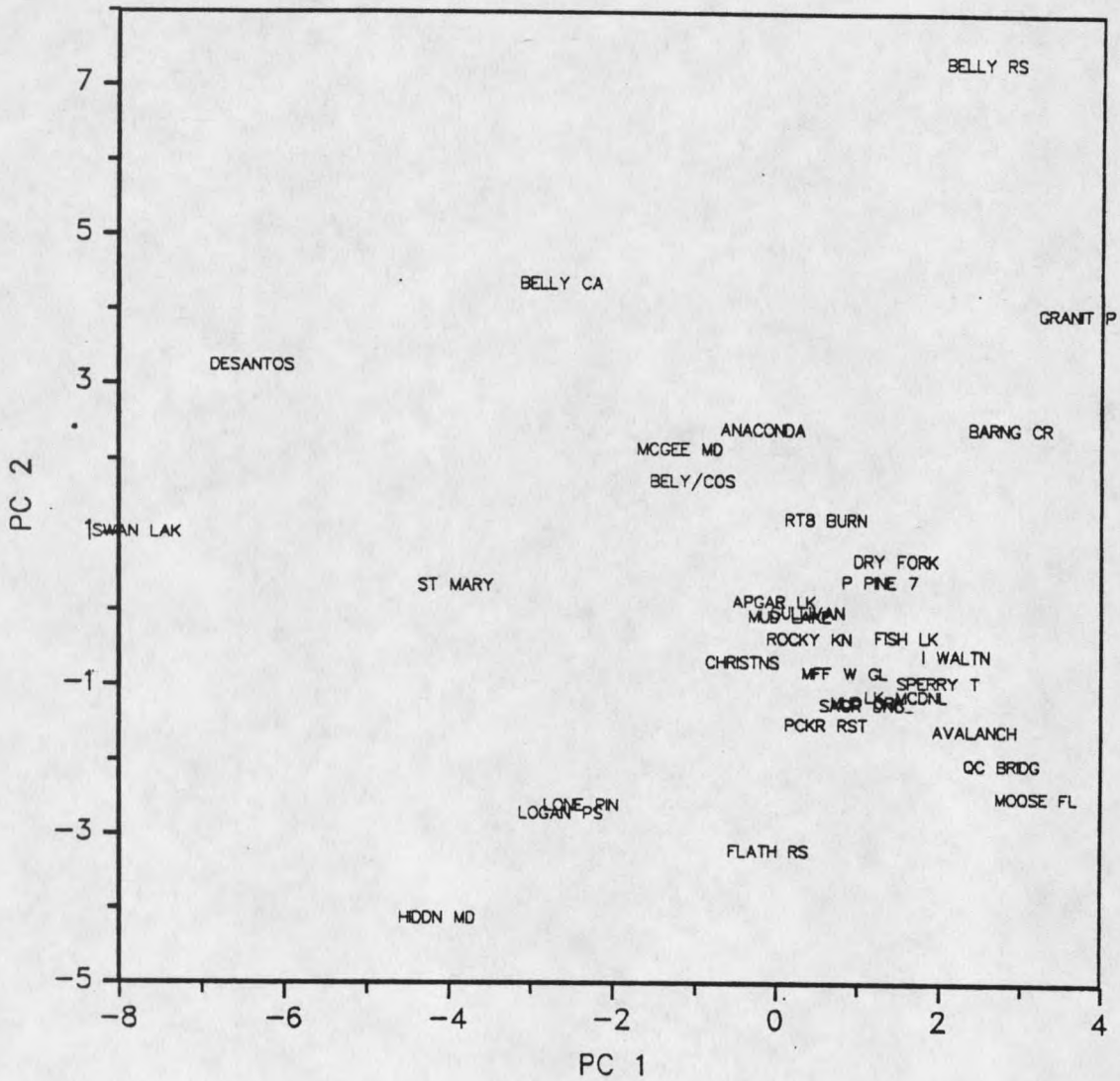
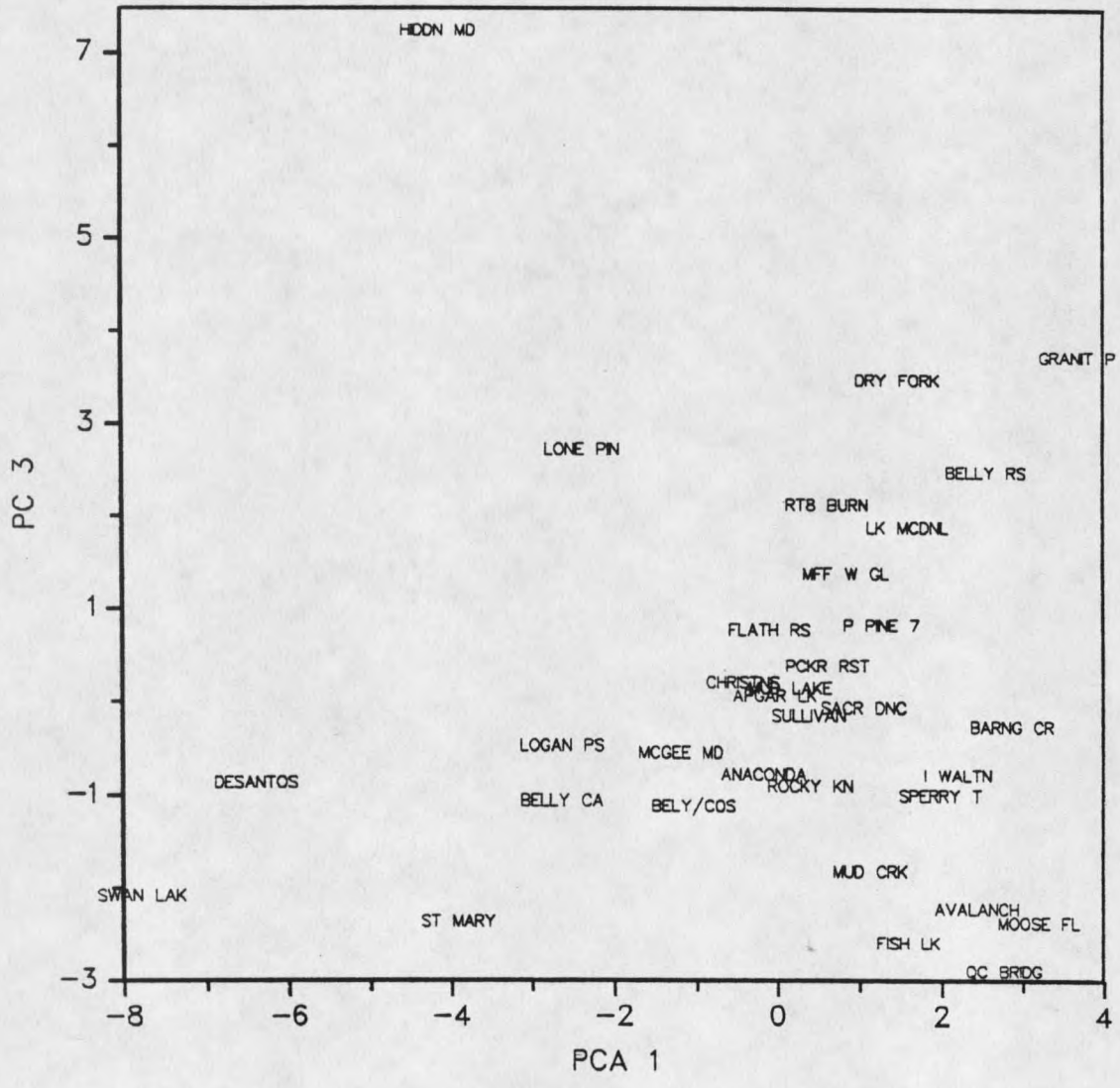


Fig. 15. Bird PCA 1988



the correlation matrix.

Butterfly 1989 PCA The first three variables explained 60% of the variation in this test. Figures 16-18 show the PC plots and cluster analysis. Elevation was correlated with PC 2 (r=-.30), but the correlation was not significant. Characterization of PC 1 as moisture is based upon the array of sites, with moister areas on the lower end of the scale. PC 3 separates some sites into east and west sides relative to the continental divide, but the fit is entirely consistent. There are few east side sites clustered with west side sites. Cluster analysis revealed high and low elevation grouping similar to that of 1988.

PC 1: moisture
PC 2: elevation
PC 3: east/west of continental divide

Bird 1989 PCA The first three PC's explained half of the variation in the data. Figures 19-21 show the PC plots and cluster analysis. Interpretation of the axes yielded the following characterizations of PC's:

PC 1: moisture
PC 2: elevation
PC 3: coniferous forests to deciduous forests and thickets

Elevation was significantly correlated with PC 2 (r=-.62, $p<.01$). Other variables were not as easily tested. The arrangement of the sites clustered riparian areas with higher values of PC 1, suggesting a moisture gradient. The habitat requirements of species characterizing the extremes

Fig. 16. Butterfly PCA 1989

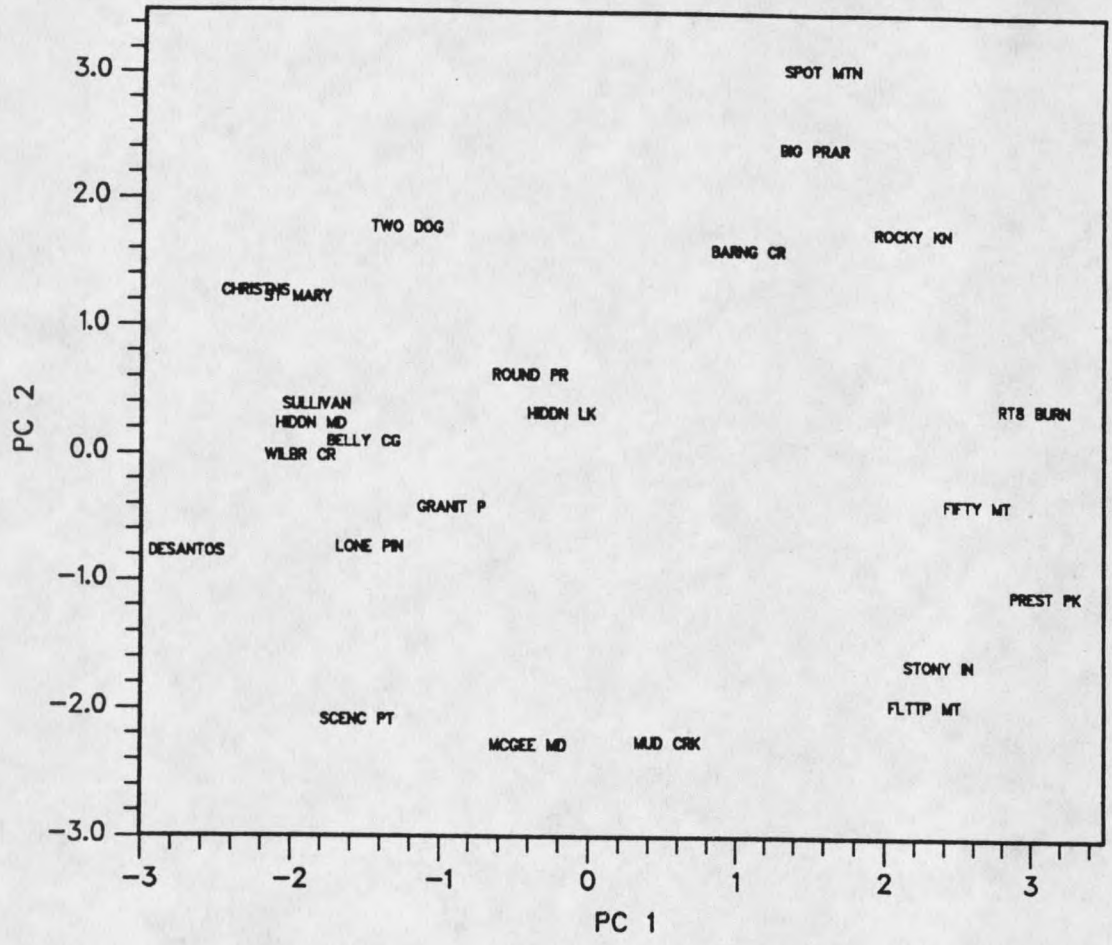


Fig. 17. Butterfly PCA 1989

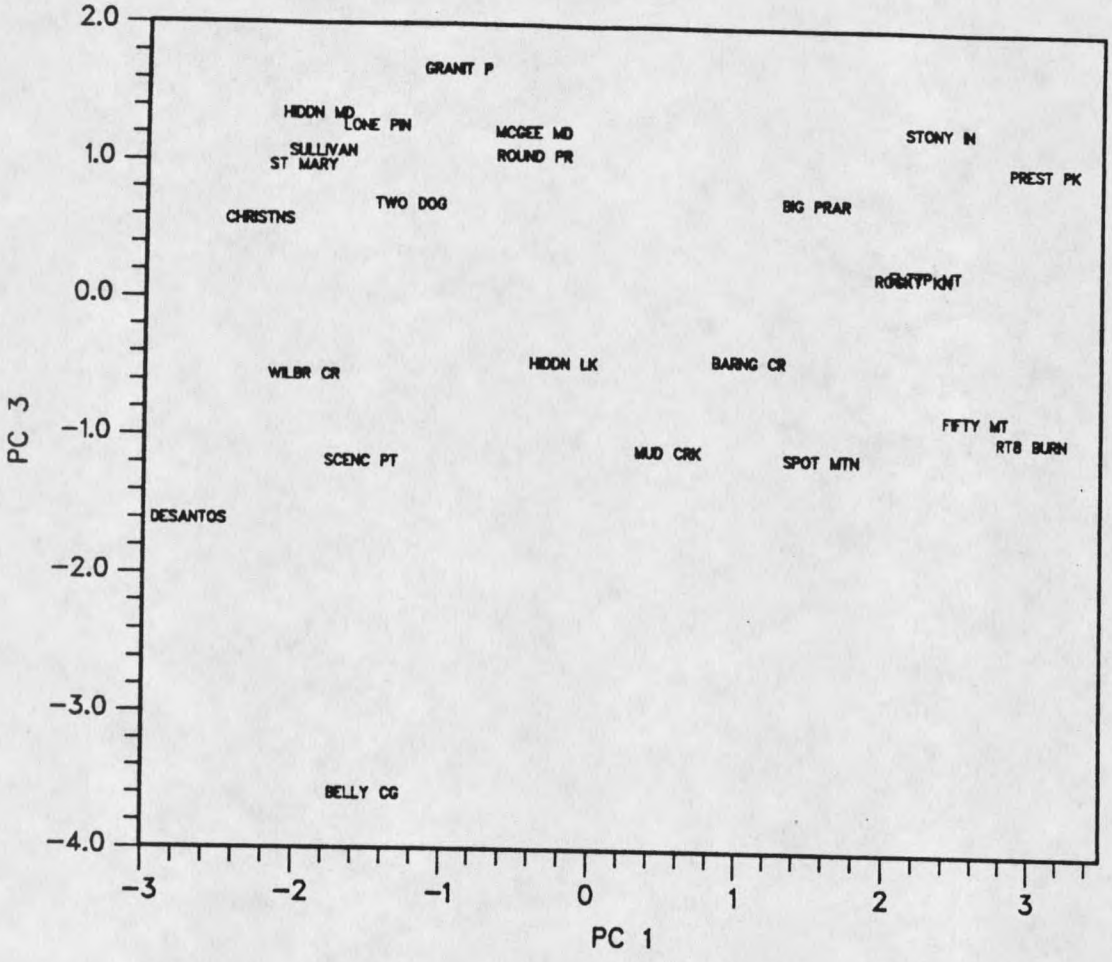


Fig. 18. Butterfly Cluster Analysis - 1989

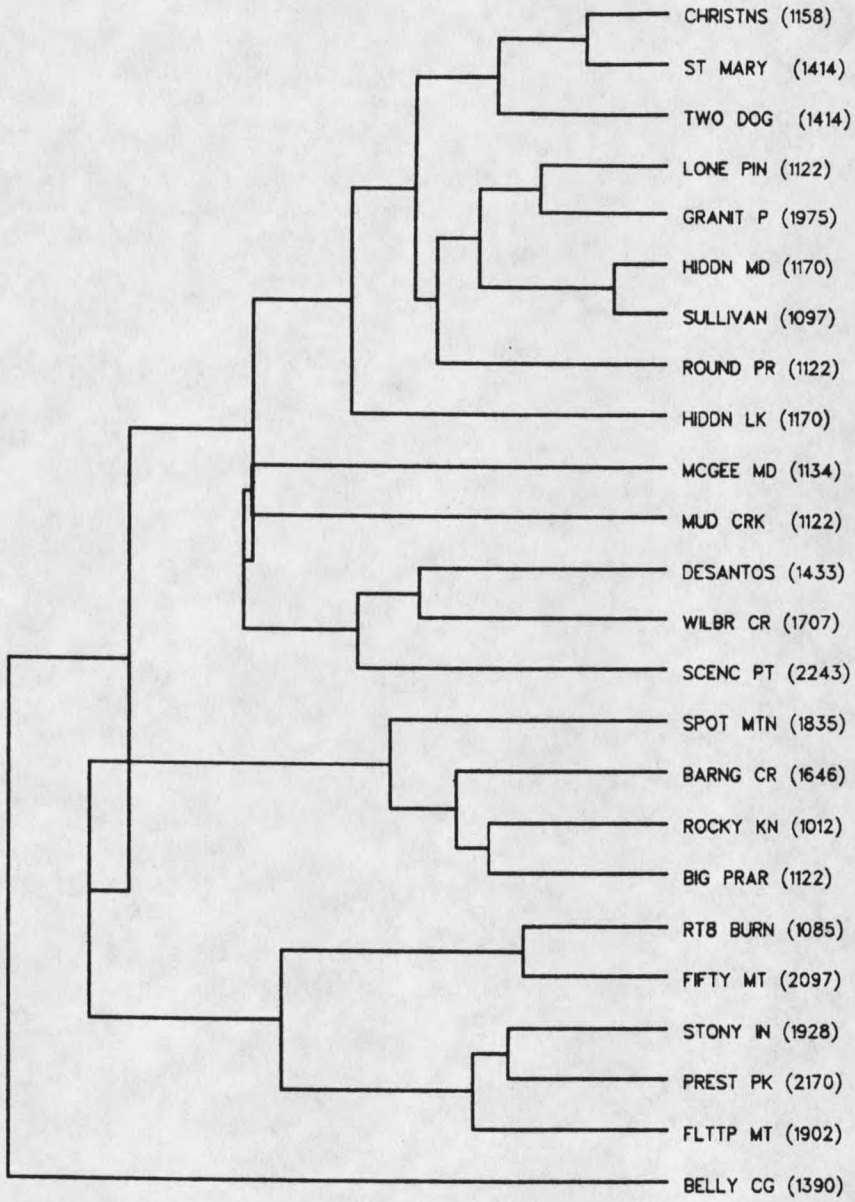


Fig. 19. Bird PCA 1989

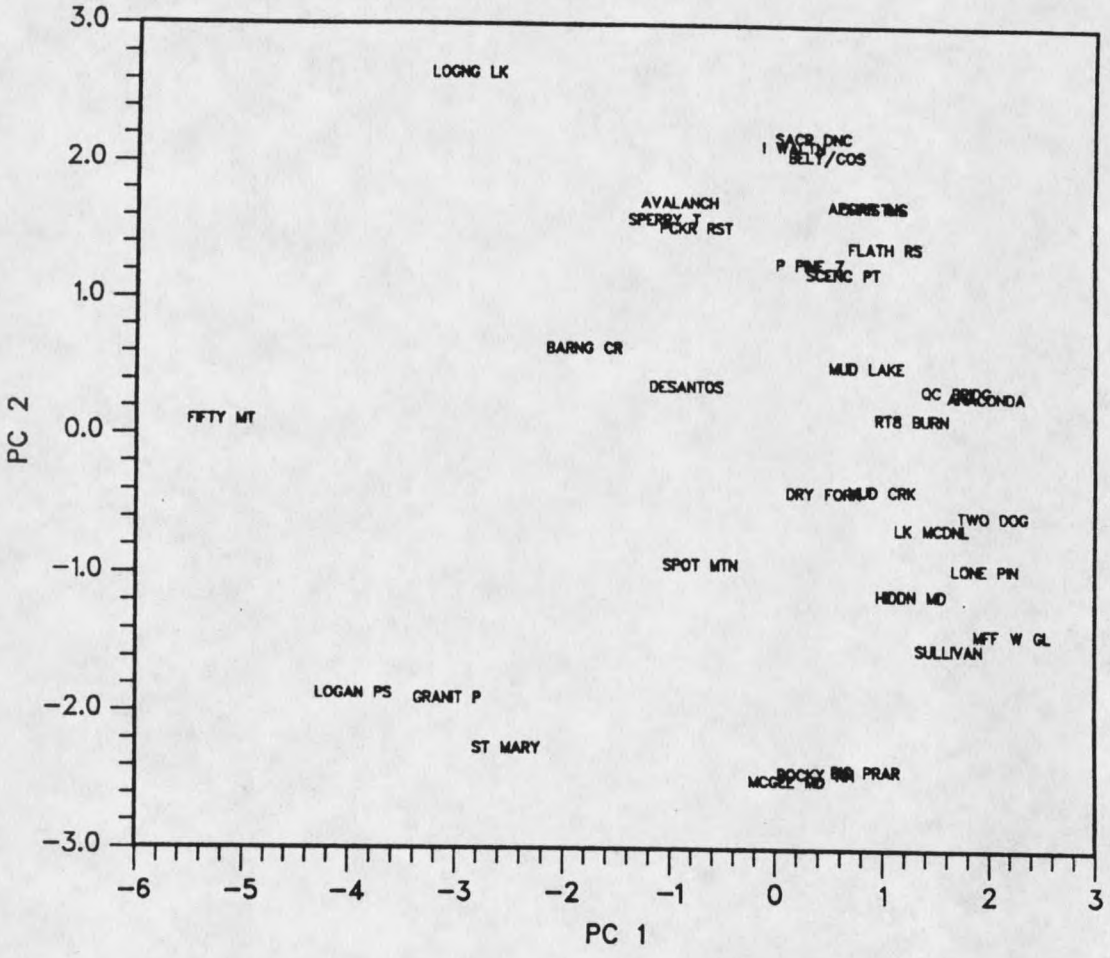


Fig. 20. Bird PCA 1989

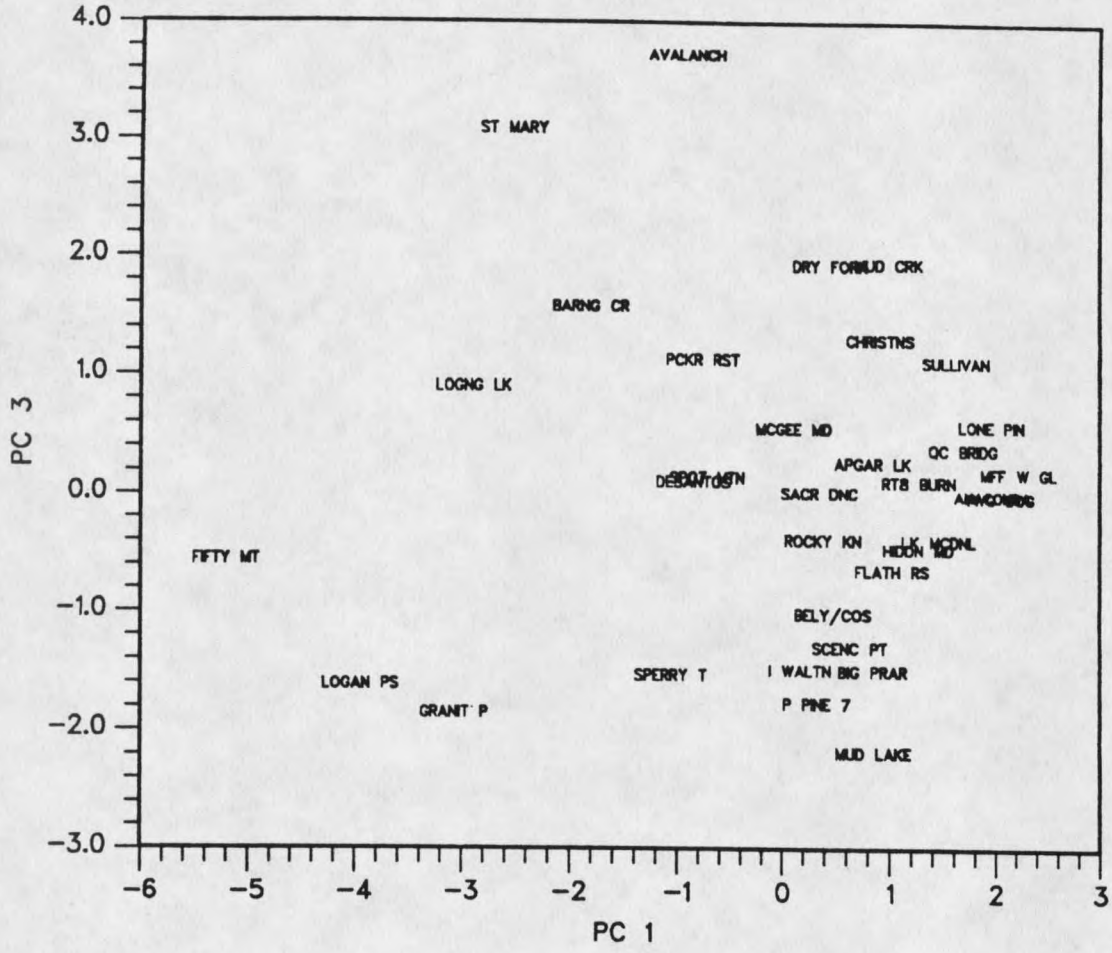
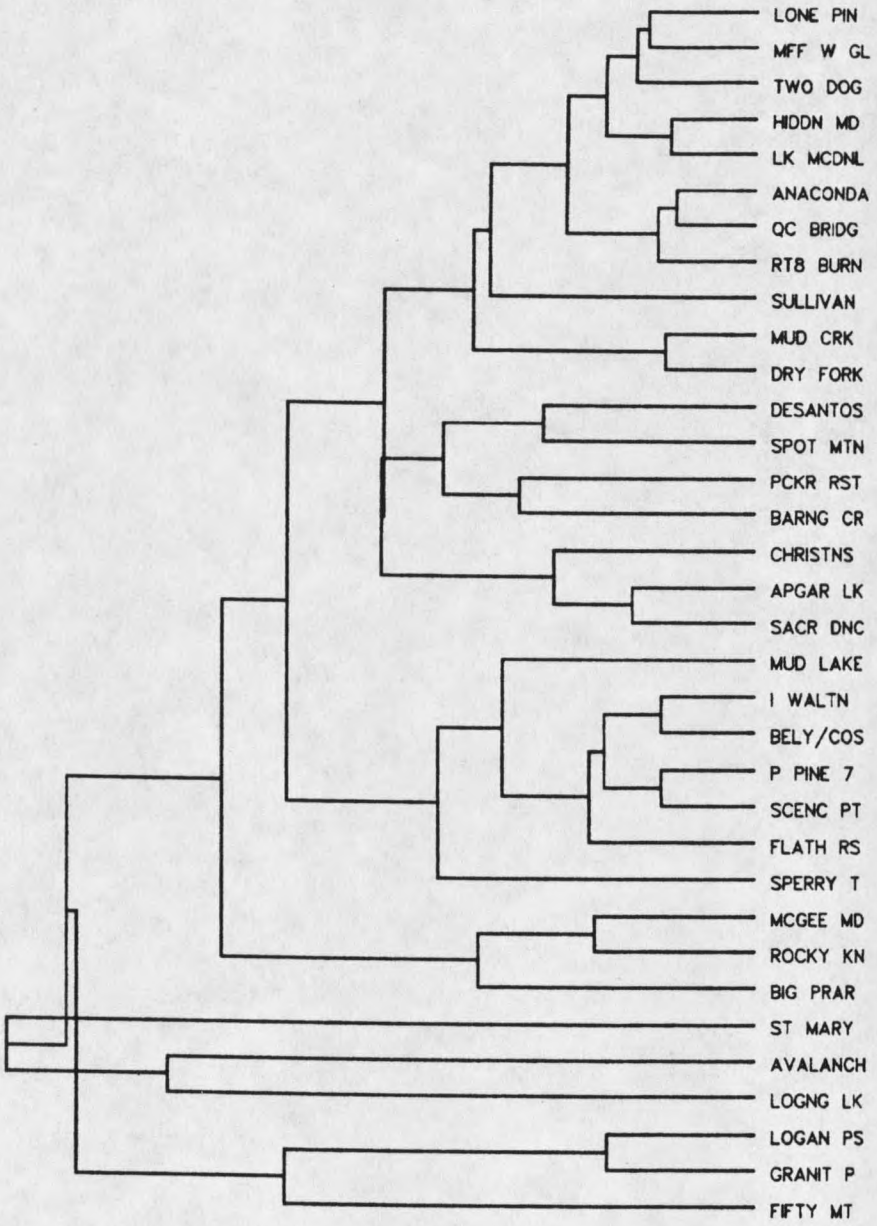


Fig. 21. Bird Cluster Analysis - 1989



of PC 3 suggested a coniferous species to deciduous gradient. Cluster analysis of this data did not reveal any easily distinguished groupings.

ANOVA and Discriminant Analysis for Species/Habitat Associations An ANOVA was conducted on the species by site matrix to determine which species, if any, exhibited a tendency to be associated with a particular habitat type or east/west orientation. There was a marked difference between the results of the butterfly data (Table 13) and that of the bird data (Table 14). While 10 birds exhibited a significant east/west preference and 17 birds exhibited a significant habitat preference, only two species of butterflies exhibited an east/west preference and only three species exhibited a habitat preference.

Table 13. Habitat Anova Results - Butterflies 1989.

Species that discriminated between habitats with $p<.05$

East/West Differentiation

Species	p value	Habitat Preference
Coenonympha inornata	.014	East
Euphydryas anicia	.006	West

Habitat Preference

Species	p val.	Hydr.	Mes.	Xeric	Alpine
Phyciodes campestris	.008		Y	Y	
Speyeria atlantis	.004	Y	Y		
Nymphalis antiopa	.002	Y			

Table 14. Habitat Anova Results - Birds 1989.

Species that discriminated between habitats with p<.05

East/West Differentiation

Species	p value	Habitat Preference
Swainson's thrush	.027	West
yellow rumped warbler	.027	West
American redstart	.000	West
Wilson's warbler	.042	West
western tanager	.016	West
varried thrush	.008	West
piliated woodpecker	.014	West
orange-crowned warbler	.014	West
Clarke's nutcracker	.026	East
white-crowned sparrow	.000	East

Habitat Preference

Species	p value	Int. For.	For. Mead. Edge	For Rip. Edge	Alpine
swainson's thrush	.041	Y	Y	Y	
golden kinglet	.035	Y		Y	
warbling vireo	.037		Y	Y	
blackcapped chickadee	.025		Y	Y	
American redstart	.034	Y	Y	Y	N
chipping sparrow	.001	N	Y		
cedar waxwing	.000	N	Y	Y	
wilson's warbler	.025	Y			N
yellow-bellied sapsucker	.040		Y	Y	N
brown-headed cowbird	.000	N	Y		N
willow flycatcher	.014		Y	Y	N
hammond's flycatcher	.013		Y	Y	N
song sparrow	.014		Y	Y	N
yellow warbler	.014			Y	N
varried thrush	.003	Y			N
white-crowned sparrow	.022	N			Y
common yellowthroat	.018	N	Y		N

A discriminant analysis (DA) was conducted to determine the level of accuracy obtained when species assemblages were used to predict habitat type or east/west orientation

relative to the continental divide. The initial analysis was conducted using common species as variables. Rare species provide little information mathematically if they occur in fewer sites than the smallest group. As such, they cannot be used to define a group, so they are not appropriate choices for DA variables. A second DA was conducted using only species which ranked p<=.05 in the ANOVA. In both cases, the results were similar. While some DA results showed a high number of correct categorizations, jackknifing always revealed overfitting. That is, there were many more variables relative to the number of observations, confounding the ability to make rigorous predictions.

Gradient Analysis

Elevation Gradients Species richness (S), when plotted against elevation for the 1987 butterfly data, produced a strong peak at 1150 m and two lesser peaks 1950 and 2250 m (Figure 22). These sites correspond to low elevation and alpine meadow habitats, respectively.

Bird species richness peaked near 1000 m and also near 1400 m elevation (Figure 23), in riparian habitats. Variance in species richness relative to elevation decreased with increasing elevation for both birds and butterflies.

Fig. 22. Elev. Grad.- Butterflies

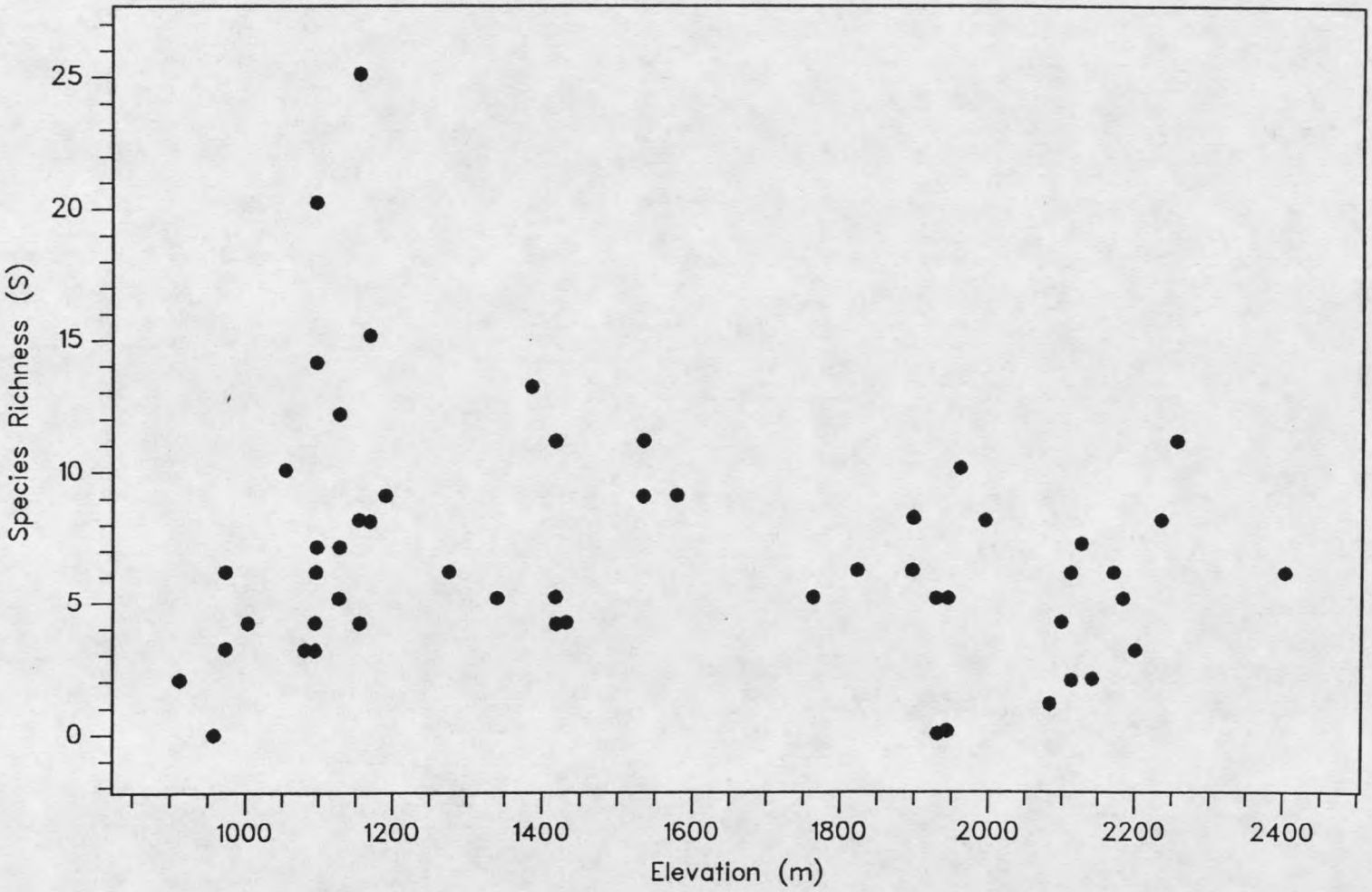
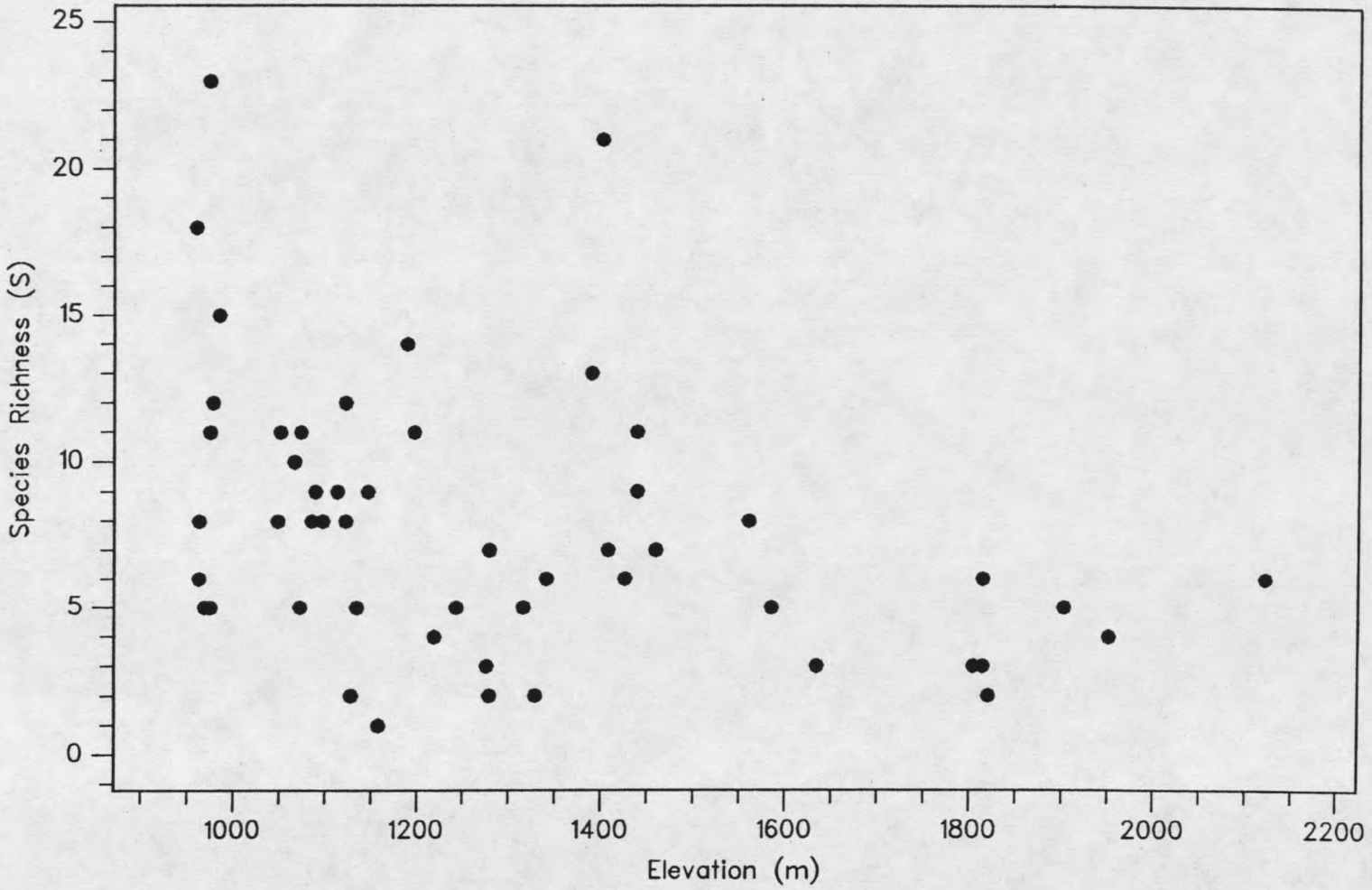


Fig. 23. Elevation Grad.- Birds



Moisture Gradients A sorting of 14 of the 1987 meadow habitats by moisture gradients (hydric, mesic, and xeric), revealed that mesic meadows had over twice the butterfly species diversity relative to hydric or xeric meadows (Table 15). Despite the small sample size, there is an obvious difference between habitats. Mesic meadows support a higher diversity of species. The mean number of species present in each meadow type was as follows: hydric (n=3): 6 species, mesic (n=8): 13.5 species, and xeric (n=3): 6.33 species.

Table 15. Moisture Gradient Analysis.

1987 Butterfly Species Richness Relative to Moisture of Site

Hydric Meadows	Mesic Meadows	Xeric Meadows
Mud Creek (7)	Christensens (25)	Big Prairie (3)
Bowman (7)	Lone Pine (13)	Round Pr. (5)
McGee (4)	Sullivan (20)	Two Dog Fl.(11)
	Anaconda (14)	
	Deer Lick (15)	
	Dutch Creek (10)	
	Fern Creek (6)	
	Flathead R.S. (5)	
Total Sp.= 18	Total Sp. = 108	Total Sp. = 19
n = 3	n = 8	n = 3
mean = 6	mean = 13.5	mean = 6.33

Edge Effects Defining an edge and measuring its dimensions is a difficult task because of the numerous variables that could be considered (i.e., initiation of edge, height requirements, visual components, etc.). Further, the effective edge width may vary between species.

Despite these constraints, a subjective analysis of edge effects was conducted. Some of the butterfly sample subplots could be classified as meadow/forest edges while others were in the middle of a relatively homogeneous meadow. Edge sites tended to have a higher diversity of flower species and consequently had a higher diversity of butterfly species (Table 16). For example, Lone Pine Prairie, on two occasions, exhibited greater species diversity on the edge plot, as did Christensen Meadow and Round Prairie. Two Dog Flats did not exhibit consistent results; one non-edge site exhibited higher species diversity (7 species near edge relative to 5 species farthest from edge) while the other exhibited lower species diversity relative to the edge subplot (7 species near edge relative to 8 species farthest from edge).

Bird sites were separated into several different categories with respect to edges: (1) meadow/forest edge, (2) riparian edge, (3) habitat complex, (4) interior forest, and (5) meadow. Table 17 shows that on average, meadow/forest edge sites had 50% more species compared to the interior forest edge sites (means of 31.2 and 18.8 species respectively with n=6 for each habitat type).

Table 16. Forest Edges And Butterfly Diversity.

A comparison of subplots nearest forest edges with subplots farthest from forest edge (# in parentheses = replicates).

Site	Nearest to Edges # Species	Farthest from Edges # Species
Lone Pine Prairie		
6/22/89	7 (3)	1 (2) and 2 (3)
7/28/89	7 (8)	5 (4) and 3 (6)
Christensen Meadow		
7/6/89	11(5) and 12 (4)	6 (4)
7/18/88	7 (4) and 9 (5)	5 (2)
Two Dog Flats		
7/12/89	7 (6)	8 (7) and 5 (6)
Round Prairie		
7/21/89	7 (5) and 7 (5)	4 (3)

Table 17. Forest Edges And Bird Diversity.

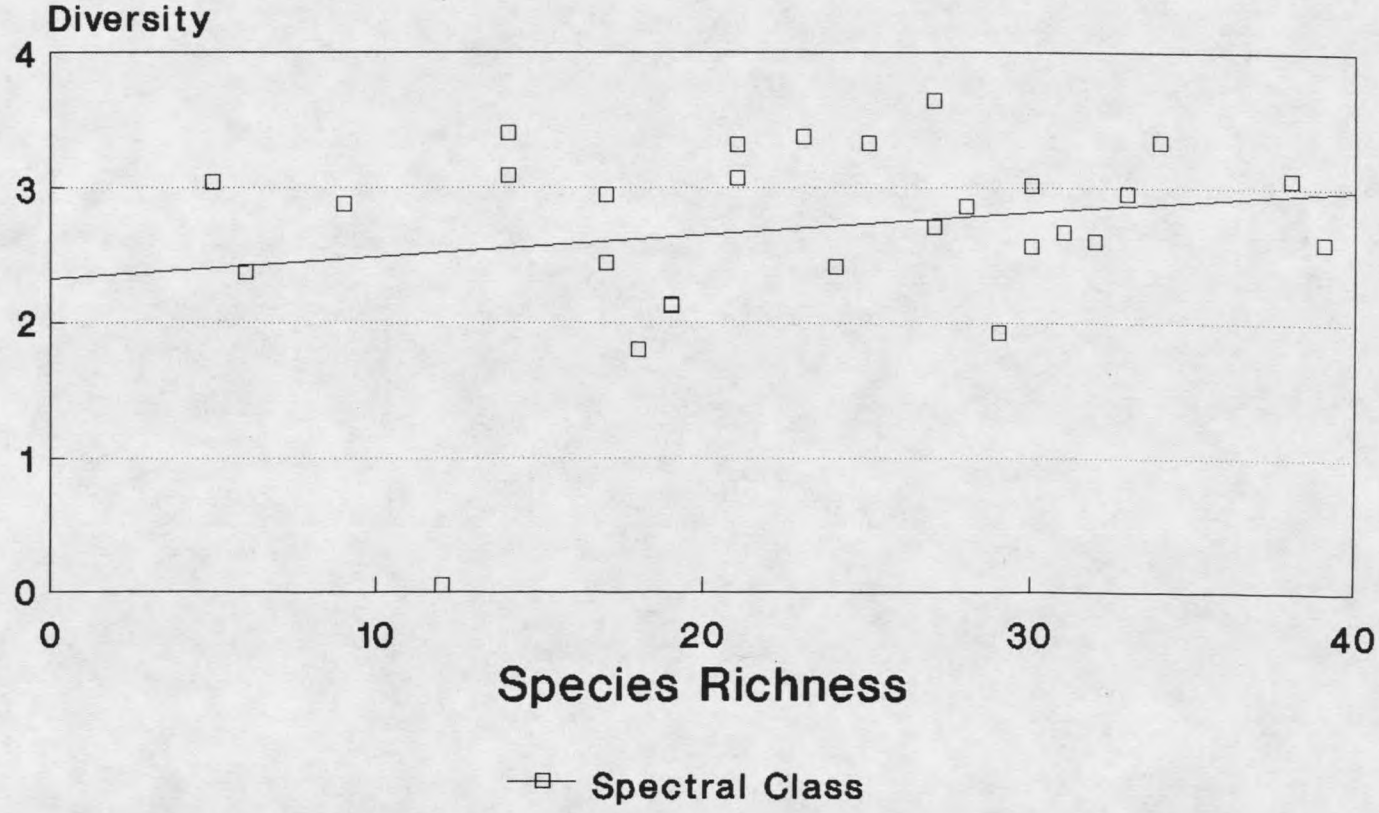
A comparison of plots where the forest/meadow edge is dominant with plots where the dominant habitat influence is an interior forest. S represents cumulative species richness from 1989 censuses.

Forest/Meadow Edge	S	Interior Forest	S
Sullivan Meadow	33	Avalanche Lake Trail	17
Christensen Meadow	28	Apgar Lookout Trail	19
Lone Pine Prairie	39	Ponderosa Pine Stand	17
McGee Meadow	24	Packer's Roost	20
Anaconda Meadow	31	Isaak Walton R.S.	22
Two Dog Flats	32	Sacred Dancing Trail	18
Mean = 31.2		Mean = 18.8	

Habitat Diversity and Species Richness Analysis of site-specific species richness (S) was tested for correlations with topographic diversity using a variety of habitat measures. GNP's GIS characterizes each 50 x 50 m plot of land across the entire park using 99 spectral classes (based upon ultra-violet reflectance from satellite photography), aspect, slope, and elevation. Thus, each square kilometer plot is characterized by 400 50 x 50 m subplots, and each subplot is described by 102 variables. Separate Shannon habitat diversity indices were calculated for elevation, aspect and slope using the 400 subplots within each of the biodiversity sites. These habitat diversity indices were plotted against species richness (S) for each of the sites to test for a correlation between habitat diversity and species richness (Figures 24-31).

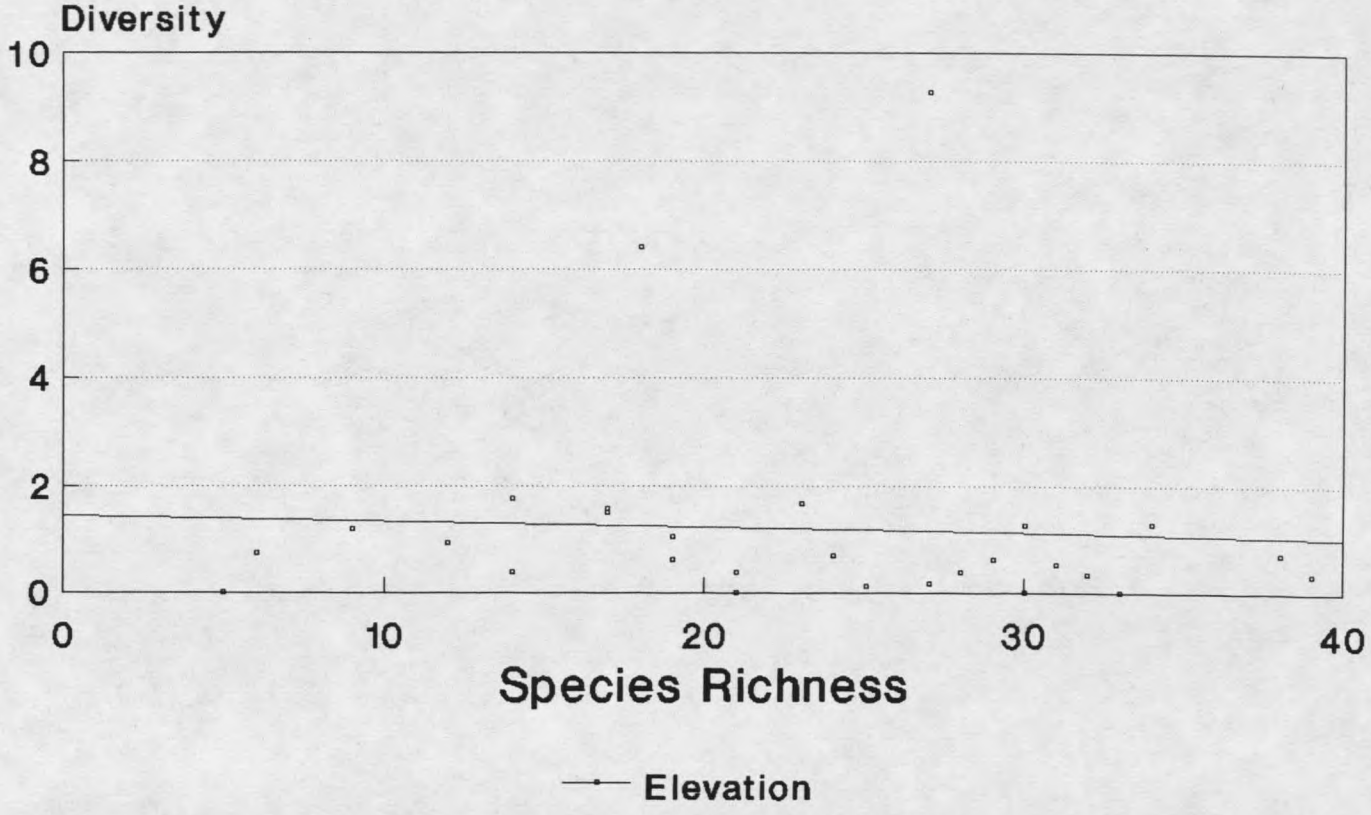
Spectral class diversity, which is indicative of habitat type diversity, had the expected positive correlation with species diversity; however, the relationship was much more marked in butterflies than in birds. Aspect diversity (i.e. sites with a diversity of aspects) had a very slight negative correlation with species diversity in both butterflies and birds. Slope diversity had a negative correlation with species diversity in both butterflies and birds, but the relationship was again more marked for butterflies. Elevation diversity exhibited a different correlation between taxa. The correlation was

Fig. 24. GIS Habitat Diversity
Versus Species Richness



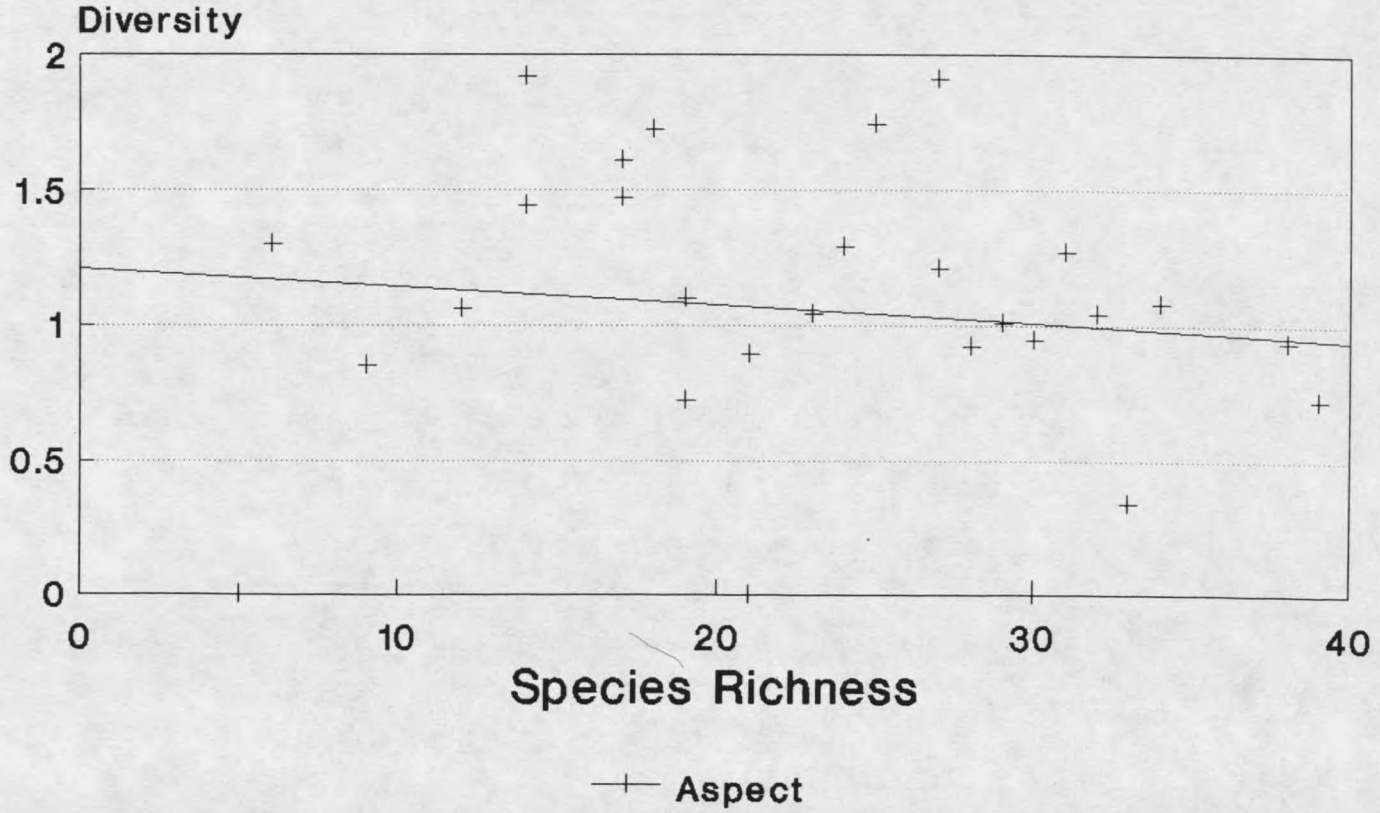
Birds 1989

Fig. 25. Elevation Diversity
Versus Species Richness



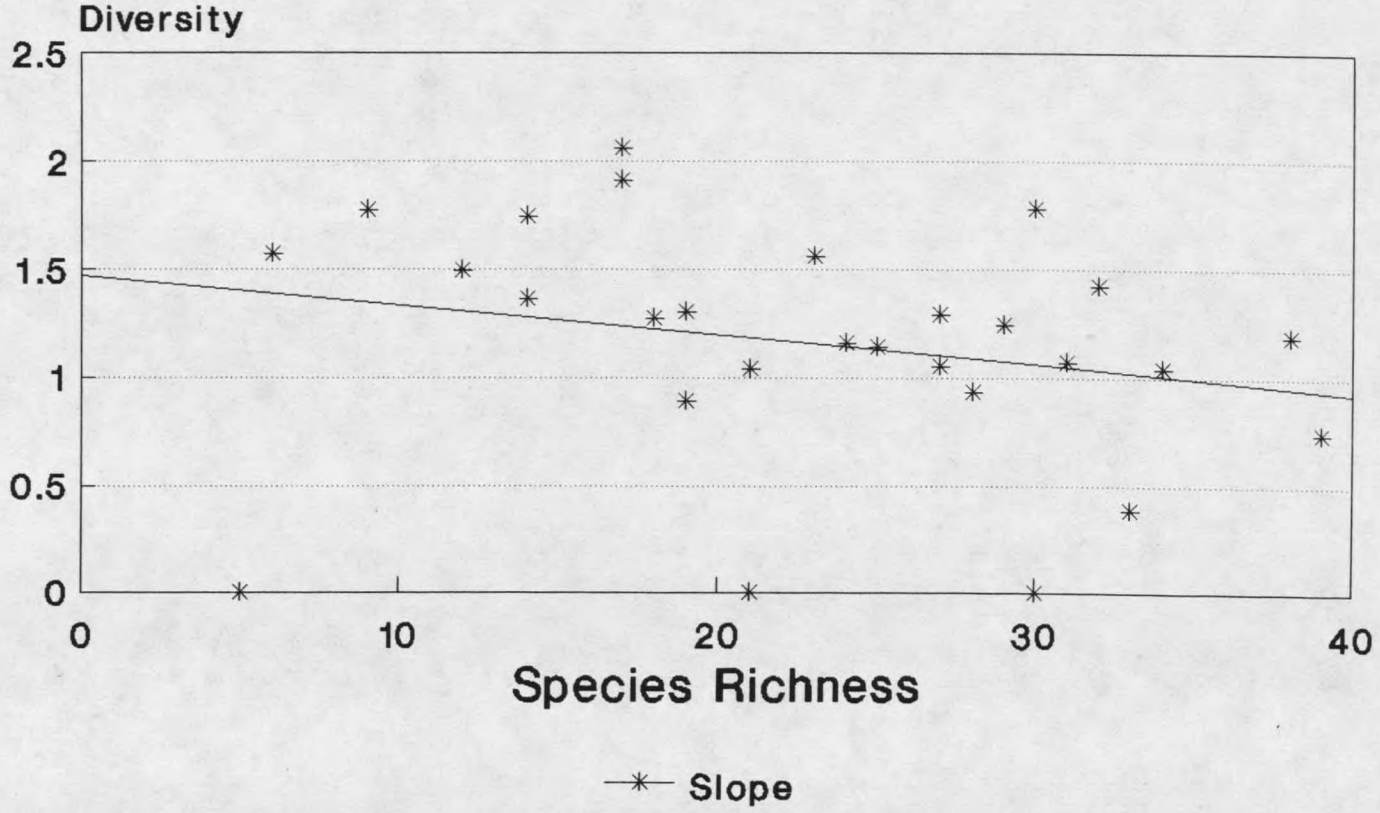
Birds 1989

Fig. 26. Aspect Diversity
Versus Species Richness



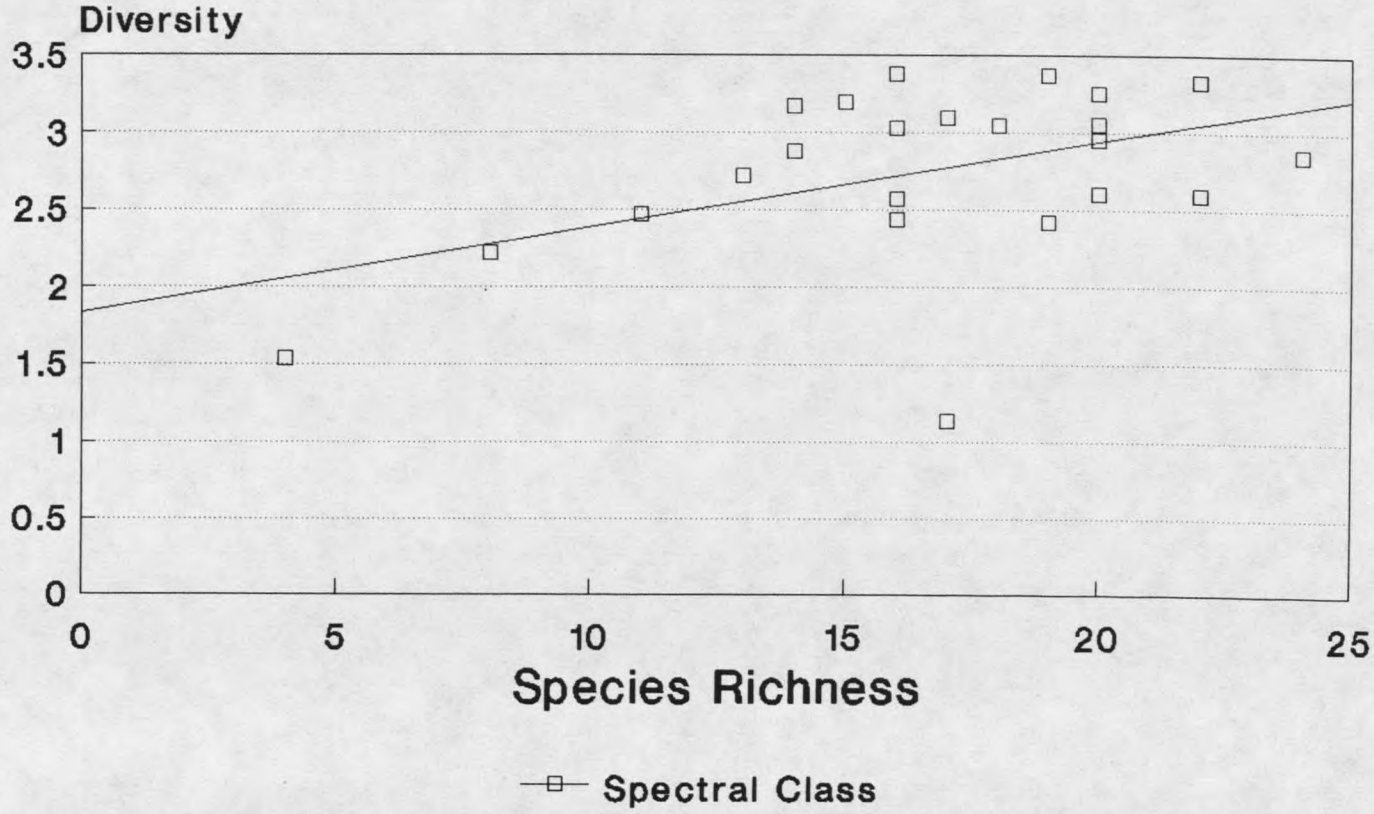
Birds 1989

Fig. 27. Slope Diversity
Versus Species Richness



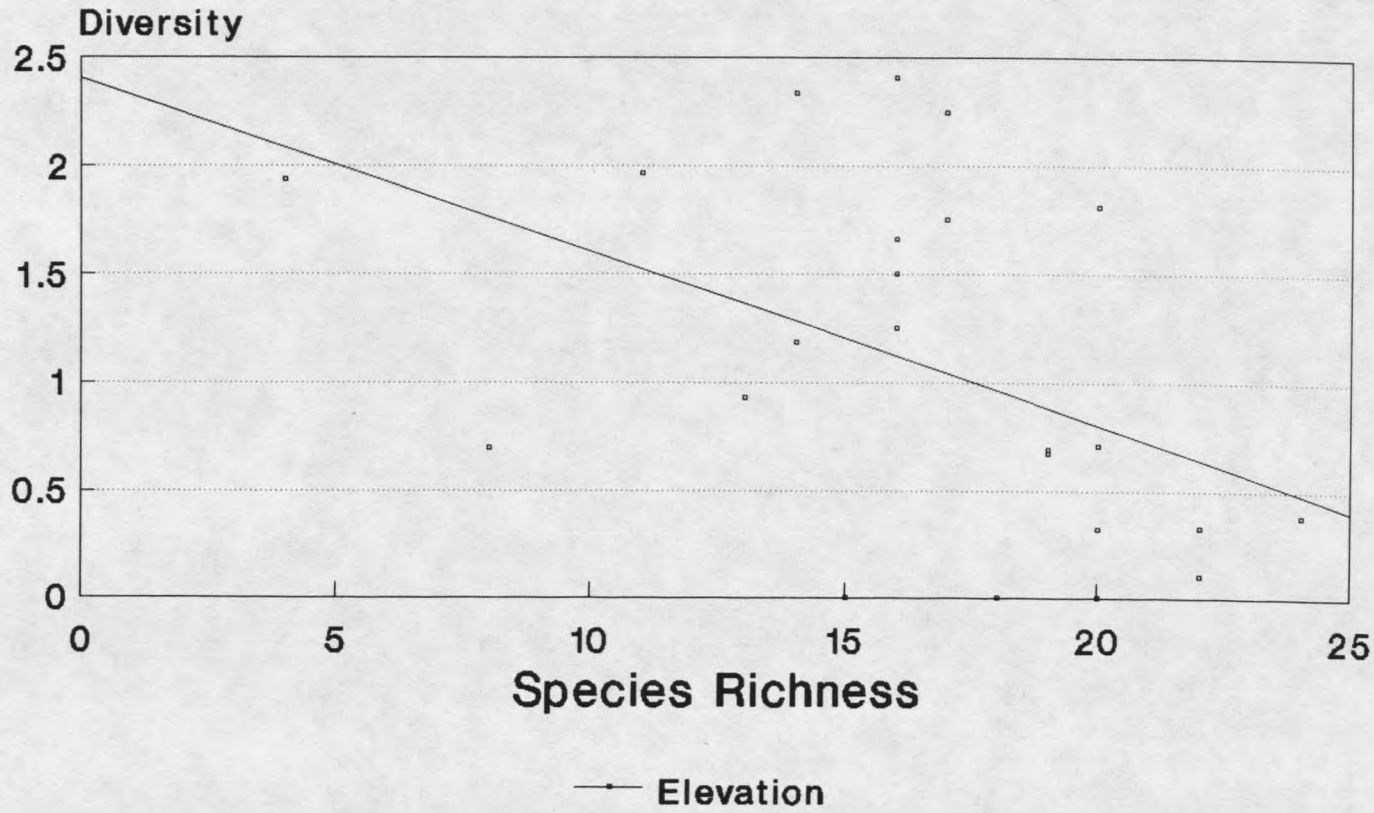
Birds 1989

Fig. 28. GIS Habitat Diversity
Versus Species Richness



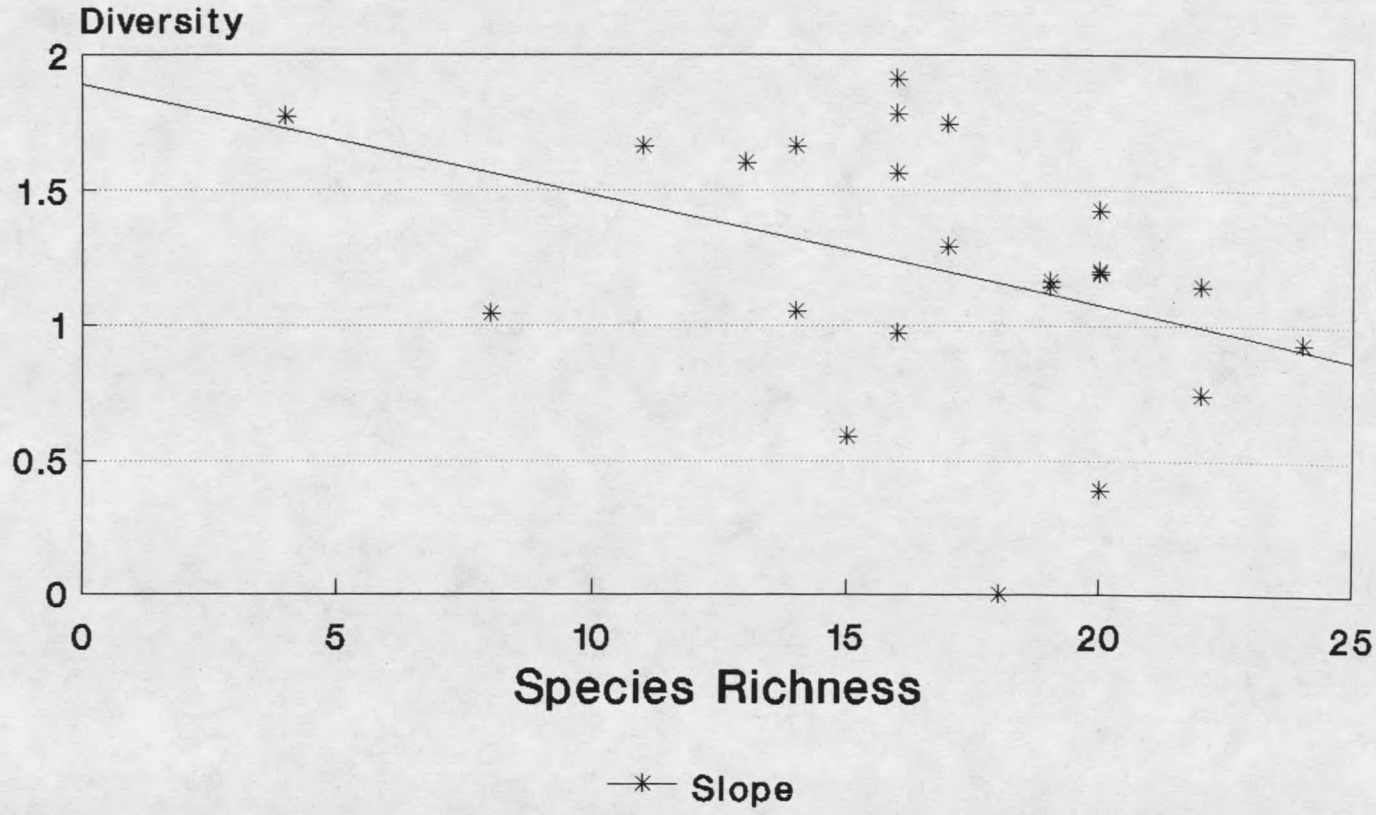
Butterflies 1989

Fig. 29. Elevation Diversity
Versus Species Richness



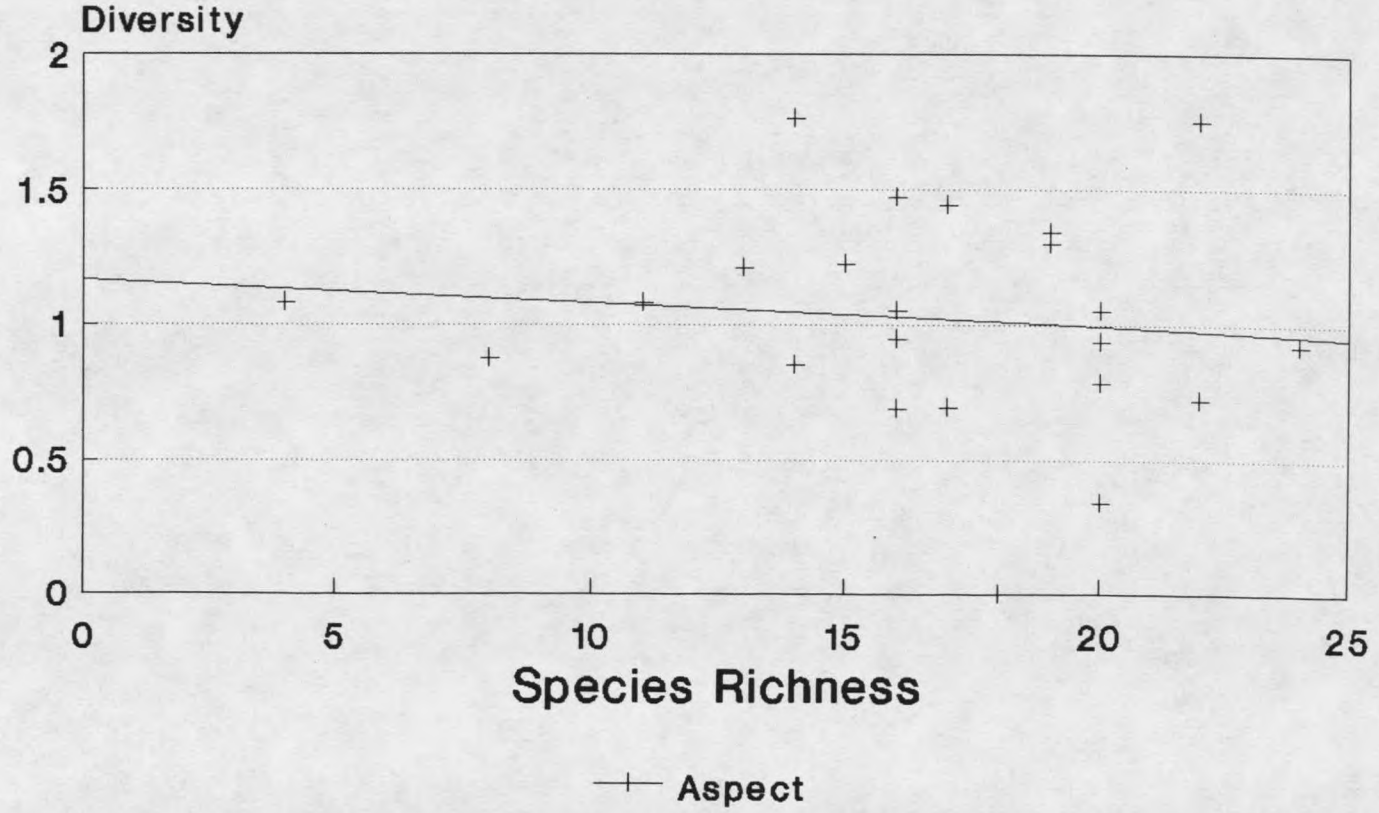
Butterflies 1989

Fig. 30. Slope Diversity
Versus Species Richness



Butterflies 1989

Fig. 31. Aspect Diversity
Versus Species Richness



Butterflies 1989

extremely marked and negative for butterfly species, yet there was no correlation whatsoever for bird species diversity.

Sampling Efficiency Analysis

Spatial & Temporal Fluctuations in Species Distribution & Diversity Jaccard's coefficient was used to estimate (1) the similarity in bird species composition between temporal replicates at the same site and (2) similarity in butterfly species composition between spatial replicates within the same site. Table 18 compares bird census data from 1989. Surprisingly, the similarity between temporal replicates was usually lower than 50%, and the mean was 37.5%.

The expression was modified to compare three spatial replicates (subplots within the 1 sq. km) when analyzing the butterfly data. The formulas used are noted below:

3 - Site Comparison	Pairwise Comparison (Jaccard's)
$C/(N1 + N2 + N3 - C)$	$C/(N1 + N2 - C)$

C is the number of species common to the plots compared and N1, N2, and N3 are the total species in each plot. It should be noted that the maximum value of Jaccard's pairwise comparison is 1.0, while the maximum value for a 3-Site comparison is 0.5. The results from butterflies in 1988 are indicated in Table 19. The comparison between the three replicates is noted in the first column, and the mean of the three pairwise comparisons is noted in the second column.

It is readily apparent in both cases that site replicates do not rank high in biotic similarity. Triplicate similarities for butterflies in 1988 range from 0.0 to .25, while the mean pairwise similarities range from .075 to .666.

Table 18. Index of Biotic Similarity between temporal replicates in the 1 sq. km sample plots - Birds 1989.

Site	Jaccard's Coefficient
Fire Scar	.25
Avalanche Lake	.27
Christensen Meadow	.40
West Glacier	.38
Sacred Dancing Cascade	.35
Logan Pass	.31
St. Mary Campground	.48
Two Dog Flats	.42
Desanto's	.50
Ponderosa Pines	.69
Sullivan Meadow	.47
Quarter Circle Bridge	.30
Rocky Knob	.46
Baring Creek	.21
Belly River/Cosley	.50
Fish Creek	.32
Sperry Trail	.14
Isaac Walton Ranger Station	.17
Anaconda Meadow	.47
Lone Pine Prairie	.46
Apgar Lookout	.30
Hidden Meadow	.55
Mud Lake	.50
mean = 0.375	

Table 19. Index of Biotic Similarity between spatial replicates in the 1 sq. km sample plots - Butterflies 1988.

Site	3 Replicates	Mean Pairwise
Barring Creek	.091	.328
Preston Park	.125	.400
Christensen Mead.	.125	.308
St. Mary	.154	.384
Granite Park	.154	.261
Stony Indian Pass	.000	.075
Desantos	.250	.666
Fifty Mt.	.250	.565
Sullivan Meadow	.200	.411
Round Prairie	.250	.444
Big Prairie	.143	.233
Belly River	.066	.239
Siyeh Pass	.000	.114
Scenic Point	.182	.430
Flattop Mt.	.143	.394
maximum	.500	1.000

G-Test for Changes Between Years Because the data on species diversity are being recorded as presence/absence, the significance of changes in species occurrences over time can be tested by the use of simple contingency tables and G-tests (Sokal and Rohlf 1981). For example, if a bird species "x" had been recorded in 13/30 plots in 1988 and 10/30 plots in 1989, this is not a significant change ($G = 0.64$, d.f. = 1, $p > .5$). On the other hand if it had been recorded in only 5/30 plots in 1989, the decline would be significant ($G = 5.22$, d.f. = 1, $p < .025$). A quick examination of the site location maps would allow one to discer whether the decline were concentrated in any

particular area or if it appeared to be random. A further check of the plots' positions in ecological space would reveal if the decline appeared to be associated with any particular elevations or exposures.

Butterflies: Application of a G-test to the 1988 and 1989 butterfly data revealed several significant differences (Table 3). Twenty-four of the 102 species exhibited significant changes in frequency between the two years, fifteen higher in 1988 and nine higher in 1989.

Birds: A comparison between 1988 and 1989 revealed that for each bird species that had significantly different frequencies of occurrence between the two years (Table 4), the frequencies were always higher in 1989.

Cost/Benefit Analysis of Sampling Effort An important question in sampling is the number of square kilometer plots that must be censused before one can be 90% certain of finding a species that occurs in 400 (10%) of the 4000 square kilometers in the park. This question was addressed by using a binomial equation for calculating the probability of detecting a species given certain potential and realized sites. The following expression was used to estimate the number of samples needed (k), with a probability, P, given that a species occurs in n sites out of a potential N sites:

$$P = 1 - \sum_{i=1}^{k} (1 - n/(N - i + 1))$$

The most difficult aspect of solving this equation is estimating the true value of N, the potential number of sites where a species could occur. For most species, potential habitat will be a fraction of the entire 4000 sq km of Glacier. For example, the butterfly *Colias nastes* only occurs in alpine habitats, and so would be limited to areas of the park above a certain minimum elevation. Potential habitat for this species would be relatively easy to calculate from topographic maps and aerial photographs. On the other hand, estimating total potential habitat area for other species such as *Euphydryas gillettii* which requires wet, sunny meadows with black twinberry *(Lonicera involucrata)* would be much more difficult.

Table 20 shows the output from a program used to calculate sample size with the formula above. Three different scenarios were constructed, assuming that the species could potentially inhabit 400, 1000 or 3000 of the 4000 sq km in the park. Significance levels were set at .05, .10, and .10 respectively. Lower significance levels (.10) were used in cases where N was in the thousands so that the magnitude of the number of samples needed would be comparable to this sampling design. The number of sites a species actually inhabited ranged from 5 to 275 sites.

Table 20. Sample Size Necessary for Detecting Rare Species.

Frequency	N = 400 alpha = .05 Samples	N = 1000 alpha = .10 Samples	N = 3000 alpha =.10 Samples
5	148	370	1108
15	57	143	427
25	36	88	264
35	26	64	191
45	20	50	150
55	17	41	123
65	14	35	105
75	12	31	91
85	11	27	81
115	8	20	60
175	5	13	40
275	3	9	25

N = # of sites (1 sq. km. a species could potentially inhabit

n = frequency = # sites a species actually inhabits

The output shows that if the species is extremely rare (existing in 5 sites), hundreds to thousands of samples are needed to detect it. On the other hand, if it occurs in hundreds of sites, only a few samples are needed to detect it.

Discussion

Describing the Data

Historic Species Lists The total number of species increased each year for both birds and butterflies. Two new butterfly species were added to park records in 1987, four in 1988, and three in 1989. Unfortunately, a comparison between the number of species found using the more extensive sampling scheme of 1987 relative to that of the more intensive design of 1988 and 1989 was not possible. Several factors confounded this comparison. For example, sampling in 1987 started three weeks later than it did during the two later years, so several of the early emerging species were missed. Some species are biennial, so some will always be missed during any one year. Perhaps most importantly, the skills of the investigators as lepidopterists and ornithologists increased over time, affecting the accuracy of both bird and butterfly detection.

Possible reasons for discrepancies between historic lists and present census results for both taxonomic groups are as follows:

1. Missed spring or early summer species - due to the late start of censusing season.
2. Strays or accidental sitings (gamma rarities): 29 of 47 of the bird species that were not observed are noted as accidental or rare in the GNP Bird List.
3. Misidentifications of original list (eg. 2 butterflies)

4. Taxonomic changes (esp. butterflies)
5. Extinctions

Reliability of Species Diversity Data Biodiversity data must be scrutinized for reliability from two perspectives: (1) reliability of presence data and (2) reliability of absence data. In general, presence data is much more reliable than absence data. Most species identifications can be assumed correct. Questionable butterfly species assignments were verified by S. Kohler, and bird identifications were discussed by two or three observers at the time of census. Yet, how certain can the observer be that a species that did not appear during a census was really not present? Unfortunately this second question is much more difficult to resolve. In evaluating presence/absence data, there is a learning curve associated with the skill of the observer. The following remarks are in order:

The bird data from 1989 differ significantly from that of 1987 and 1988. The 1989 data are more complete for two reasons - the censuses were always longer in duration, and the censusers were far better birders after two years of experience. As a result, comparisons between years should be interpreted conservatively. For example, many of the most productive sites in 1989 ranked much lower in previous years. Butterfly data are much more reliable, as

unrecognized species were collected and pinned, allowing for identification in the lab.

Analysis of Commonness and Rarity Some of the birds were under-represented in the biodiversity sites relative to their commonness on the park checklist. These groups include species specific to three habitat types: interior forest dwellers such as evening and pine grosbeaks, cassin's finch, red crossbill, and brown creeper, grassland inhabitants such as the vesper and savannah sparrows and horned larks, and Townsend's solitaires (forest birds which prefer mountain slopes). Interior forest species (including the less-observed woodpeckers) probably had lower detectability, relative to other birds, in a census. Several of the bird biodiversity sites can be considered interior forest: Packer's Roost, Avalanche Lake, Belly River near Cosley Lake trail, Fish Creek, and others.

In two ways, the sampling method employed may have selected against these birds. First, while the majority of the park area is forest, this habitat was proportionately under-represented in the sampling scheme in order to include some of the more rare habitat types. Secondly, many of the censuses include a large proportion of edge habitat; specifically forest/meadow or forest/riparian edge (eg. Christensen Meadow, Sullivan Meadow, Two Dog Flats, or Hidden Meadow). Edge-inhabitants are easily detected as one

follows the meadow/forest edge. In contrast, the interior forest (or grassland) dwelling species are not as easily detected. Assuming relative homogeneity of the forest, deep forest dwelling birds will be dispersed more or less evenly throughout the entire area. Because the volume of available habitat is greater for forest and grassland species, a greater effort is necessary to detect them. In contrast, an edge habitat is sampled more efficiently than a three-dimensional space because the habitat is more accessible to the observer.

An added complication is song volume. Sound does not travel through a dense forest as well as it does from the edge of a forest to a listener in a meadow. Furthermore, some forest dwellers sing at a low volume (e.g. pine grosbeaks).

Among the species commonness/rarity discrepancies that are not explained by the dimensions of sampling, included the occurences of the redpoll and the nighthawk. These discrepancies may be explained by temporal sampling problems. The season and time of the day affects the occurence of species. The redpoll is less common during the summer months and the nighthawk is much more active in the evenings, both being less available for detection during this study.

Finally, categorization of common or rare may be confounded by the under-representation of human-inhabited

areas. In contrast, some of the birds on the park list may be classified as common because they are seen frequently around human dwellings. For example, the mourning dove and evening grosbeak are frequently found in association with humans. Thus, species considered common on the park list may in fact be uncommon or even rare in the larger ecosystem.

Analysis of Rarity Rare species may be important to monitor, as they may be particularly vulnerable to environmental change. For example, the loss of specific habitat types (alpine, successional, etc.) may lead to the decline of a rare species dependent solely upon such habitat. Predictions of extirpations are contingent upon knowledge of both species natural history and future park management scenarios (eg. plans to alter specific habitats).

Many questions pertinent to management can be associated with the study of rarity. For example: Do rare species occur only in specific habitats? Do rare species associate? Are rare species found in areas of high or low habitat diversity? Are rare species found with common species of similar size or food habits? Can species be identified as alpha, beta, or gamma rarities? Which species are most vulnerable to environmental changes or habitat loss and/or fragmentation?

At this point alpha and beta rarities cannot be distinguished. These categorizations are based upon a knowledge of habitat rarity relative to each species' requirements. Further analysis of the sampling sites based upon GIS classification relative to the distribution of other types of habitats within the park could be used to classify sites as common or rare habitats (see recommended expansion of project). Once this task is accomplished, alpha and beta rarities can be distinguished.

Rank Occurrence Analysis What is the distribution of rare and common species in each of the taxonomic groups? Do the data fit a standard species distribution curve? For example, using rank abundance analysis, the log normal distribution is said to be indicative of a large, mature community. The log series is characterized by a small number of abundant and a large number of rare species. The geometric series distribution describes a niche pre-emption model characteristic of harsh environments. The broken stick model characterizes an environment where resources are more equitably shared between species. Fig. 7 from Magurran (1988) shows an example of each of these distributions.

Rank occurrence curves showed a lognornal distribution for both taxa. Fitting the data to one of these models mathematically presumably describes potential ecological and evolutionary processes that determine community structure.

Interpretation may be limited, however. Occurrence values were estimated using frequency over all biodiversity sites in the park rather than a sum of true abundances over all sites. Because this sampling methodology over-represents rare habitats relative to their frequency in the park, the rarity estimates are probably under-estimates of the actual level of rarity within the park.

Another pitfall in analyzing rank abundance data is that mathematical distributions describe various types of community assemblage rules, but they may also arise as a result of sampling. For example, when sample sizes are small, the log series may arise as a sampling distribution. Alternatively, the log normal distribution may arise as a consequence of the Central Limit Theorem. When a large number of factors act to determine the amount of a variable (i.e. number of species standardized by log transformation), random variation in those factors will result in the variable being normally distributed (Magurran 1988).

The final problem in analyzing rank abundance curve arises when one tries to compare two curves. Statistical comparisons may be made to measure differences in the shapes of rank abundance curves, but there are no criteria available to interpret the biological meaning of these differences (May 1975). Therefore rank abundance analysis results must be interpreted with extreme care; especially in the case where frequency rather than abundance is used.

Rank abundance may be more useful on a parkwide basis.

Diversity Hotspots Which sites are most species-rich? Do certain habitat types harbor more rare species or support larger numbers of species than others? Are there distinct characteristics of these sites that may explain their high species diversity?

Three low elevation meadows were diversity hotspots for both birds and butterflies, and two of these meadows consistently ranked highest in species richness for two consecutive years. These meadows tended to have a diversity of trees at their border and supported a high diversity of flowers. They were both mesic meadows, and one of them had a lake, while the other had a stream flowing through it. Another interesting finding was a correlation between sites that supported high species diversity and sites that supported rare species.

Species/Habitat Relationships

Species Assemblage Analysis - Principal Components Analysis What environmental variables exhibit the strongest influence upon species diversity or the presence of rare species? Elevation was a common PC for both taxonomic groups during each of the two years. Structural diversity was an important PC for birds in 1988, but in 1989 there was more of distinction between coniferous and deciduous habitats. Commonness and rarity was a PC for butterflies in

1988. Moisture was a PC for butterflies in 1989, and for birds in both years. East/west orientation were PC's for the butterfly data of 1989.

Unfortunately, PCA's based upon presence/absence data cannot be interpreted with the same level of rigor as those based upon abundance data. The percentage of explained variance never topped 60% for the first three PC's for the butterfly data. Thus, the axis interpretations must be viewed conservatively.

The bird data of 1988 demonstrate an interesting result. Using a correlation matrix, the highest eigenvalue was 6.97 and explained 9.97 of the variance, while using a covariance matrix the highest eigenvalue was 1.02 and explained 11.8 percent of the variance. The analysis revealed a continuous level of explained variation throughout the variables. In effect, the PCA results indicated that the bird data exist as a spherical data cloud. No major axis could be found to separate the sites, because each site was characterized by a unique species assemblage. The management implication of this result is that each of these sites is worth preserving because it supports its own distinct species assemblage. This does not necessarily mean that all changes should be prohibited. It is not surprizing that each site is different given the small number of sites and the desire to maximize the different habitats surveyed. A more thorough survey of

species distribution within the park would be necessary before one would be capable of prioritizing preservation values of various sites based upon their distinctness.

Species Assemblage Analysis - Cluster Analysis Cluster analysis groups similar census sites based upon the species that inhabit the sites. Used alone, it is not regarded as a highly reliable statistical technique. However, by using PC scores, only groups that exhibit real similarities are grouped as clusters. From the butterfly results presented, it is obvious that general habitat groupings (e.g. low elevation meadow or alpine meadow) can be discerned from the clusters, and therefore species presence can be used as an indicator of habitat type.

The 1988 bird PCA had such a low level of explained variance that a cluster analysis was not justified. The PCA results indicate that each site was so different that major trends could not be discerned.

Anova and Discriminant Analysis for Species/Habitat Associations While 10 birds exhibited a significant east/west preference and 17 birds exhibited a significant habitat preference, only two species of butterflies exhibited an east/west preference, and only three species exhibited a habitat preference. The marked difference between the taxonomic groups is of interest. It appears

that birds are more inclined to be habitat specialists than butterflies. Further, because birds and butterflies are differentially affected by environmental cues, one should not expect one group to be a surrogate for the other.

While some of the DA results showed a high number of correct categorizations, jackknifing always revealed overfitting. Overfitting occurs because there are so many descriptor variables (species) relative to the number of sites (the dependent variable). For this reason, discriminant analysis has limited reliability.

Gradient Analysis Gradient analysis addresses the question of how organisms are distributed along environmental gradients, both in relation to each other and in relation to the gradient itself. The general approach of gradient analysis is: (1) Select gradient variables, such as temperature, moisture, or pH. (2) Arrange population samples along the gradient with respect to frequency or density. (3) Interpret the pattern. For example, are population samples correlated with the gradient? Amplitudes, centroids, and lengths of the gradient are used in this analysis.

Elevation Gradients: Plotting species occurrences against elevation showed that higher elevations supported fewer species of birds. This might be explained because lower elevation sites often included riparian habitats which

tended to have higher species richness. Lower structural diversity of vegetation in the high elevation habitats may also contribute to lower species richness at high elevations, but these data do not allow a test of this hypothesis. The elevational peaks of species richness in butterflies correspond to those elevations where meadow habitats predominate--mesic meadows at lower elevations, alpine meadows at higher elevations. The large variance in species richness along the elevational gradient is probably related to differences in species richness between meadows, trailsides, riparian zones, and alpine areas.

Moisture Gradients: Moisture gradient analysis of butterflies showed that mesic meadows support a higher diversity of species. This result may be explained by a greater diversity of flowering food plants and larval host plants in mesic meadows. Hydric meadows restrict plants with low water tolerance, while xeric environments restrict plants that cannot tolerate drought conditions.

Edge Effects Leopold (1933) noted that species diversity increases with habitat complexity due to the simultaneous availability of more than one habitat. Even standard habitat management guides suggest that managers create as much "edge" as possible because wildlife is a product of the places where two habitats meet (Yoakum &

Dasmann 1971).

Spatial heterogeneity in landscapes creates horizontal patchiness while the spatial heterogeneity at the edge (caused by the complex vegetation composition and structure) creates vertical patchiness. Edges modify species distribution and dispersal, increase nest predation and parasitism, and provide browse for wildlife. Other effects include microhabitat changes in temperature, light, and humidity.

Some species are edge-loving, while others specifically avoid edges. Edge species conduct all or most of their activities at or near the edge, while interior species conduct most of their activities away from edges.

Preliminary results showed that meadow/forest edge sites had 50 % more species relative to interior forest sites. Further research should be done to determine the significance of this relationship, but from the initial results it does not appear trivial.

Habitat Diversity and Species Richness Sites with higher habitat complexity would be expected to support higher species diversity, and thus a strong positive correlation was expected between habitat diversity and species diversity. The habitat diversity variable that best correlated with species richness was spectral class diversity. The habitat diversity parameter showing the most

marked inverse relationship with species richness was elevation diversity. One would not intuitively expect a site with less elevational diversity to have lower species richness, as higher topographic diversity often provides more microhabitats and thus more different species. However, on a scale of one square kilometer, perhaps too much topographic diversity is not conducive to supporting a diversity of species. It makes sense that aspect diversity and slope diversity are probably not as significant in dictating species diversity. One might expect the actual vegetation and topographical diversity to be more influential factors.

Sampling Efficiency Analysis

Spatial and Temporal Replication Temporal replicates of bird surveys within the same year showed a surprisingly low level of similarity. Because replicate censuses were usually separated by one month, the dissimilarity may result from the replacement of nesting species by migrants; however, changes in detectability between the nesting and post-nesting season cannot be discounted. In either event, such low levels of similarity indicate that more than two samples per year are necessary (Magurran, 1988).

There was also a very low level of similarity between butterfly subplots within the square km sites. This was expected since the subplots were selected to maximize

butterfly species diversity within each site; however, higher replication would have enabled us to estimate the relative contributions of habitat differences and sampling error due to heterogeneity.

If the sample sizes were larger, additional analyses could include the following two steps:

(1) Determine what percentage of the total species would have been found using only one or two of the three replicates.
(2) Calculate biotic similarity coefficients between sites of the same habitat type (rather than replicates within the same site).

Cost/Benefit Analysis of Sampling Effort In reviewing the results of the cost-benefit analysis, one immediately notices that an intensive effort is required to detect a rare species. For example, sampling 30 sites will only detect a species that occurs in 35 out of 400 sites (confidence = 95%), 80 out of 1000 sites or 275 out of 3000 sites (confidence = 90%). If the species frequency is lower, or the number of potential sites is higher, more samples will be needed. This formula also assumes that if an observer samples a site, he or she definitely finds the species. Depending upon the weather and the flight season of a butterfly, this might not be a valid assumption.

According to binomial calculations, a minimum of 150 sites sampled at least three times a year would be provide the level of detection necessary.

Monitoring Twenty-four of the butterfly species found in 1988 and 1989 exhibited significant changes in frequency between the two years. Fifteen species were found in more sites in 1988 than in 1989; nine were found in more sites in 1989 than in 1988. Five of these species are biennial (*V. cardui, B. titania, N. vau-album, N. californica,* and *P. phoebus*; thus, they would be expected to show large fluctuations in occurrence between years. The change in frequencies in two other species (*P. glaucus rutulus* and *P. icariodes*) can perhaps be attributed to misidentification; the underlying reasons for the changes in the others are unknown.

Several hypotheses can be proposed to explain the universal increase in frequencies of occurrence of bird species between 1988 and 1989. A drought year occured in 1988, and fires burned extensive areas during August and September. However, the fires may have created additional habitat favorable to certain species in 1989. Unfortunately, these data do not allow a test of these hypotheses with any degree of confidence. The birding skills of the observers increased between 1988 and 1989; and extra effort was made to find rare species during 1989, and

replication during 1989 was higher.

Regular monitoring of species occurrences in the square kilometer plots is a necessary component of biodiversity monitoring. The data base increases in value with each subsequent monitoring event, and repeated censusing insures that any changes in biological diversity can be detected. Although the status of rare species should be checked yearly (along with annual plants and fungi), it will probably be necessary to completely resurvey each site for species diversity in all indicator groups only every three to five years. Likewise, subsequent surveys must be done to determine whether or not genetic diversity in the targeted species is remaining constant or decreasing.

Because complete inventories are not necessary every year, the monitoring procedure actually can be carried out by a small number of well-trained personnel. For example, since only annual plants, fungi, and rare species need to be resurveyed every year, a sampling schedule could be developed as follows in Glacier. Year 1: Survey for butterflies, birds, vascular plants. Year 2: Survey for carabids, small mammals, and drosophilids plus additional annual plants and fungi; monitor populations of rare birds and butterflies. Year 3: Survey for dragonflies, mollusks, and bumblebees plus additional annual plants and fungi; monitor rare species of birds, butterflies, carabids, small mammals, and drosophilids. Year 4: Resurvey butterflies,

birds, all vascular plants and fungi; monitor rare species of carabids, small mammals, drosophilids, dragonflies, mollusks, and bumblebee, and so on.

After several years of data have been collected, it may be possible to find answers to important questions. For example, if species A is seen in 10 sites in 1995 and six sites in 1996, what is the probability that it is becoming more vulnerable to extinction (by smaller population size, or fragmentation through local extirpation)? How many times does a decline in the frequency of occurrence in the data correspond to an actual decline in the population? Does frequency of occurrence have any predictive power? If the frequency index has a high level of variance, a decline may be a false alarm while some declines may not be detected in time for action. Trends in species occurrences can also be examined using linear regression analysis using census year as the independent variable and number of sampling plots occupied by a certain group of species as the dependent variable.

Sites of special importance can be identified based upon high species richness or because a certain species is restricted to it. The variety of habitats necessary to maximize the total park species diversity could also be determined. This value would be taxon-specific, however, and assemblages of taxa would have to be considered in order to manage the entire ecosystem.

During the GNP study, many species were detected only in one or two sites. If the next year they are not detected, should the park be concerned? More importantly, if they continue to be detected in only one or two sites, should the park be concerned? Ironically, at the present intensity of sampling (30 1 sq. km. biodiversity sites with presence/absence data) population trends can best be detected for common species. This does not imply that these data are useless, however. The present biodiversity assessment was intended to be a pilot project. Increasing the number of sampling sites and monitoring over longer time periods will enhance the value of the data.

Suggestions for Future Research at Glacier

Additional Taxa to be Included Although this pilot study only involves smaller terrestrial birds and butterflies, the following groups should eventually be included in the biodiversity assessment:

1. Vascular plants. The value of species and genetic diversity in vascular plants is well-known, so the inclusion of this group should be self-evident.

2. Fungi. Fungi are important agents of decay in forest ecosystems, and many species form critical micorrizal associations with plants.

Because both of these groups are sedentary and most are conspicuous and easy to sample (with the exception of

hypogeous fungi), obtaining species lists from each site should be relatively straightforward. However, annual plants and fungi are often sporatic in their appearances, so several years of sampling will be required before all species present in a sampling site have been recorded. Even though quantitative estimates of plant species abundances (as frequency, density, or cover) can also be obtained relatively easily, it is best to not spend efforts on this initially, although it may be desirable to do so at a later date.

3. Vertebrates. Medium to large vertebrates such as ungulates, carnivores, raptorial and large water birds, etc., cannot be reasonably sampled using this biodiversity assessment technique. However, population trends in many of these species are monitored in Glacier already, so this is not seen as a serious problem. However, if these species or their sign is seen in a sampling site, their presence there is noted. Likewise, the few species of amphibians and reptiles in Glacier should be noted when encountered, but intensive efforts to determine whether or not these species are present in each sampling site are not likely to be particularly productive and might involve a considerable amount of habitat destruction.

Thus, a biodiversity assessment would ideally include the following vertebrate groups:

a. Small to medium-sized land birds. These are

taxonomically and biologically well-known, ecologically diverse (granivores, insectivores, carnivores, etc.), relatively easy to observe, and poltically popular. During the pilot project all sites are censused for breeding species by visual and aural surveys. This effort will be expanded to include migrants and winter residents if funds and off-season access permit. Mist net sampling also may be added at a later date to insure that all species present in the sites are being recorded.

b. Small mammals (bats, shrews, and small rodents). This group is ecologically diverse (insectivores, granivores, herbivores), well-known biologically, and relatively easily sampled. Bats in particular are apparently quite sensitive to environmental changes; at least three species are declining precipitously in Montana. Shrews and rodents will be sampled in pitfall, snap, and small live traps, and bats with mist nets and electronic devices.

4. Invertebrates. Information on invertebrate species diversity will be far more difficult to obtain than it will be for plants or vertebrates. There are probably several orders of magnitude more species, and most taxa are poorly known systematically. However, the following groups seem to be particularly amenable to biodiversity assessment, and all three should be incorporated into the procedure as soon as possible.

a. Butterflies. Taxonomically and ecologically well-known, butterflies are easy to capture and identify and represent the ecologically important insec herbivore guild. These are the main reasons for choosing them for the pilot project.

b. Carabid beetles. Carabids have been extensively studied in Glacier (eg. Edwards 1975), can be censused easily by pitfall traps (Newton and Peck 1975), and represent the insect predator/scavenger guild.

c. Terrestrial mollusks. There is an endemic subfamily of slugs (Ariolimacinae) found only in northwestern North America. Many species are confined to old-growth forests, and a few are found in Glacier. The "mountain snails" (genus *Oreohelix*) are Rocky Mountain endemics and also are found in Glacier. Snails are often used as biological indicators of climate change. Finally, a large number of land mollusks in the North American fauna are exotics, and thus are of special concern to the Park Service.

The following invertebrate taxa are under consideration for eventual inclusion, pending more information on their diversity and abundance and on sampling feasibility in the park.

d. Drosophilids. Many species of flies in this genus have been studied extensively by geneticists and

evolutionary biologists. As a result they are taxonomically well-known and moderately well-known ecologically, and they may be important components of detritivore food webs in forest ecosystems. Many species are easily sampled with banana-baited traps. Unfortunately, the potential attractiveness of these traps to bears may preclude drosophilids from assessment in Glacier.

e. Bumblebees. These are important pollinators, especially in alpine meadows. They are diurnal, presumably easily recognizedc in the field, and their ecology has been extensively studied elsewhere in the Rocky Mountain region.

f. Dragonflies. This group, with both aquatic and terrestrial life stages, should be a particularly useful one to begin to incorporate aquatic environments into biodiversity asssessment.

Using the GIS in Concert with Present Biodiversity Data

Glacier National Park has recently developed a sophisticated GIS. GIS spectral analysis combined with aspect, slope, and elevation data can be used as a method of habitat typing. GIS habitat typing could be used in conjunction with the biodiversity data and sampling program to accomplish the following tasks: (1) Detect unsurveyed sites that may support rare species or high biodiversity by comparing their GIS classification to previously surveyed sites.

(2) Ground-truth the GIS habitat classification system by comparing known sites and unsurveyed sites that would be predicted to be similar based upon their GIS classifications.

(3) Determine habitat types that have not yet been surveyed by comparing surveyed site GIS classification to the entire array of GIS habitat types throughout the park. These sites would be prime candidates for survey should the project be expanded.

(4) Develop a full scale biodiversity sampling scheme. Given the fact that this project was a pilot project, if one were to design a full-scale biodiversity inventory and monitoring program, GIS habitat typing and habitat frequency analysis could be used to insure that the sampling represented the full range of habitat types within the park.

(5) Classify present biodiversity sites with respect to habitat commonness and rarity. This knowledge would provide the information necessary to distinguish between alpha or beta rarities in the existing species diversity database.

(6) Predict species assemblages and distribution patterns in other areas of the park based upon GIS classification and biodiversity data from this survey. Predictions could then be tested with future fieldwork.

Summary

Species Detection

Approximately 86% of the historically recorded butterflies and 70% of the historically recorded bird species have been observed in the three years of sampling. The analyses presented here have proven that increased effort both in terms of the number of sampling sites and the number of replicates is necessary to improve the detection of species and the reliability of the results. For example, species that occur at a frequency of 8% to 9% were being detected with a 90% - 95% probability. That is, species were detected that occured in 35 out of 400, 80 out of 1000, or 275 out of 3000 sites. Species that had rarities below these levels will not be detected. One hundred and fifty sites would have provided a much more thorough assessment. This would have allowed detection of species that occured at frequencies of 1% to 1.5%.

Habitats of Significance

A major goal of this research was to identify habitats that are important for preserving biodiversity. These types of habitats include sites of high biodiversity, sites supporting relatively rare species, successional habitats, and habitats that are range edges for rare species. Although the sampling was limited in both space and time, some examples of these habitats were identified A few examples are listed below.

Christensen Meadow and Hidden Meadow are examples of important habitats because of their high bird and butterfly richness. Range edges are important because the loss of such an area may contract a species' range. For example, *Colias nastes* is an arctic species and Glacier may be the southernmost extension of its range. It occurs only at high elevations within the park. Loss of habitats such as Siyeh Pass might result in the shrinkage of the total range of this species. The value of sites supporting rare species is widely accepted. Finally, successional habitats are important to monitor. Species such as *Euphydryas gillettii* depend on wet meadows where the larval host plant *Lonicera involucrata* is present. These types of meadows are often in the early stages of succession. If large trees begin to encroach, blocking the sun, the habitat may no longer be suitable for the species. Management that would preserve the meadow and prevent succession may be called for in this case.

During the three years of this study, there was a striking continuity of species richness per site. Sites supporting the highest number of species consistently ranked high, year after year. There was also a striking overlap between sites that support high species diversity and sites that support rare species. Several sites that supported high species richness often supported a number of rare

species as well. This generalization applies more strongly to butterflies than birds. Birds seem to be more habitat-specialists than butterflies.

Habitat's significance may change over time because of human-induced or natural influences. For this reason, many years of monitoring (e.g., one or two year inventories every five years) will be necessary to detect temporal changes in habitats. Ideally, this project would be continued for twenty years or more. With monitoring intervals of five years, after twenty years, one could differentiate real trends from natural fluctuations.

Techniques for Analyzing Biodiversity Data

A simple ANOVA on years and on habitat associations provided some insights into species/habitat relationships, but discriminant analysis had limited robustness because of the large number of variables.

Distinct peaks of species richness occurred at low elevations and high elevations for butterflies while lower richness values were observed at mid-elevation sites. Bird species richness peaked at low elevations only.

Analysis of species richness relative to edges revealed the expected increase of species richness at the junction of two habitat types for both birds and butterflies.

Habitat diversity analyses demonstrated a positive correlation between GIS spectral class diversity and species

richness for both birds and butterflies. Aspect, slope and elevation diversity had a negative or negligible relationship with species richness.

Jacaard's coefficients and ANOVAs were used to interpret spatial and temporal fluctuations of species diversity. Variance between temporal and spatial replicates within a site was high, both for birds and butterflies, indicating that more replicates are needed both in time and in space. The cost/benefit analysis reiterated these same results. The ANOVA on years revealed a striking increase in species sited in 1989 relative to 1988.

Recommendations for future Biodiversity Inventories

This was a pilot inventory and monitoring project. If one were to establish a large-scale inventory in a park such as Glacier, the number of samples should be increased both spatially and temporally. Both bird and butterfly censusing should occur at least three times per year, and 100-150 sites should be sampled, allowing for a larger number of replicates in each habitat type. The present sampling strategy uses pseudoreplicates rather than a true replicates. With only 24 to 33 sites, there is a high level of variation between sites. Attempting to maximize coverage of all the different habitats in the park allowed for few samples in each habitat type. Ideally, one would prefer to have at least 10 sites of each habitat type.

Conclusions

Three years of field work has provided considerable insight into the distributional ecology of butterflies and small land birds in Glacier National Park. Analysis of the GNP biodiversity data has allowed this investigator to (1) obtain baseline data on species occurrences and map them in both topographic and ecological space so that long-term trends in species distribution and abundance can be tracked, (2) identify locations and habitats that are particularly species-rich for each indicator group (e.g. Christensen meadow, Spot Mt., Hidden Lake, Preston Park, Hidden Meadow, Desantos, and the Rt. 8 Burnscar), (3) discriminate common, widely distributed species from uncommon, local ones, (4) reveale species assemblages that are indicative of a specialized habitat types, and (5) reveal variables (elevation, moisture, structural diversity) that are influential in predicting species composition of a site. Although specifically designed for Glacier National Park, these techniques should be adaptable, with minor modifications, to any other relatively large reserve.

This research emphasized a new approach which provides information on the dynamics of local extirpations and colonizations. The presence/absence data were used to assess patterns of species distribution and abundance and will prove valuable in the future by documenting changes in these patterns over time.

Some goals, however, were not achieved to the intended level of satisfaction. During this period, the degree of statistical reliability was not as high as desired. Many rare species almost certainly remain undetected, the relative merit of sampling over wide areas versus repeated sampling in fewer discrete sites remains unresolved, and the ability to distinguish sampling artifact from biological causation of changes in species' distributional patterns is questionable. Several more years of field work will be required before these problems can be solved.

This work has proved to be very beneficial in highlighting the problems associated with an accurate assessment of species diversity in a few taxonomic groups in a large area such as Glacier. First, traditional ecological methods emphasize intense sampling; biodiversity surveys require an extensive approach. This means that several years of working out the most appropriate sampling design--in the field--is necessary before statistically satisfying data can be produced. Second, choosing "indicator taxa" seems to be a methodologically sound approach; however, even groups as well-known and tractable as birds and butterflies present challenges in the field that can only be met by very experienced observers. Third, documenting the presence or absence of a species in an area requires considerable skill and experience; estimating its abundance requires considerably more. Thus, biodiversity surveys will have to

use presence/absence data, and more attention should be paid to developing appropriate statistical methodology for dealing with such data. Finally, adequate coverage of an area as large as GNP requires much more effort than can be provided by two field workers. At the sampling intensity that was possible during 1988 and 1989 (33 square km sites for birds, 24 for butterflies), trends in frequency of occurrence over this two year period are probably reliably documented for only the common species. Considerably more effort must be expended to achieve the same degree of resolution for rare species, which tend to be those of most conservation concern.

CHAPTER 3

GENETIC DIVERSITY ASSESSMENT

Introduction

In order to address adequately the preservation of biological diversity at all levels of organization, it is also necessary to inventory and monitor genetic diversity in selected species. The specific levels that need be considered include 1) the diversity of gene pools within a species, and 2) the diversity of genetic information within these gene pools. Scientists are mainly concerned with issues related to the amount of genetic variation, the factors that reduce it, and the effects such reductions have on the populations concerned. Clearly, population size and gene flow are of utmost import. The smaller the effective population size, the more important stochastic events (genetic drift) become (Schonewald-Cox et al. 1983).

This chapter focuses upon the genetic aspects of biodiversity assessment. Topics of discussion will include 1) types of species most appropriate for genetic analysis, 2) techniques used in genetic diversity assessment, 3) implications of spatial distribution to maintenance of

genetic diversity, 4) life history of the species chosen for analysis, 5) results of the genetic analysis of the species in #4 above, and 6) conservation and management implications of the analysis.

Choosing Species for Genetic Diversity Assessment

Rare species are logical candidates for surveys of genetic variation because they are most vulnerable to loss of genetic diversity. Some species may be rare because they are near the boundaries of their ranges, but are more abundant elsewhere (e.g., Brown 1984, Brussard 1985). These so-called marginal populations may have important adaptations and gene combinations that are not found in the rest of the species' range, and their conservation may be important for preserving the full range of genetic variability in these species. Thus, they are likely candidates for surveys of genetic variation.

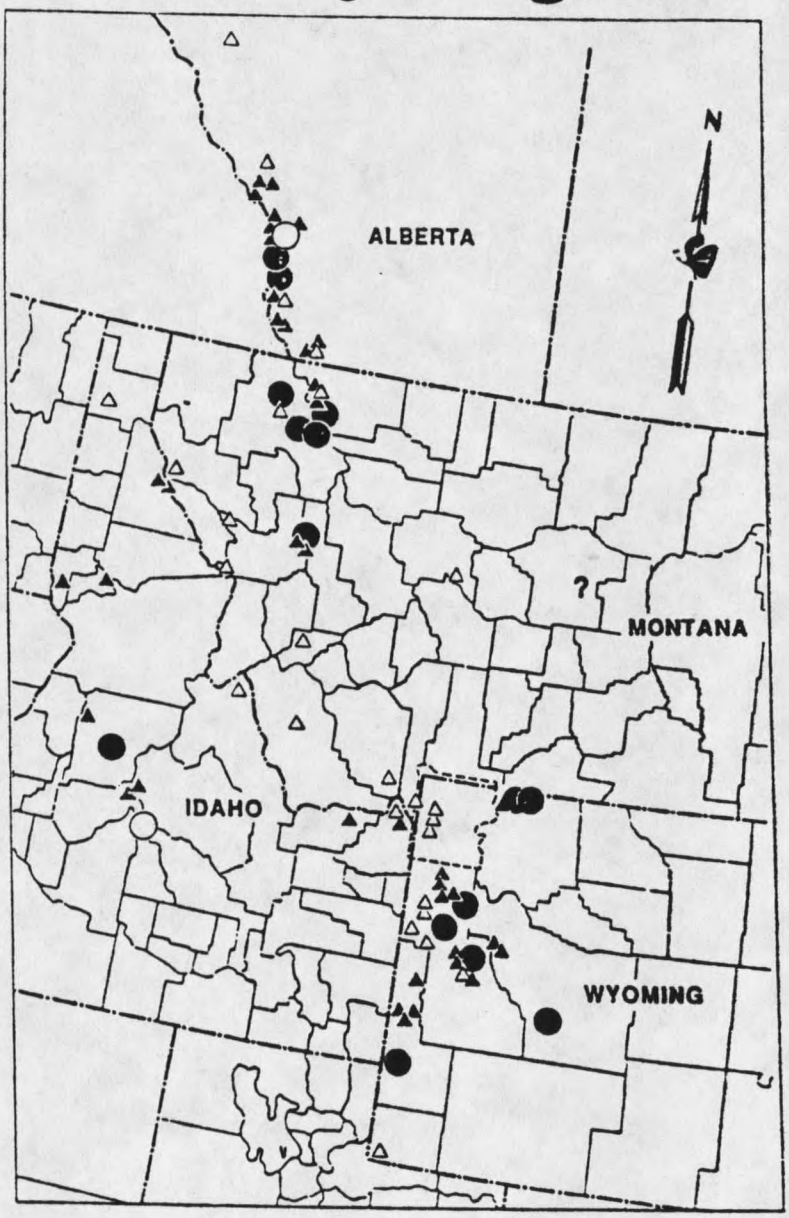
Other groups that might be inventoried genetically are dominant and keystone species and species that are economically or recreationally important. The decline or loss of these species would have serious ecological or political consequences, and managers should have as much information as possible available on the biology of these species, including their genetics.

Finally, organisms that are distributed in small, highly fragmented populations may be most important to

monitor. These populations may be highly extinction-prone, depending upon the size of the population and the distance from the nearest occupied habitat. Because population sizes are frequently small, historic bottleneck events can leave the population depleted of genetic diversity. The question of interest is how much genetic variation exists within and among populations. Such information is very useful to management decisions, especially if transplants to enhance gene flow or to increase population numbers are contemplated.

In Glacier, the techniques of monitoring genetic variation were demonstrated with the checkerspot butterfly, *Euphydryas gillettii*. This northern Rocky Mountain endemic is distributed in small, widely separated patches, and its populations appear to be declining. Williams (1988) visited 29 localities where *E. gillettii* had been collected in the past and found extant populations in only 13 of them (Figure 32). In addition, the ecology and population genetics of several species of checkerspot butterflies, including *E. gillettii*, have been under intensive study in the western United States for the past quarter century; thus, ample comparative data exist. Many of these data already have made important contributions to the theory and practice of conservation biology (e.g. Ehrlich and Murphy 1987). Thus, *E. gillettii* appears to be an ideal choice for genetic inventory.

Fig. 32. Range of Euphydryas gillettii



Range of *Euphydryas gillettii*. Closed circles are sites described in Williams (1988); open circles are locations of populations believed to be extinct; closed triangles are locations where *E. gillettii* has been seen since 1960; question marks denote uncertain record. After Williams (1988)

Estimating Genetic Diversity

Genetic diversity is necessary for a population to adapt to environmental changes. As such, measurements of genetic diversity provide an indication of the long-term survivability of a population to changes in the environment (e.g. global warming). Genetic diversity is commonly categorized in three ways 1) at single loci, 2) as quantitative polygenic characters, or 3) as chromosomal variations. Single locus variations manifest themselves as mutant phenotypes, single gene polymorphisms with major phenotypic effects, or enzyme polymorphisms. Quantitative polygenic characters are those that vary in a meristic (countable) or continuous fashion (e.g. height, weight, or number of fingers). Most adaptive evolution is based upon these characters. Chromosomal variation has been commonly studied, but is not found in all organisms, and the adaptive basis is not at all clear.

There are several ways to estimate genetic diversity and its loss. Heterozygosity (the proportion of individuals heterozygous at surveyed loci in a population) is widely used because it lends itself readily to theoretical considerations on the effect of limited population size on genetic variation (Allendorf 1986). A second measure of genetic variation that can be used is the actual number of alleles present at a locus. Allelic variation is lost much more quickly than heterozygosity and can only be restored by

mutations (Fuerst and Maruyama 1986). Both heterozygosity and allelic variation can be estimated using protein electrophoresis. Accuracy of estimation is maximized by increasing the number of loci rather than total number of individuals (Nei 1987).

An alternative method of measuring genetic variability is through morphological assays; morphological variation within populations often (but not always) varies inversely with genetic variation. Increased morphological variation is a reflection of increased homozygosity of polymorphic loci that quantitatively affect development. High levels of heterozygosity provide a developmental buffering that limits individual variation. When heterozygosity decreases, this buffering effect is lost, and individual variation increases (Allendorf & Leary 1986).

Morphological variation can be evaluated in two ways (Wayne et al. 1986). The first is by calculating the coefficient of variation (CV) of a trait (e.g., tooth length, spot width, etc.) and comparing it to the CV of the same trait in a different population or in the same population at a different time. Larger CVs may indicate reduced genetic variation. The second method is to compare the extent of fluctuating asymmetry of traits, the magnitude of differences between right and left measurements of bilateral characters. Increases in fluctuating asymmetry in a population may indicate an underlying loss of genetic

variation, inbreeding, or environmental stress (Valentine et al. 1973, Palmer and Strobeck 1986).

The research described in this chapter used electrophoresis as a tool to estimate genetic diversity. Electrophoresis can be used as a conservation biology tool to estimate overall genetic variation, to partition genetic diversity (as measured by protein variation), and to determine the level of genetic differentiation between populations. Specific estimates include overall similarity, sharing of rare alleles, and comparisons of genetic diversity within, versus among, populations.

Baseline estimates of genetic diversity indicate that, on average, a species will have about 25% of its loci polymorphic and an average heterozygosity per individual of 7%. Such figures conceal considerable variation, as these are averages over a range of life forms. Invertebrates have higher levels of heterozygosity on average relative to vertebrates, with plants being intermediate (Beardmore 1983). Ayala (1982) lists invertebrates as having an average polymorphism of 47% and an average heterozygosity of 13%. Kitching (1989) noted Danaid butterfly heterozygosity ranging from 10% to 25%. Porter & Geiger (1988) note that *Coenonympha tullia* in the western U.S have heterozygosities ranging from 12%-19% and polymorphism levels from 32.9% to 58.8%. Brussard and Vawter (1975) note that *Euphydryas phaeton*

populations have a high variance in heterozygosity levels ranging from 22% to 72% with 43% of surveyed loci being polymorphic.

Although genetic diversity is generally thought to convey adaptive advantages, the correlation between electrophoretically assayed heterozygosity and fitness is not yet understood. Lab experiments have shown populations with greater degrees of heterozygosity maintain a larger population size or biomass than less heterozygous populations (Ayala 1968). Growth rate and heterozygosity correlations are not always consistent. The selectionist explanation of the heterozygous advantage is that "heterozygotes have greater biochemical flexibility and hence are able to buffer the internal environment of the organism more effectively than homozygotes" (Beardmore 1983). However, a more plausible hypothesis is that more heterozygous individuals are more outbred. Assuming simple dominance, the benefits of heterozygosity should reach a threshold in large outbreeding populations that are at equilibrium for the mutational gain and selective purging of deleterious mutations (Vrijenhoek 1985).

Metapopulations

Definition

A species whose range is composed of more or less geographically isolated patches, interconnected through

patterns of gene flow, extinction, and recolonization is said to form a "metapopulation", or "population of populations" (Lande and Barrowclough 1987). Each population is spatially and often genetically distinct from the others, but each is still a component of the larger metapopulation, a term coined by Levins (1969). Levins' (1969) mathematical model showed that metapopulation viability is dependent upon maintaining a critical balance between patch colonization and extinction.

Habitat patches alternate between two states: inhabited and uninhabited. Inhabited patches send propagules (colonizers) to uninhabited patches, recolonizing suitable habitat. Patch extinction (turnover) may occur on a regular basis. This will not necessarily be detrimental to the metapopulation unless there is a cumulative effect of demographic instability and/or loss of genetic variation. If these factors build up, recolonization may not keep pace with local extinction, and the result will be extinction of the metapopulation. Gilpin and Soule (1986) discuss these issues with respect to population viability analysis.

The movement of individuals among patches is of major importance in studies of metapopulations. The rate of immigration affects the genetic differentiation of patches and the population dynamics within them (the "rescue effect" of Brown and Kodric-Brown 1977). Rates of immigration depend upon distance between patches, configuration of the

metapopulation, and the number of individuals (which is often related to area) in each patch (Gilpin 1987).

Relevance of Metapopulations to Conservation Biology

The dynamics of simple populations have been well understood for some time. However, metapopulations are of special interest to conservation biology because their size and spatial distribution allow the effects of genetic drift, natural selection, and environmental stresses to be manifested over a shorter period of time on a per-patch basis. Single patches of a metapopulation often have low effective population size (N_e) and thus become prime candidates for the study of demographic, genetic, and environmental stochasticity. The metapopulation itself also has an effective population size (N_{me}) and an associated extinction probability.

Some endangered and threatened populations are naturally distributed as metapopulations (e.g. their habitats are patchily distributed). Other species that once had large, contiguous ranges are becoming distributed as metapopulations because of habitat loss and fragmentation. Smith & Peacock (1990) note that "Natural habitats, hence animal populations, are becoming increasingly fragmented and vulnerable as a result of man's activities". The meta-population concept (Levins 1970; Gilpin 1987, Hanski 1989, Harrison et al. 1988), consisting of interdependent patches

of occupied and unoccupied habitat, can be used to describe the dynamics of these fragmented populations. "The ultimate goal is to understand these systems well enough to predict their behavior and manage for their persistence" (Gilpin 1987).

Life History Of *Euphydryas Gillettii*

The checkerspot butterfly, *E. gillettii*, is often found in populations of 30 adults or less (Table 21, Williams 1988). Its range includes western Wyoming, northwestern Montana, northeastern Idaho, and southwestern Alberta, and it has a fragmented distribution, with distances of 20 to 40 miles between populations, in some cases (Figure 32). *E. gillettii's* fragmented distribution can be partially explained by its larval foodplant specificity. *E. gillettii* lays its eggs solely on the black twinberry, *Lonicera involucrata*. This perennial shrub must be located in a wet, sunny area for the butterfly to find it suitable, and these requirements often restrict it to early successional habitats.

Disturbances are also an important factor contributing to *E. gillettii* habitat abundance. According to Williams (1988), fire is the single most important factor in creating *E. gillettii* habitat, and extensive fire suppression in the Rocky Mountains prior to 1975 may have significantly reduced *E. gillettii* habitat. Encroachment by surrounding forests shades

Table 21. Characteristics of 15 sites occupied by *Euphydryas gillettii after Williams (1988)*

Site no	Colony size[1]	*Lonicera involucrata* abundance[2]	Nectar availability	Nearby trees (age of largest to nearest 5 yr)	Water (stream width)	Disturbance
1	>30	>30	High	Lodgepole pine (75) Engelmann spruce (65)	Stream (<1 m)	Fire[3]
2	>30	>30	High	Quaking aspen (60) Subalpine fir (75)	Streams (<1 m)	None; meadow edge
3	7	10	Low	Engelmann spruce (150)	Stream (1–3 m)	None; meadow edge
4	2	10	Low	Lodgepole pine (55)	Marshy	Fire; wet soil
5	4	20	Low	Lodgepole pine (90) Quaking aspen (65)	Stream (<1 m)	Fire; logging
6	>30	20	High	Subalpine fir (155) Lodgepole pine (15)	Streams (<1 m)	Fire[3]; logging
7	18	10	Low	Cottonwood (40) Lodgepole pine	Stream (1–3 m)	Beaver activity
8	21	10	High	Lodgepole pine (65)	Stream (>5 m)	Flooding
9	22	20	Low	Lodgepole pine (95) Engelmann spruce (70)	Marshy, stream (<1 m)	Wet soil
10	8	>30	High	Lodgepole pine (55) Engelmann spruce (50) Subalpine fir (40)	Stream (<1 m)	Fire?; meadow edge
11	7	5	Low	Subalpine fir (95) Engelmann spruce	Marshy	Fire[3]
12	3	>30	Low	Lodgepole pine	Stream (1–3 m)	Flooding; fire?
13	1	20	Low	Engelmann spruce (195) Lodgepole pine (40)	Stream (1–3 m)	Fire[3]
14	2	20	Low	Willow (no trees)	Marshy, stream (<1 m)	Wet soil; grazing
15	>30	5	High	Lodgepole pine (75)	Marshy	None; meadow edge

[1] Total number eggs and adults.
[2] Approximate number *Lonicera* clumps in 30 × 30 m quadrat.
[3] Charred tree trunks.

the *Lonicera* leaves, making them unattractive to females, which always lay their eggs on sunny leaves. Other important disturbances include floods and the creation of forest openings by beavers and logging.

Williams and others have conducted extensive research on the life history, habitat requirements, and distribution of *E. gillettii*. Williams (1988) notes that some *E. gillettii* populations may fluctuate greatly in abundance from year to

year. Effective sizes for such populations are calculated using the harmonic mean of the annual population sizes. In such cases the effective population size can be much smaller than the actual population size because the harmonic mean is most strongly influenced by the smallest values. There may also be certain high-elevation populations that are biennial because the warm season is too short for the larvae to mature in one summer.

It appears that a major factor limiting the recolonization of sites is the inability of dispersing individuals to reach a suitable habitat (Holdren & Ehrlich 1981). Areas that appear perfectly habitable are perhaps never colonized by *E. gillettii* due to the insect's poor dispersal ability. An artificial introduction of *E. gillettii* in Colorado resulted in a range expansion of the species. The success of this project indicated that dispersal, and not lack of suitable habitat, may have inhibited the species from extending its range into Colorado (Holdren & Ehrlich 1981).

Because of its fragmented distribution and small population size, *E. gillettii* is an ideal organism for demonstrating the techniques of genetic diversity assessment. Historically, five colonies were known to exist in the Glacier National Park (GNP) ecosystem (Kohler 1980).

Research Plan/Methodology

The goal of this project was to assess genetic diversity within and among *E. gillettii* colonies composing the GNP metapopulation. Four colonies were assayed within GNP and two outgroups, colonies from Idaho and Wyoming, were also compared with the GNP population for allelic uniqueness and heterozygosity. Because the entire metapopulation could not be surveyed, this subsample was used as a model for the greater metapopulation. Electrophoretic analysis was used to determine the level of heterozygosity at twenty-four presumptive enzyme loci (Table 22). A minimum of seventeen individuals was assayed from each site. The methodology for starch gel electrophoresis is similar to that developed by May et al (1979) and is descibed in Appendix C.

Questions related to genetic diversity assessment include:

(1) What is the level of genetic diversity among gene pools within the park relative to the diversity among regions (ID, WY, MT)? Given the short dispersal distance of the organism (Holdren & Ehrlich 1981) one would expect a high degree of differentiation between regions.

(2) Is the park large enough to support more than one viable gene pool over the long-term (a hundred years or more)?

(3) Are gene pools potentially mergeable without adverse consequences?

(4) What management decisions within or around the park might result in the merging or destruction of gene pools?

Table 22. Enzymes used in Genetic Analysis of *Euphydryas* spp.

Locus	Enzyme	Buffer
AAT-1,2	Aspartate aminotransferase	C
AGP	Alpha-gylcerophospatase	4
DIA-1,2	NADH diaphorase	4
G6PDH	Glucose-6-phospate dehydrogenase	C
GAPDH	Galactosaminidase	C
GP	General protein	all
GPI	Glucosephosphate isomerase	4
HBDH	Hydroxybutyric dehydrogenase	C
GK-1,2	Glucokinase	R
IDH-1,2	Isocitrate dehydrogenase	C
LDH	Lactate dehydrogenase	C
MDH-1,2	Malate dehydrogenase	4
MPI	Mannosephospate isomerase	R
PEP-GL	Peptidase (glycyl-leucine)	R
PGD	Phosphoglycerate kinase	C
SOD-1,2	Superoxide dismutase	4
XDH	Xanthine dehydrogenase	R
PGM	Phosphoglucomutase	4

Results

Colonies

Kohler (1980) noted that five colonies were historically known to exist in the GNP ecosystem (Christensen Meadow, near Kiowa, Blacktail Hills, Swiftcurrent, and McGee Meadow). During the course of this research, previously known colonies were located in Christensen Meadow, Marias Pass, and north of Kiowa, and

four new colonies were identified: Red Meadow Creek Road, Spot Mt., Elizabeth Lake, and Belly River. No *E. gillettii* were observed at McGee Meadow during 1987-1989, and interestingly, only one eggsac was found at Swiftcurrent Lake in 1990 (surveyed 1989 and 1990). The Blacktail Hills site was not surveyed due to grizzly activity; thus, *E. gillettii's* current status there is unknown.

Population Sizes

A short mark-recapture study in 1989 revealed a higher population size than Williams had estimated. Initial estimates of colony size during 1987 and 1988 suggested colonies of 20 or fewer individuals. However, during 1989, a brief mark-recapture experiment produced minimum population estimates of 142, 98, 56, and 28 individuals at each of the colonies (Table 23). These data are based on 2-4 census dates per site, and the low number of recaptures suggests that the true population size was much larger than the censused population size, or that the disturbance affected recapture rates. Evidently this species becomes locally abundant during certain years. During other years, the species appears to be rare everywhere.

Genetic Analysis

Males of the species were collected from four sites in GNP during 1988 and 1989 as well as central Idaho and central Wyoming in 1989 (Table 24). Females were not collected so recruitment into the population would not be adversely affected.

Table 23. Colony Sizes and Mark-Recapture Data for *E. gillettii* in Glacier National Park Ecosystem - Summer 1989.

Date	New Males	New Females	New Total	Minimum Pop.
Christensen Meadow				
7/11	3	17	20	
7/7	3	5	8	28
Belly River				
6/28	9	6	15	
7/14	9	23	32 *	
7/15	49	47	96	142
* all marked 7/14, out of 96 captures on 7/15 none was marked				
Red Meadow				
7/4	11	16	27	
7/11	9	19	28	56
* 15 females marked on 7/4; no recaptures on 7/11				
Marias Pass				
7/4	3	4	7	
7/18	12	31 (marked)	43	
7/20	17	27 (8 rcpts)	34	
7/24	1	18 (5 rcpts)	14	98

Note: rcpts = recaptures

Table 24. Sample sizes for electrophoresis.

Collection Sites	Total Individuals Collected	
	1988	1989
Glacier Park		
Christensen Meadow	17	
Belly River	23	9
Red Meadow		25
Marias Pass		21
Outgroups		
W. Central Idaho		20
W. Central Wyoming (Granite Creek)		22

1988 Results

Heterozygosity A total of 19 loci from two populations in GNP were surveyed electrophoretically (Tables 24 and 25). Seven loci were found to be polymorphic in the Belly River population (AGP, IDH-2, PGD, GPI, MDH-1, PGM, and DIA-2), while four loci were found polymorphic in the Christensen meadow population (PGD, MDH-1, AGP AND DIA-2). All polymorphic loci in the Christensen meadow population were also polymorphic in the Belly River population. Appendix D provides a detailed description of allelic frequencies and genetic variability in 1988.

Belly River had a population mean heterozygosity of 0.084 with S.E.=0.038 (unbiased estimate, Nei 1978). The mean number of alleles per locus was 1.5 (S.E.= .17). The

Table 25. Polymorphic Loci of *E. gillettii* - 1988 Glacier National Park, MT

Locus	Alleles Present Christensen Meadow	Belly River
IDH-2	C	C,D
PGD	A,B,C	A,B,C
GPI	C	C,F
MDH-1	C,E	E,F
PGM	G	F,G,H
DIA -2	C,D	C,D
AGP	A,B,C	A,B,C
MDH-2	C	C
GP	C	C
IDH-1	G	G
AAT-1	C	C
AAT-2	C	C
GAPDH	C	C
LDH	B	B
SOD-1	D	D
SOD-2	B	B
DIA-1	B	B
HBDH	B	B
PEP	C	C
#polymor. loci	4/19	7/19
%polymor. loci	22%	35%

percentage of the loci polymorphic was 20% by the .95 criterion and 35% by the .99 criterion.

Christensen meadow had only four polymorphic loci with a mean heterozygosity of .079, S.E.=.037 (unbiased estimate). The mean number of alleles per locus was 1.25 (S.E.= .12), and the percentage of loci polymorphic was 20% by the .95 criterion and 20% by the .99 criterion.

Wright's Inbreeding Coefficients The summarized F statistics over all loci (Table 26) revealed inbreeding coeffients as follows: F_{IS} = -.125, F_{IT} = .079, and FS_T = .041.

Table 26. Summary of F-Statistics - all Loci in Belly River and Christensen Meadow - 1988

Locus	F_{IS}	F_{IT}	F_{ST}
AGP-1	-.006	.049	.055
IDH-2	-.024	-.012	.012
PGD-1	-.089	-.059	.028
GPI-1	-.026	-.013	.013
MDH-1	-.208	-.108	.083
DIA-2	-.319	-.292	.020
PGM-1	-.076	-.037	.037
Mean	-.125	-.079	.041

Chi-Square Analysis AGP, PGD, and MDH-1 exhibited significant differences in frequency between the Christensen Meadow and Belly River population in 1988 (Table 27). The total chi-square was 26.505, with a corresponding probability of .00545, highly significant.

Genetic Identity Nei (1978) unbiased genetic identity between the two populations was .997, while the Nei (1978) unbiased genetic distance was .003.

Table 27. Contingency Chi-Square analysis - all loci 1988

Locus	#alleles	X^2	d.f.	p
AGP-1	3	6.657	2	.03584
IDH-2	2	0.724	1	.39472
PGD-1	3	6.600	2	.03688
GPI-1	2	0.811	1	.36775
MDH-1	3	8.461	2	.01454
DIA-2	2	0.317	1	.57314
PGM-1	3	2.933	2	.23073
totals		26.505	11	.00545

1989 Results

Heterozygosity A total of 23 loci from Wyoming, Idaho, and Montana were analyzed (Table 28). The Montana population, however, consisted of three separate sub-populations, Marias Pass (n=20), Red Meadow (n=25), and Belly River (n=9) which were analyzed separately. The Idaho and Wyoming samples each came from only one population of 20 and 22 individuals respectively.

Six of the 23 assayed loci were polymorphic (26%) in the Montana and Idaho populations, while Wyoming had five of 23 loci polymorphic (22%). Allelic composition is shown in Table 28. Appendix E provides a detailed description of allelic frequencies and genetic variability in 1989.

Table 28. Polymorphic Loci of *E. gillettii* - *1989*

Locus	Alleles Present				
	Wyoming N=22	Idaho N=20	Red Mead. N=25	Marias P. N=21	Belly R. N=9
IDH-2	C	C	C	C	C
PGD	A,B	B,C	B	B	B
GPI	B,C	B,C	C,D	C	C
MDH-1	D,E	D,E	D,E	E	E
PGM	G	G,H	G	G	G
AGP	A,B	A,B	A,B	A,B	A,B
MDH-2	C	C	B,C	C	C
MPI	C,D	B,C	B,C	B,C	B,C
GK-2	C	C	B,C	C	C
GP	C	C	C	C	C
IDH-1	G	G	G	G	G
AAT-1	C	C	C	C	C
AAT-2	C	C	C	C	C
G6PDH	C	C	C	C	C
GAPDH	C	C	C	C	C
LDH	B	B	B	B	B
SOD-1	D	D	D	D	D
SOD-2	B	B	B	B	B
DIA-1	B	B	B	B	B
XDH	C	C	C	C	C
HBDH	B	B	B	B	B
PEP	C	C	C	C	C
GK-1	C	C	C	C	C
#polym. loci	5/23	6/23	6/23	2/23	2/23
%polym. loci	22%	26%	26%	9%	9%

The diversity of alleles at each locus was relatively equivalent across the three populations. In several cases, a population could be distinguished by the presence or absence of certain alleles. For example, Wyoming had the A and B alleles for PGD, while Idaho had the B and C alleles. Montana populations only had the B allele. Similarly,

Wyoming and Idaho had the C allele for MDH-2 and GK-2, but Montana's Red Meadow population had B and C. At the MPI locus the Idaho and Montana populations were similar, exhibiting the B and C alleles, while the Wyoming had both C and D alleles. PGM was polymorphic only in Idaho. At GPI, Wyoming and Idaho were most similar, exibiting the B and C alleles, while Montana exhibited the C and D alleles. The same alleles were present in all three populations at the AGP and MDH-1 loci.

Genetic analyses revealed that the populations with higher allelic diversity exhibited higher polymorphism. Populations in Idaho, Wyoming, and Red Meadow, MT had six, five, and six polymorphic loci respectively, compared to Marias Pass, MT and Belly River, MT's two. The level of heterozygosity was near 0.05 in the Idaho, Wyoming, and Red Meadow populations, while it was .030 and .035 for the Belly River and Marias Pass populations (Table 29). Belly River's low polymorphism estimate may not be as reliable as the others, however, because of small sample size (N=9).

Table 29. Heterozygosity at Variable Loci - 1989

Locus (n)	Wyoming (22)	Idaho (20)	Belly R. (9)	Marias P. (20)	Red M. (25)
PGD	.044	.095	n.a.	.153	.000
GPI	.463	.049	.000	.000	.113
MDH-1	.449	.180	.000	.000	.039
PGM	.000	.145	.000	.000	.000
AGP	.172	.180	.490	.498	.500
MDH-2	.000	.000	.000	.000	.077
MPI	.139	.480	.198	.133	.365
GK-2	.000	.000	.000	.000	.127
mean H	.056	.050	.030	.035	.053
S.E.	.029	.024	.023	.024	.026

Wright's Inbreeding Coefficients The summarized F statistics over all loci (Table 30) revealed inbreeding coeffients as follows: F_{IS} = .011, F_{IT} = .333, and F_{ST} = .325.

Table 30. Summary of F-Statistics over all Loci within MT, WY, and ID - 1989

Locus	F_{IS}	F_{IT}	F_{ST}
AGP-1	.206	.533	.413
MPI-1	.121	.442	.366
PGM-1	-.086	-.016	.064
PGD-1	-.068	-.028	.038
GPI-1	-.437	-.086	.244
MDH-1	-.379	-.102	.201
MDH-2	-.042	-.008	.032
GK-02	.642	.662	.055
Mean	.011	.333	.325

Chi Square Analysis Three chi-square analyses were conducted; one which included all populations in 1989, and a second for the GNP 1989 populations only, and a third that compared Belly River populations in 1988 and 1989. Table 31 shows significant differences among all 1989 populations at the following loci: AGP, MPI, PGM, GPI, MDH-1, and GK-02. The GNP populations are distinguished by significant variation at the MPI locus only (Table 32). Belly River populations differ significantly between years at loci AGP and IDH-2 (Table 33).

Table 31. Contingency Chi-Square analysis - all loci, all populations 1989.

Locus	alleles	X^2	d.f.	p
AGP-1	4	204.45	12	.00000
MPI-1	3	90.5898	8	.00000
PGM-1	2	11.717	4	.01958
PGD-1	3	4.432	8	.81621
GPI-1	3	61.085	8	.00000
MDH-1	2	36.401	4	.00000
MDH-2	2	5.660	4	.22606
GK-02	2	9.977	4	.04081
totals		424.307	52	.00000

Table 32. Contingency Chi-Square analysis - all loci, Glacier populations 1989.

Locus	#alleles	X^2	d.f.	p
AGP-1	2	.240	2	.88670
MPI-1	2	52.530	2	.00000
PGD-1	2	.356	2	.83713
GPI-1	2	3.458	2	.17747
MDH-1	2	1.131	2	.56817
MDH-2	2	1.283	2	.31933
GK-02	2	4.212	2	.12170
totals		26.505	11	.00000

Table 33. Contingency Chi-Square analysis - Belly River 1988 and 1989.

Locus	#alleles	X^2	d.f.	p
AGP-1	3	12.441	2	.00199
IDH-2	3	60.000	2	.00000
PGM-1	3	1.670	2	.43397
PGD-1	3	.696	2	.70622
GPI-1	2	.357	1	.55040
MDH-1	2	.376	1	.53994
totals		75.539	10	.00000

Genetic Identity Nei's (1978) unbiased genetic identity (I) (Table 34) grouped Belly River and Marias Pass as a cluster (I=1.00). Marias Pass and Belly River, MT were grouped most similar to Wyoming populations (genetic identity = .983 and .985 respectively). The Red Meadow population of Montana was slightly more distinct, with an identity of .982

relative to the Belly River population. Idaho was the outlier, being most closely related to the Belly River and Marias Pass populations at I=.967 and I=.966, respectively. The most dissimilar populations were Wyoming and Idaho (I=.949).

The cluster analysis (Figure 33) using unweighted pair group method and Nei (1978) unbiased genetic identity portrays these similarities as a composite. Two of the Montana populations are clearly segregated from the others in a clump of high similarity (I=1.0). The closer identity between Belly River & Marias Pass, Montana and Wyoming (.98) is also portrayed, leaving Red Meadow, MT as an outlier to this group (I=.974). Idaho is the most different with an identity of .956 relative to the other populations.

Table 34. Matrix of Genetic Similarity and/or Distance Coefficients

Below Diagonal: Nei (1978) unbiased genetic identity
Above Diagonal: Nei (1978) unbiased genetic distance

Population	Idaho	Belly R.	Red Mead.	Marias P.	Wyoming
Idaho	*****	.034	.037	.035	.052
Belly R.	.967	*****	.018	.000	.015
Red Mead.	.964	.982	*****	.021	.042
Marias P.	.966	1.000	.979	*****	.017
Wyoming	.949	.985	.959	.983	*****

Similarity and distance estimates were also calculated using Rogers (1972) equations. Rogers' distance considers two populations with fixation for different alleles farther apart than ones where one or both are heteroallelic even though they have no common allele (Wright 1978).

In both tables 38 and 39, Wyoming and Idaho populations are the most dissimilar and Marias Pass and Belly River populations are the most similar. However, while the Nei (1978) indices would have grouped Belly River, Marias Pass and Wyoming as most similar (Fig. 33), the Rogers (1972) indices group all of the Montana populations together prior to including Wyoming (Fig. 34). The latter diagram is what one would expect based upon the geography of the sample sites. The Idaho site is closer to the Montana sites (283 miles) than Wyoming is to the Montana sites (303 miles). There is also more continuous montane habitat connnecting the Idaho and Montana sites relative to Wyoming and Montana sites. Moving south from GNP, there are breaks between Helena, MT and the Beartooth Mts. of Wyoming, whereas there are virtually no breaks from GNP to the Idaho site in the Sawtooth mountains.

Fig. 33. Cluster Nei (1978)

Cluster analysis using unweighted pair group method
Coefficient used: Nei (1978) unbiased genetic identity.

Population or cluster numbers joined		Clustering level	Cycle
2	4	1.00000	1
2	5	.98415	2
2	3	.97337	3
1	2	.96140	4

Goodness of fit statistics
****
Farris (1972) "f" = .055
Prager and Wilson (1976) "F" = .564
Percent standard deviation (Fitch and Margoliash,1967) = .788
Cophenetic correlation = .864

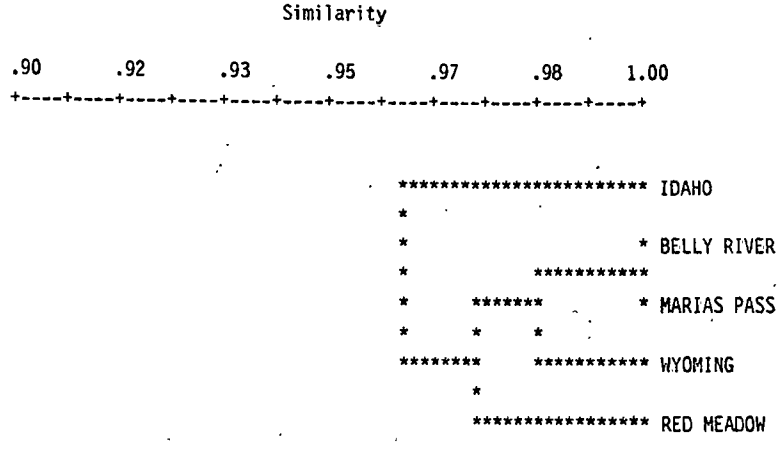


Fig. 34. Cluster Rogers (1972)

Cluster analysis using unweighted pair group method
Coefficient used: Rogers (1972) genetic similarity.

Population or cluster numbers joined		Clustering level	Cycle
2	4	.99282	1
2	3	.95874	2
1	2	.93799	3
1	5	.93170	4

Goodness of fit statistics
****

Farris (1972) "f" = .079
Prager and Wilson (1976) "F" = .839
Percent standard deviation (Fitch and Margoliash,1967) = 1.203
Cophenetic correlation = .870

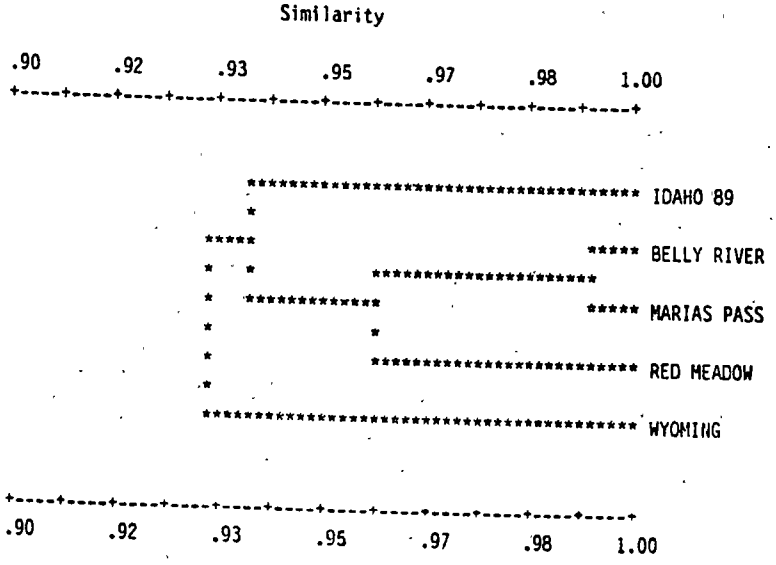


Table 35. Matrix of Genetic Similarity and/or Distance Coefficients

Below Diagonal: Rogers (1972) unbiased genetic identity
Above Diagonal: Rogers (1972) unbiased genetic distance

Population	Idaho	Belly R.	Red Mead.	Marias P.	Wyoming
Idaho	*****	.059	.067	.060	.086
Belly R.	.941	*****	.039	.007	.050
Red Mead.	.933	.961	*****	.043	.083
Marias P.	.940	.993	.957	*****	.053
Wyoming	.914	.950	.917	.947	*****

Discussion

Colony Numbers and Distribution

Given the results of the brief mark-recapture project,the reported rarity of *E. gillettii* must be questioned. More rigorous censusing and a search for new colony sites may prove the organism to be more common than historically noted. Since many of the historic colony sites are within easy access of roads, there undoubtedly could be many more colonies in remote areas that have not yet been discovered. This hypothesis is supported by the discovery of four previously unknown populations during the species diversity inventory project.

Both the Belly River and Red Meadow populations are spread out over long, linear sites. Because *L. involucrata* is a disturbance species, it tends to be distributed along trails or roadsides, suggesting that *E. gillettii* distributions may mimic the distribution of its host plant. In other sites, such as moist meadows, *E. gillettii* populations are distributed in more of a rectangular fashion. In this case, the rectangular distribution may be a consequence of nectar plant distribution.

Genetic Diversity

The electrophoretic analysis revealed that *E. gillettii* populations in GNP, Montana, may consist of two separate biennial populations. This hypothesis is supported by the major genetic differences between the Belly River 1988 and 1989 analysis. Chi-square analysis showed significant differences in allele frequencies at the AGP and IDH-2 loci between the two broods. The 1989 population had only two polymorphic loci, while the 1988 population had seven polymorphic loci. Further, the C allele did not appear in the 1989 population at the AGP locus. This apparent difference may be a result of small sample sizes (n= 23 in 1988 while n=9 in 1989); however, the results are so strikingly different that they probably result from more than simple sampling error. Simple calculations using 1988

allele frequencies to estimate 1989 allele frequencies revealed major differences between observed and expected results. Several alleles present in 1988 were not observed in 1989. The possibility of *E. gillettii's* biennial nature is suggested in Scott (1986): "J. Harry found that the subalpine ecotype hibernates in the second, third, or fourth stage after feeding for 2 weeks, then hibernates the second winter in the unfed fifth stage."

A biennial life history could actually offer the species a longer expected persistence time, as the two populations may experience the environment in different ways. For example, eggs, larvae, and pupae may be susceptible to different environmental perturbations relative to adults. During an extreme drought year, the population that is flying could become extinct. Presumably, the hibernating population would also be affected, but perhaps not quite so significantly. If the hibernating population is protected from a "bad year", the species could persist as one population that flies every other year. This has been observed in Colorado populations of *Boloria acronema* (Brussard & Britten 1989). Thus, two alternating biennial populations may increase persistence time for rare species. If extinction probabilities are independent, one population may go extinct regardless of the fate of the other. In some lepidopteran populations, such as *Boloria acronema*, there can be

variance in developmental time. If some larvae take longer to develop, "leakage" may permit gene flow between populations, thus allowing the re-establishment of an extirpated brood (Brussard & Britten 1989).

In planning the sampling scheme, it would have been preferable to combine samples at each site between years, thereby affording a larger sample size and a four-site comparison. Large samples were never taken from any population. However, due to the disparate results between the two years, this lumping was not justified. Because the between-year differences were significant, the most appropriate analysis was a between-population within-year comparison.

As such, the 1988 results can only be used to compare two populations within the GNP ecosystem; Belly River and Christensen Meadow. Belly River had almost twice the level of polymorphism (49%) as Christensen Meadow (25%), but similar levels of mean heterozygosity were found (Belly River = .084 and Christensen Meadow = .079). AGP, LDH-1, and GPI significantly differentiated the populations based upon chi-square results.

The 1989 survey allowed for comparisons among three populations in GNP, as well as an inter-state comparison. Wyoming, Idaho, and Red Meadow, MT had comparable levels of heterozygosity (.055, .049, and .053 respectively). Montana's Marias Pass and Belly River populations had the

lowest heterozygosity (.035 and .030 respectively). Polymorphism was similarly distributed; WY = 22%, ID = 26%, and Red Meadow, MT = 26%, while Marias Pass and Belly River, MT were both polymorphic at only 9% of the loci surveyed. However, small sample size hindered thorough analysis of the Belly River population.

The chi-square analysis of MT, WY, and ID populations identified significant differences at six out of eight polymorphic loci. This is not surprising, given the fact that these populations are separated by hundreds of miles. When GNP 1989 populations were compared using the chi-square analysis, there were differences only at the MPI locus, but this difference was highly significant ($p = 0.00000$). The C allele was predominant in Belly River and Marias Pass populations, but the B allele was predominant in the Red Meadow population.

Within the park, spatial distribution of the population may be correlated with genetic diversity. For example, the long, narrow populations distributed over a few miles (e.g. Belly River and Red Meadow) exhibited a higher level of heterozygosity than the rectangular meadow populations that were less than one half of a mile on a side (e.g. Christensen Meadow). The long, narrow populations may also be much larger than the meadow populations.

F-Statistics and Genetic Similarity

Wright's inbreeding coefficients showed different results between years, but this may be expected due to the different scales of analyses. In 1988 F_{IS} was negative, and F_{IT} was intermediate, and F_{ST} exhibited the highest value. In 1989, F_{IS} was small but not negative, and F_{IT} was highest, and F_{ST} was intermediate, but all values were larger than in 1988 (Tables 26 & 30).

Hartl (1980) describes the meaning of F_{ST} as follows: Population subdivision and its attendant random genetic drift causes the average subpopulation heterozygosity to be smaller than what the heterozygosity would be were the subpopulations combined into a single large randomly mating unit. F_{ST} measures the extent of this reduction in heterozygosity. In other words, the quantity F_{ST} estimates the amount of genetic variation in the whole population that is attributable to genetic differentiation among subpopulations; when $F_{ST} = 0$, for example, there is no genetic differentiation among subpopulations. Values for F_{ST} are quite variable in this study. In general, F_{ST} is influenced by the amount and pattern of migration between subpopulations, among other factors.

F-statistics revealed that the two GNP sub-populations (1988 data) were more similar ($F_{ST} = .263$) than the 1989 sample of Montana, Wyoming, and Idaho populations ($F_{ST} = .441$). This implies, as one would expect, that

subpopulations between states are more isolated, or more structured, than those within GNP.

Comparing populations in different states, Idaho and Montana were much more similar than either is to Wyoming. This is also to be expected given the fact that the Idaho and Montana populations are closer spatially. If *E. gillettii* is truly limited in dispersal ability, one would expect more geographically isolated populations to be more genetically distinct.

Implications for Management

The level of heterozygosity within the park is comparable to the diversity within other regions. Heterozygosity and percent polymorphic loci were the same or slightly higher in Red Meadow, MT relative to the ID and WY populations.

The PGD locus singled out Wyoming and Idaho by characteristic alleles found nowhere else. GPI, MDH-1, MDH-2, PGM, MPI, and GK-2 also were helpful in distinguishing among state populations, as some sampled WY and ID populations were fixed for certain alleles at these loci.

Gene pools within GNP were somewhat different but may be mergeable without adverse consequences. It appears that the genetic variation in some populations is a subset of the variation expressed in the others. In 1988, Christensen

Meadow and Belly River were significantly different at AGP, MDH-1, and PGD based upon chi-square results. In 1989, Belly River and Marias Pass ranked high in similarity, but both were different in allelic composition relative to the Red Meadow population at GPI, MDH-1, MDH-2, MPI, and GK-2.

How might park management result in the merging or destruction of gene pools? Park management decisions are not likely to result in the merging of gene pools, as geographical distance is probably the largest separating factor given the low vagility of this butterfly. However, management decisions could lead to the destruction of gene pools. The butterfly's host-plant specificity, combined with the disturbance-loving nature of the host plant, suggests that maintenance of successional-stage habitats is imperative to the survival of *E. gillettii*.

Management policies that prevent natural changes could deleteriously affect populations of this species. For example, fire suppression policies will be detrimental, as new openings will not be created. As successional changes occur in meadows such as Christensen Meadow, the area will become too dry or shaded for the butterfly to persist. If new openings are not created, the species will face a continuous loss of habitat. Similarly, areas that are opened outside of the park (through development, for example), may create new habitat. This dependence on

disturbed areas may be one of the explanations for the species' patchy distribution.

Corridors are also an important habitat variable in the maintenance of the park's *E. gillettii* populations. *E. gillettii* moves primarily up and down streams connecting patches of good habitat; it does not use dry areas. Therefore, stream/river systems constitute the predetermined colonization and dispersal corridors (Williams, pers. com.).

If colony sizes or heterozygosity should happen to decline in the future, it would be relatively easy to transplant eggsacs between colonies. One effective migrant per generation between colonies is all that is needed to make a subdivided population "approximately panmictic" (Lande & Barrowclough 1987). However, careful consideration of differences between gene pools should be accomplished prior to such a management activity.

According to Ehrlich (1983), natural extinctions of butterfly populations appear to be common occurrences, especially in response to stresses on their larval food plants. These extinctions, however, are normally followed by recolonization of habitat patches, and a mosaic pattern of population "regulation" prevails. Anthropogenic extinctions of butterflies are becoming increasingly common as a result of widespread habitat destruction. In the case of *E. gillettii*, habitat destruction could be synonymous with

fire suppression.

Given the results of the genetic analyses, it is unclear whether the park is large enough to support more than one viable gene pool over the long term. It appears that there are minor differences in genetic composition of populations within the park. However, dispersal distance is the critical factor in determining the true level of isolation between populations. Heterozygosity levels are higher than one would expect for populations of 30 individuals. Thus, dispersal between populations may be maintaining genetic diversity within the population. Some of the smaller populations may be sink populations relative to the larger source populations (e.g. Pulliam 1988). However, more research is necessary before this question can be answered. Actual population sizes need to be estimated more rigorously, and determination of potential dispersal distances would be highly advantageous.

Given the potential rarity of *E. gillettii* compounded with its hypothesized biennial nature (Scott 1986), continued population monitoring and genetic analysis is critical. Genetic analysis is the only realistic way to distinguish between an annual and biennial population structure. *E. gillettii* is known to exhibit major fluctuations in population size, and its persistence at small population numbers is not easily explained. A biennial population structure could be

the explanation for the observed allelic differences, population size fluctuations, and its continued persistence. If this hypothesis is correct, the even year populations should be much more similar to each other genetically than they are to the odd years.

Summary

This chapter shows how electrophoretic techniques can be used for genetic diversity assessment. This research corroborates most of Williams' (1988) ideas, who has studied *E. gillettii* most extensively. *E. gillettii* exists in small, fragmented populations in the GNP ecosystem, and seems to exhibit large fluctuations in population size. However, some of the populations observed in GNP may be on the order of hundreds of individuals, rather than the small population sizes Williams reports.

Electrophoretic analyses revealed moderate levels of heterogeneity both within and between the colonies studied, and a potential biennial nature of the organism. A biennial life history is consistent with the expected findings, given the distance between patches, the large fluctuations in population sizes, and the small overall colony sizes. However, the level of heterozygosity was higher than expected for population sizes of one hundred or more. It may be that dispersal between populations is maintaining a

higher level of heterozygosity.

Using the WY and ID populations for comparison, the GNP, MT population has an equivalent genetic diversity relative to other areas. Highest levels of polymorphism (35%) and mean heterozygosity (.084) were both found in 1988 Belly River, Montana. Lower values for these variables were found in 1989 Marias Pass and Belly River populations, but the Belly River estimate may be too low because of small sample size. With respect to genetic identity, the Rogers similarity index gave the result most consistent with expectations. Two Montana populations (Belly River and Marias Pass) were extremely similar, while Red Meadow, MT was slightly different. The Montana cluster was most similar to Idaho. The Wyoming population was the outlier.

CHAPTER 4

PROBLEMS IN BIODIVERSITY ASSESSMENT AND MANAGEMENT

One goal in assessing biodiversity is to obtain a reliable, repeatable characterization of species distribution patterns in the community examined. In this fashion, baseline inventory can be established, and future monitoring can then be employed to document changes - both natural and human-induced - over time. If the fluctuations observed are greater than the expected natural fluctuations, then alternative, potentially human-induced, causes can be discerned.

There are far fewer papers describing empirical biodiversity assessments than those discussing the theoretical and ethical reasons for preserving biodiversity. The few projects that are implemented are often scaled down to incorporate financial considerations, time constraints, and personnel limitations (Chapter 2).

By scaling down these projects, conservation biologists face problems obtaining adequate databases. With very few exceptions, we have neither the resources nor the time to do a complete inventory of species diversity. Thus, we are faced with problems of sampling, some of which are listed

below. This chapter is a discussion of these problems, and a set of suggestions is provided as to how they might be resolved.

Problems Inherent in Assessing Biodiversity

- Replication both in space and time is necessary to distinguish natural background variation in species distribution from true changes and sampling artifact.

- The degree of within-site habitat heterogeneity can strongly influence the number and types of species observed.

- Sampling effort must be standardized for each taxon to ensure the sample continues until one reaches a saturation point in species found relative to effort exerted.

- Observer bias, as a result of different levels of expertise, can lead to major differences in sample results.

- It is difficult to know when sampling has been adequate enough to detect the last rare species, or the hottest hotspots.

- It is difficult to associate changes in biodiversity with specific environmental changes.

Sampling Problems in Biodiversity Assessment

Ecological phenomena often operate on spatial scales far larger than our bodies and temporal scales longer than our lifetime. The choice of time scale for a study of population dynamics depends not only on generation time of the species of interest, but also on the generation times of the other species with which it interacts. Until a study has been repeated many times at many sites, a biologist has only a restricted idea about the range of applicability of the study's conclusions. Similarly, long-term dynamics at a

single site provide very different conclusions relative to a short-term study of a similar community at many different sites distributed over a large area (Wiens et al. 1986).

Spatial Scales Diversity generally increases with larger geographic scale, but the factors contributing to this increase are not the same at all scales (Cody 1986). Because species richness increases as a function of area, it is important to document the area surveyed when describing the species richness of a site. To date, the only generalized formula that accounts for both species richness and area is that advanced by island biogeographers: $S = cA^z$, where S = number of species, c is a constant, A = area, and z is the slope of the species/area function. Another approximation is the distinction between point diversity, alpha, beta and gamma diversity.

Point diversity results from the overlap of different species' home ranges. On a somewhat larger spatial scale, alpha diversity measures the variety of species present in a given habitat. Beta diversity is found on a larger geographic scale that includes several habitat types. Finally, gamma diversity measures the accidental species occurrences attributable to historic events, such as storms (Cody 1986). These definitions provide a generalized spatial context, but their specificity is dependent upon the classifications of "habitat" and "region."

It is not simple to delineate habitat edges. Furthermore, landscapes may appear to be heterogeneous at one scale but quite homogeneous at another. Scale can affect the properties of a system, including the degree of equilibrium, degree of closedness versus openness, and whether a disturbance agent is endogenous or exogenous. Moving to a coarser scale means becoming further removed from the basic processes (Meetenmeyer & Box 1987).

When considering the size of the census area, one must keep in mind that spatial scale changes should not be viewed as simple linear changes. As an example, doubling a map scale produces a four-fold increase in the size of the map required (Meetenmeyer & Box 1987). Similarly the number of interactions represented as scale increases may not necessarily be linear relations.

The spatial scale perceived by the researcher should also take into consideration the spatial scale perceived by the organism. Patches or microhabitats may be much more significant as reservoirs of biodiversity than the observer may think. For example, intermittent streambeds support much higher levels of butterfly species diversity than do the surrounding meadows (pers. obs.).

Weiss and Murphy (in press) attribute great significance to microhabitats, noting "the great variety of temperature and water regimes mediated by topography is responsible for much of the biological diversity supported

by landscapes, since many plants and animals have restricted thermal and hydrologic requirements." In lepidoptera, population size itself is mediated by topoclimates. For example, females that emerge early and lay eggs on cool slopes where host plants senesce later may have higher reproductive success than late-flying females that oviposit on warm slopes. This is because warm-slope larvae will not have a chance to mature before the host plants senesce. Narrow east-west running ridgelines and v-shaped gullies provide major thermal changes over a short distance since they create north and south-facing slopes. These microclimates can be critical in years of climatic extremes as postdiapause larvae can disperse short distances to find thermal retreat.

Microhabitats may exist as a result of the patches creating and perpetuating their own abiotic environment. It seems that larger patches have a greater ability to create their own microenvironment. However, even small patches, such as windbreaks, can increase their moisture supply by capturing snow (Miller 1978). This added moisture can make a critical difference in vegetation composition, diversity, and size to lepidopteran species.

Habitat Heterogeneity How should census sites be chosen? It is much easier to census for species composition in a homogeneous habitat, as each species assemblage can be associated with a particular habitat type. However, some species thrive on habitat edges or in microhabitats, and by censusing only the middle of a homogeneous site, these species are missed. For example, one can census for birds in the middle of a field or in the middle of a forest, but if one walks the edge between these two habitats, the number of species observed increases dramatically (Chapter 2). Thus, the chances of finding more species increases as one includes several habitats. A large site that incorporates several habitats will be a much more productive site to census if the goal is to find as many species as possible, given limited resources. For example, one might sample a site that contains meadow, forest, and meadow/forest edge. There is one problem with this technique, however. To use the avian taxon as an example, edge avoidance is a characteristic of interior forest dwelling birds. By sampling near an edge, one may miss interior forest species.

Habitat Site Selection If the goal of a biodiversity assessment is to compare the relative abundances of species within a taxonomic group over an entire reserve, replication of habitats in the biodiversity sampling sites should be directly proportional to their frequency of occurrence. For

example, if lodgepole pine forests cover 80% of the reserve, 80% of the censuses should be conducted in lodgepole sites. However, the rare, scattered habitats could potentially be more critical as centers of endemism. Unusual habitats are generally of interest because of the unique species they contain.

Of course, species distribution will not be known until a preliminary inventory is completed. For example, if rare habitats support 80% of the species diversity, and 20% of the species diversity is harbored in lodgepole forests, the sites of high species diversity should be sampled at a frequency much higher than their relative frequency in the park. In this case, the sampling regime could be set up so that less frequently-occurring habitats are intentionally over-represented (as was done in this study). This methodology does not provide a true representation of proportional frequency of species. Instead, by representing a wide variety of habitat types it maximizes the opportunity to sample different (and potentially rare) species. Austin & Heyligers (1989) sum up the reality of sampling problems as follows: "In theory, each grid point in each environmental cell should have an equal, or at least known, probability of being sampled to ensure a lack of bias. In practice this is impossible: access to many grid points would require days of walking and/or use of helicopters." Further, areas of conservation significance may be small and

unlikely to be detected by arbitrary traverse survey or random sampling. Bias introduced by selecting accessible grid points is unavoidable. However, by adopting explicit sampling procedure, one can ensure consistency of sampling and provide the opportunity for others to determine the degree of bias.

The application of this strategy must be standardized in order to allow comparability between different surveys. Otherwise, the perceived species rarity throughout the park will not be indicative of the true level of rarity. In fact, rare species found in rare habitats would be even rarer than first estimated if rare habitats were proportionally oversampled. This problem may be ameliorated by classifying census sites according to a GIS habitat designation. Using such a tool, the relative frequency of the habitat type can be used to weight each species frequency, thereby obtaining the true species frequency within the reserve. A GIS can also be used to calculate spatial autocorrelations, plot residuals, and manipulate scale to assess effects of scale changes (Meetenmeyer & Box 1987).

Sampling Effort and Replication Once the sites are established, how does one determine the optimal plot size, amount of census time and number of replicates? A species effort curve can be used to determine optimal sampling time

(Chapter 2). Steele et al. (1984) suggests that 3 replications of a 2 km. transect are required to obtain reliable estimates of avian community characteristics (abundance, species richness and species diversity). He found that five repetitions (1 per day) were sufficient to quantify bird community characteristics. Species richness results collected from three days of sampling predicted the results from five days of sampling with high probability (r=.97), and predictions from two days were only slightly worse. Results from an ANOVA on total population and species diversity showed significant differences among years, months, and habitats. Further, more birds were seen in riparian areas than any other habitat type.

Subset plots can be used to determine the minimum size plot necessary to estimate species richness, abundance, and diversity. For example, Steele et al. (1984) calculated the correlation between 12 x 12 m plots and each of 5 x 5, 6 x 6, 7 x 7 . . . to 11 x 11. He found that abundance, rather than richness or diversity had the highest correlation with plot size over the range of plot sizes tested. Small plot sizes (5 X 5, 6 x 6, and 7 x 7) had low correlations (r^2 = .5 to .75) with species richness and diversity, but as plot size increased, all three variables (richness, abundance, and diversity) had correlations of .8 or more.

Rare Species Rare species pose difficult problems in censusing due to their small population sizes. These small populations, both in numbers of individuals and in areal extent, can create difficulties in plot placement, replication, and randomization. Small population sizes also eliminate the possibility of destructive sampling (e.g., plants).

Travis and Sutter (1986) review experimental designs for demographic studies of rare plants. They recommend hexagonal plots as a compromise between the ideal circular shape, which minimizes edge effects, and the more practical square. The sample size should be large enough to sample adequately the variation in the taxa. Modifying Travis and Sutter's (1986) vegetation sampling scheme to a multitaxa survey, the sample size should be determined by three components: 1) the variability and turnover rate of the species, 2) the variability of habitat types, and 3) the desired sensitivity of the experiment. The more innately variable the character (e.g. species composition), the larger the sample size needed to detect differences between sites. For example, if species diversity varies temporally or spatially, more replicates will be necessary to distinguish a real change from a natural fluctuation. Second, for a given level of innate variability, the greater the sample size, the more subtle differences among sites that can be detected. If the distribution is assumed to be

normal, the standard error decreases with the square root of n, where n = sample size. Thus, one must first estimate the innate variability (of species diversity, for example), then decide what level of difference one wants to detect before a sample size can be determined. For example, is the level of detection a difference in abundance in a square kilometer site, or a difference in presence/absence totals over an entire reserve? Different areas may require different sampling intensities. Sites with high species diversity may require greater sampling effort before the number of species reaches a saturation point.

Presence/Absence Sampling Habitat diversity dictates separate analyses for separate habitats, but subdividing the data by habitat types may significantly decrease sample size per type. As sample size decreases, the chance of detecting a rare species decreases. How then, do we reconcile the need for replication with the need to survey a large, diverse ecosystem?

Presence/absence sampling was used in the Glacier study to allow sampling over a wide range of moisture and elevation gradients. Reliable abundance data for each of one hundred different species in each taxonomic group was simply not a realistic goal. Presence/absence sampling allows one to replicate sampling in a wide range of habitats, and it is sensitive enough to detect changes in

occurrence over time.

Both Brown (1984) and Bock (1987) have demonstrated positive correlations between species distribution and abundance. Species that occupy the most sites tend to have the highest abundance within occupied sites. This relationship supports the use of presence/absence sampling as an alternative to the more time-consuming and costly abundance data. If enough sites are sampled, one can infer species abundance by determining their frequency of occurrence.

Bock (1984) notes that correlations between range size and abundance are significantly positive, to a greater degree within families than between them, and more within regions of the United States than across the whole continent. He also notes that the positive correlation between distribution and abundance of North American winter landbirds is not an artifact of their relative conspicuousness, nor is it dependent upon the geographic scale at which the comparison is made. Rather, it appears to be an intrinsic property of the species themselves (Bock 1987). These results further substantiate the use of presence/absence sampling, especially at a regional level or below. Because most areas surveyed will fall within a small geographic range (relative to continental scale), the correlations will be strong.

Of course, some important considerations include the precision level desired and the research question. In species of special concern, one might want to invest more time and effort to obtain abundance estimates.

Reliability of Species Diversity Data In evaluating the results of an ecological study, one must always address the question of data reliability. How good are the estimates of species presence and absence? How do we know that we have not missed some rare species? The biodiversity data must be scrutinized from two perspectives: (1) reliability of presence data and (2) reliability of absence data. In general, presence data are much more reliable than absence data. Species identifications can be verified if a sample is collected or a bird song is recorded. Bird identifications can also be discussed by two or three observers at the time of census. Yet, how certain can the observer be that a species that did not appear during a census was really not present? Unfortunately this second question is much more difficult to resolve. In evaluating presence/absence data, one must also realize that there is a learning curve associated with the skill of the observer. Ideally, well-trained researchers will be collecting the data, but this is not always the case in reality.

Major discrepancies between historic lists and census results are potentially attributable to several causes,

including 1) temporal or seasonal variation in species activity, 2) strays or accidental sightings, 3) misidentifications of the historic list, 4) taxonomic changes, and 5) extinctions. Careful consideration should be given to each of these possible causes before a valid assessment can be made.

Detectability Profile Some species may be observed, but their overall commonness and rarity may differ relative to historic lists. For each species on the list, one can speculate separately why it is under- or over-represented in the survey sites relative to the checklist categorization. General habitat requirements are worth considering first. Is each species given equal probability of being included in a census? For example, the sampling method employed may have selected against certain species. If most surveys are conducted near human structures or roads, the species composition and distribution may differ greatly from results that might be obtained in wild areas. As an example, barn swallows and other birds that nest in buildings might be noted as common if censuses are conducted near buildings, but rare if censuses are conducted in undisturbed sites.

Permanent Versus Migratory Species Some birds are year-round residents, while most are migratory species residing in the park only during the spring and summer. A few butterfly species are also migratory, but the percentage that fall into this category is less than 10%. Changes exhibited by migratory species could be a reaction to conditions on their wintering grounds or migratory pathway. Hence, changes in their abundance and distribution must not automatically be assumed to be a result of changes in Glacier.

Natural Fluctuations Bird populations are not static; they vary in space and time on several scales of resolution. Similarly, lepidopteran populations are known to fluctuate greatly between years. In birds, the variation itself is not smooth and continuous but changes as a function of scale. Analyses of breeding bird habitat occupancy spanning different spatial scales reveal different patterns. Similarly, factors that account for variations in bird community diversity are affected by scale. Temporal variations in population densities at local scales may also complicate the interpretations of bird-habitat associations, especially if populations do not completely saturate the available habitat. Only by recognizing that ecological processes operate with different intensities at different scales of space and time and then attempting to match the

scale of censusing or habitat evaluation with the scale(s) of operation of these processes can we hope to derive a correct understanding of the patterns of nature (Wiens et al. 1986).

Monitoring Many species were detected in only one or two sites in the Glacier survey. If they are not detected in the next year, should the park be concerned? More importantly, if they continue to be detected in only one or two sites, should the park be concerned?

If species A is seen in 10 sites in 1995 and six sites in 1996, what is the probability that it is becoming more vulnerable to extinction (by smaller population size, or fragmentation through local extirpation)? How many times does a decline in the frequency of occurrence in the data correspond to an actual decline in the population? Does frequency of occurrence have any predictive power? If the frequency index has a high level of variance, a decline may be a false alarm while some declines may not be detected in time for action.

How does one discriminate between natural variation and a development-related impact? Bird community density changes have been found to be highly correlated with precipitation, butterflies with precipitation and temperature. By looking for changes not explained by the driving variables (e.g., precipitation), but coincident with

impact events, one can potentially determine the effects attributable to development (Steele et al. 1984).

Describing changes in community structure requires density estimates and thus more extensive data. Comparing species or groups between years within one habitat can be done with simple counts. However, to compare habitats, seasons, or relative abundance of different species, one needs density (enumeration over-estimates conspicuous species in habitats or seasons where detectability is high) (Steele et al. 1984).

Sites of special importance can be identified based upon high species richness or because a certain species absolutely requires it. The variety of habitats necessary to maximize the park species diversity could also be determined. This value would be taxon-specific, however, and all taxa would have to be considered in order to manage the entire ecosystem.

Summary of Sampling Problems If monitoring is to be valuable, sampling must be rigorous enough to allow the researcher to understand the level of background fluctuations in species occurrence. Short term, small-scale inventory projects will not provide statistically viable data with which to discern trends. Rapid assessment may be valuable for detecting hotspots now, but it will not begin to provide information on expected variation in species

distribution. The sampling methodology applied may also influence the type of results obtained. Large areas of critical conservation concern may be glossed over if sampling focuses upon preconceived notions regarding the relationship between habitat type and hotspots.

Biodiversity as an Indicator of Environmental Change

One of the most difficult applications of biodiversity assessment is that of using biodiversity as an indicator of environmental change or ecosystem health. Let's first review the notion of ecological indicators with respect to indicator species. Then the limitations of using biodiversity as an indicator of environmental change will be more apparent.

Indicator Species vs. Indicator Taxa

Indicator species have been pursued for decades as the cost-effective answer to problems of environmental monitoring. For example, aquatic toxicologists have been searching for 30 years to find "the most sensitive species" (Cairns 1986). The idea of using the most sensitive species stems from several assumptions: (1) The response of the indicator species at least partly corresponds to those of a much larger array of exposed organisms in a natural system. (2) There are not significant responses at any level of biological organization that are more sensitive than the

chosen endpoints. (3) Savings are not offset by the costs of making bad decisions. (4) Species shown to be most sensitive to a limited array of toxic substances will invariably be so for a much larger array of toxic substances.

Cairns (1986) argues that these statements are actually myths rather than truth and that "these short-term laboratory tests infer a degree of protection to the environment that is not warranted by the evidence at hand." Morrison (1986) argues that the term "indicator species" has been used too broadly. Simply responding to a change does not make a species a useful indicator. Rather, a clear relationship must be drawn between the response and the causative agent in order to monitor change in a meaningful way. Direct statistical relationships between a species and its environment are necessary to prove that species is a good indicator, and its value as an indicator is specific only to those substances for which a statistical relationship has been determined. Just because a species is a good indicator of acid rain does not mean that it is a good indicator of pesticide contamination or radioactivity.

Granted, there are times when the "most sensitive species" can be identified, and the protection of this species provides an umbrella of protection for the rest of the community. But how often can one species represent an entire community under all circumstances? In essence, it is

difficult to find one organism representative of the entire ecosystem in all situations. The cost-effective argument must be used cautiously because the mitigation dictated by the most sensitive species may serve as overprotection for the remaining species.

In biodiversity assessment, we discard the idea of using indicator species, under the guise that "indicator taxa" will provide a better assay of ecosystem health. In other words, using a diverse group of species representing a wide variety of niches, trophic levels, and tolerances to environmental perturbations allows management decisions to be based on a larger, more thorough set of considerations. Taxa would be chosen as indicators based upon their sensitivity, distribution, or level in the food chain.

However, indicator taxa are simply a collection of indicator species. Certainly, monitoring several species is preferable to monitoring one species. However, as noted above, an indicator is only valuable if its sensitivities are specific and well-understood. Understanding the dynamics of an assemblage of indicators is even more difficult than understanding the dynamics of a single indicator species. For this reason, using biodiversity assessment as an ecological indicator is a challenging task. What kinds of change are we monitoring for? Is it acid rain, global warming, toxic pollution, population viability, or habitat fragmentation? If an indicator responds

similarly to more than one event, it is not a good indicator of a specific event. Each indicator must respond independently and consistently to each specific change.

Therefore, if we want to monitor for a range of environmental changes, we must have several indicators whose dynamics are well understood. Otherwise, we would simply be monitoring species distribution without causally linking it to environmental change. This may be a worthy goal in itself, but it should be distinguished from monitoring for environmental change.

Birds and Butterflies as Indicator Taxa

The two taxonomic groups chosen for this biodiversity assessment, butterflies and birds, are considered to be some of the best indicators available for terrestrial habitats, but even they have their drawbacks.

Morrison (1986) reviews the use of bird populations as indicators of habitat or environmental change. He concludes that birds are poor indicators of specific forest types relative to more direct measurements of vegetation type. Forest types are reflected in bird community structure, but bird communities should not be used to classify forest types. In terms of monitoring human disturbances or natural phenomena, it is difficult to distinguish between a direct response to a changing environment and a secondary effect of that change. Birds cannot be used to indicate that a

specific event is taking place. They indicate that a change has occurred, and the researcher must sort out the many possible causes of the effect. However, birds can be very useful in detecting processes that are not directly visible to the human eye, such as pesticide contamination, or herbicide changes that alter the distribution of insects. Birds tend to be more sensitive to environmental contaminants than other vertebrates. Thus, birds are good indicators of general changes in the environment, but they rarely can serve to provide a direct cause/effect relationship. The researcher must interpret the meanings of population changes with respect to the situation at hand.

Lepidoptera are also highly visible and highly diverse organisms. In the Insecta, butterflies are the most extensively studied taxonomic group and have proven to be particularly sensitive to environmental changes (Weiss and Murphy in press). Because they have narrow host ranges, feeding as larvae on one or just a few plants, they are highly sensitive to urban, agricultural, and industrial expansion that destroys habitat. Wiess and Murphy (in press) argue that most butterflies exist as metapopulations, or "populations of populations." This does emphasize the patchy nature of butterfly distributions, predisposing the taxa to major fluctuations in population size as a result of small climatic changes. Thus, background fluctuations must be known in order to use this taxa as an indicator of

environmental change.

The Relationship Between Diversity and Stability

Changes in species diversity, stability, and biomass have long been used to show the effects of disturbance on biological systems (Cole 1987). However, conflicting conclusions and problems with definitions have left scientists unable to predict the relationship between species diversity and the relative stability if the system. Goodman (1975) critically reviewed the historical literature on species diversity and stability in disturbed systems. From his assessment, species richness or species interactions seem to be a better index of a system's biological diversity than the commonly used Shannnon index. He also noted that this relative stability (in species numbers or persistence) is influenced more by species adaptations to disturbance than by a system's complexity or diversity. More recently, Zaret (1982) reviewed the subject and concluded that the relationship between diversity and stability was still unresolved.

As such, it is important that scientists avoid giving "diversity hotspots" preservation priority until a thorough analysis of species composition has been conducted. Noss (1990a) summarizes this issue nicely: "Obviously integrity is more difficult to quantify than simple concepts such as richness, evenness, and diversity; use of these simpler

measures presents enormous problems related to scale, sample size, and most importantly, lack of consideration of species identity. Who cares if one community is more diverse than another if we know nothing about their species composition? The richer community might be dominated by exotic weeds."

Additional Considerations in Managing for Biodiversity

Given this list of caveats for biodiversity inventory, monitoring, and analysis, what additional information do we need to consider with regard to protecting biodiversity? The following are a few additional considerations to be pursued after the sampling problems have been mitigated.

Sources & Sinks

Diverse habitats were recommended as prime sites for biodiversity inventory and monitoring. There is one caution, however, in data interpretation. Species that are found on the edges of two habitats may depend on a much more extensive area than simply the edge. If one preserves only the small edge site on which a species was found, one may be neglecting a larger adjacent area that is also important. Thus, edge sites cannot be assumed to be independent reservoirs of species diversity. They are largely dependent upon the greater surrounding ecosystem.

Pulliam (1988) offers a valuable lesson in differentiating between sources and sinks in population

regulation. He envisions the spatial distribution of a species in a series of patches, some of which are source populations from which propagules disperse and others which are sink populations into which propagules colonize. It is critically important to determine which patches are sources and which patches are sinks if one is going to preserve a species most effectively. For example, if several patches are protected, but most or all of them happen to be sinks, the population will eventually go extinct because the sources have not been protected.

Distance decay is a spatial concept, similar to diffusion, that occurs at many scales. The distance and density of propagule dispersion from one patch to another may show a distance-decay pattern of diffusion, although heterogeneity and disturbance patterns may alter the coefficients (Meentenmeyer & Box, 1987). For this reason, the spatial configuration of habitat patches, or, at a larger scale, reserves, is critically important in the preservation of both sources and sinks.

Reserve Boundaries

It is widely recognized that nearly all parks and reserves are too small to protect their biological diversity (Schonewald-Cox & Bayless 1986). As such, effectiveness of reserve protection is hypothesized to be more dependent upon what crosses the boundary than on any internal processes

alone. Because the amount of protection varies between the inner and outer boundaries of the reserve, a gradient of densities is often generated. For example, if predators are removed and hunting is prohibited within a reserve, populations of game may be significantly higher within the park. The number of individuals moving across the boundary is influenced by a combination of ecological, microclimatic, geologic or anthropogenic factors. Humans may transport pests and exotics unwittingly or in worse cases, act as poachers. If undesirable species are removed from a reserve, the concentration gradient will go from higher outside to lower inside the reserve, creating a sink within the reserve.

Reserves with small area to perimeter ratios are more exposed, and less buffered from the outside than those with large area to perimeter ratios (Schonewald-Cox & Bayless 1986). They will experience greater impact from edge species and internal changes. Of course, size is always a factor, and larger reserves are preferable.

Thus, even though reserves might be envisioned as islands in a sea of inhospitable terrain, for better or worse, this analogy can be extended only so far. The isolation factor of a reserve is not as drastic as that of an island. Management within a reserve must take into account the actions occurring outside of the reserve.

Summary

Biodiversity assessment, particularly with regard to species diversity assessment, is a task riddled with potential pitfalls, both in sampling and in analysis. Spatial and temporal variations, observer bias, scale and sampling problems must be addressed in establishing the sampling scheme. Detectability, sources and sinks, and reserve boundaries must be considered in analyzing the data. Further, using biodiversity as an ecological indicator can be dangerous if relationships between species occurrence and environmental changes are not well-understood. In essence, if biodiversity assessment is to be done at all, it should be done thoroughly and carefully. Otherwise, it will have neither predictive nor descriptive capabilities.

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APPENDICES

APPENDIX A

DESCRIPTION OF SAMPLE SITES

Appendix A: Description of Census Sites.

Site abbreviation is followed by the name of the 7.5 minute USGS quad upon which it is located and the elevation. The universal transverse mercator northing and easting values are given for the north east corner of square kilometer sites sampled in 1988 and 1989. UTM values of zero indicate that the site was not sampled as a square kilometer.

SITE		QUAD	ELEV (M)	NORTHING	EASTING
1	ANACND .8N	CAMAS RG W	1097	0	0
2	ANACONDA M	CAMAS RG W	1097	0	0
3	APG BIK TR	LK MCDNL W	963	0	0
4	APG LOK TR	MCGEE MEAD	1089	5376	719
5	AVALNCH LK	MT CANNON	1189	5393	294
6	BARING CRK	RISING SUN	1646	5396	308
7	BEAR CREEK	NIMROD	1183	0	0
8	BELLY R RS	GABLE MT	1433	5423	301
9	BELLY R TR	GABLE MT	1539	5428	304
10	BELY CG CA	WATER LK P	1402	0	0
11	BELY COSLY	GABLE MT	1478	0	0
12	BELY TR CG	GABLE MT	1426	5427	303
13	BELY TR MD	GABLE MT	1390	0	0
14	BIG PRARIE	POLEBRIDGE	1122	5412	695
15	BOULDER PS	MT CARTER	2277	5427	712
16	BOWMAN 1.5	POLEBRIDGE	1097	0	0
17	BOWMN L CG	MT CARTER	1228	0	0
18	CAMAS TRAL	CAMAS RG W	1188	0	0
19	CHRISMEADO	CAMAS RG W	1188	5390	719
20	CLEVELD CR	PORCUPN RG	1292	0	0
21	COAL CREEK	DEMERS RIG	1049	0	0
22	DEER LICK	CAMAS RG W	1170	0	0
23	DESANTOS	CANADA	1433	0	0
24	DRY FORK	CUT BNK PS	1585	5376	322
25	DUT CRK NW	CAMAS RG W	1113	0	0
26	DUT CRK SE	CAMAS RG W	1183	0	0
27	FERN CR MD	MCGEE MEAD	1097	0	0
28	FIFTY M SE	AHERN PASS	2111	0	0
29	FIFTY MT	AHERN PASS	2097	5415	290
30	FISH LAKE	LK MCDNL E	1301	5387	289
31	FLTHD FIRE	HUNGRY HOR	1006	0	0
32	FLTHD RGST	HUNGRY HOR	978	5372	716
33	FLTHD RS R	HUNGRY HOR	975	0	0
34	FLTP CG .5	AHERN PASS	1829	5407	291
35	FLTP MT CR	AHERN PASS	1780	0	0
36	FLTP MT LK	AHERN PASS	1902	5409	290
37	FLTP MT RG	AHERN PASS	2088	0	0
38	FNF LOGD 8	DEMERS RIG	1097	0	0
39	GOAT H TRL	PORCUP RDG	1341	0	0
40	GOATH LK T	PORCUP RDG	1279	0	0
41	GOATH RF L	PORCUP RDG	1317	0	0
42	GOATH STBL	PORCUP RDG	1279	0	0

43	GOATHNT RS	PORCUP RDG	1279	5426	288
44	GRANITE PK	AHERN PASS	1975	5405	295
45	GRANITE TR	AHERN PASS	1585	0	0
46	GUNST P TR	LOGAN PASS	1542	5390	301
47	HIDDN LAKE	MT CANNON	1975	5394	297
48	HIDDN MEAD	QUARTZ RDG	1170	5403	703
49	HIDN LK TR	LOGAN PASS	2146	5396	297
50	HIDN LK WS	MT CANNON	1975	0	0
51	HOLE N WAL	MT CARTER	1950	5427	715
52	HOLE TO BR	MT CARTER	1966	0	0
53	I WALTN AC	ESSEX	1143	0	0
54	KOOTENAI L	PORCUPN RG	1341	0	0
55	LINCN PASS	LK MCDNL E	2134	0	0
56	LK ELLEN W	LK MCDNL E	1829	5386	297
57	LK MCDNL W	LK MCDNL W	961	5382	280
58	LOG CR RT7	W GLACIER	1049	0	0
59	LOGAN PASS	LOGAN PASS	2121	5396	299
60	LONE PINE	DEMERS RID	1122	5402	702
61	MCDON CR L	LK MCDON W	957	0	0
62	MCGEE MEAD	MCGEE MEAD	1134	5385	719
63	MED/BIS MT	SQUAW MT	2408	0	0
64	MFF MCDONL	HUNGRY HOR	963	5378	278
65	MFF PAOLA	PINNACLE	1097	0	0
66	MFF SLOAN	HUNGRY HOR	951	0	0
67	MFF W GLAC	W GLACIER	1036	5375	281
68	MIN CRK DN	AHERN PASS	1183	0	0
69	MINERAL CR	AHERN PASS	1158	0	0
70	MOOSE FLAT	MT CANNON	1000	0	0
71	MUD CRK MD	POLEBRIDGE	1122	0	0
72	MUD LAKE	DEMERS RDG	1073	5400	703
73	NAPI LOWER	BABB	1780	5405	319
74	NAPI POINT	BABB	2221	5406	317
75	NFF LANDST	POLEBRIDGE	1097	0	0
76	NFF RIV CG	POLEBRIDGE	1097	0	0
77	PACKRS RST	MT CANNON	1121	5402	295
78	PPINE RT7	CAMAS RG W	1097	0	0
79	PRESTON PK	LOGAN PASS	2170	5398	305
80	QRTR CR BR	MCGEE MEAD	963	0	0
81	QRTZ LK TR	QUARTZ RDG	1295	5411	706
82	QRTZ PA CB	QUARTZ RDG	1243	0	0
83	QUARTZ CG	QUARTZ RDG	1346	5411	710
84	RAINB FALL	PORCUP RDG	1329	0	0
85	ROCKY KNOB	HUNGRY HOR	1012	5374	718
86	ROCKY PNT	LK MCDNL W	969	0	0
87	ROUND PRAR	POLEBRIDGE	1122	5415	693
88	RT8 BURNSC	CAMAS RG W	1085	5389	711
89	RT8 THINPL	DEMERS RDG	1072	0	0
90	S.BOUND TR	W. GLACIER	1113	0	0
91	SACR DANCE	MT CANNON	1000	5391	289
92	SCENIC PT	SQUAW MT	2243	5372	328
93	SIYEH BEND	LOGAN PASS	2194	0	0
94	SIYEH CIRQ	LOGAN PASS	2219	0	0

95	SIYEH PASS	RISING SUN	2362	5399	306
96	SIYEH PS-L	LOGAN PASS	2362	5399	306
97	SIYEH/PIEG	LOGAN PASS	2121	0	0
98	SPERRY DWN	LK MCDNL E	1768	0	0
99	SPERRY TR	LK MCDNL E	1024	5388	288
100	SPOT MT	KIOWA	1835	5376	327
101	ST MARY CG	BABB	1378	0	0
102	ST MARY RS	ST MARY	1414	5402	320
103	STONY I CG	MT CLEVELD	1928	0	0
104	STONY I PS	MT CLEVELD	2105	5418	289
105	STONY I TR	MT CLEVELD	1901	0	0
106	SULLIVAN M	DEMERS RID	1097	5396	708
107	SWAN LAKE	ALBERTA CA	1433	0	0
108	SWIFTCR LK	MANY GLAC	1487	5407	304
109	TWO DOG FL	ST MARY	1414	5398	317
110	TWO MED CG	E GLACIER	1585	0	0
111	WALTN SCAP	ESSEX	1317	0	0
112	WALTON OLE	ESSEX	1219	0	0
113	WALTON RS	ESSEX	1158	5349	306
114	WILBUR CR	MANY GLAC	1707	5410	303

DETAILED CENSUS SITE DESCRIPTIONS

LOCALITY ABBREVIATION IS FOLLOWED BY ITS FULL NAME, HABITAT TYPE & DESCRIPTION. THE KEY TO HABITAT TYPE ABBREVIATIONS IS AS FOLLOWS:

MM - MESIC MEADOW
HM - HYDRIC MEADOW
XM - MEADOW
M - MEADOW
W - WOODLAND
R - RIPARIAN
TR - TRAIL
HA - HIGH ALPINE
A - ALPINE
SA - SUBALPINE
AR - ALPINE/RIPARIAN
D - DISTURBED AREA (I.E. LOGGED, BURNED, ETC.)

1 ANACND .8N - ANACONDA .8 NORTH - (MM) MEADOW 0.8 MILE WEST OF ANACONDA CREEK ON THE INSIDE NORTH FORK ROAD (GLACIER RT 7) ON NORTH SIDE OF THE ROAD. (GNPA009)

2 ANACONDA M - ANACONDA MEADOW - (MM) MEADOW ON EAST SIDE OF ANACONDA CREEK. ACCESSED FROM GLACIER RT 7. LONG MEADOW (0.5 MILE LONG) RUNNING NNE FROM ROAD. (GNPL013)

3 APG BIK TR - APGAR BIKE TRAIL - (W) BIKE TRAIL FROM WEST GLACIER TO APGAR. NARROW, PAVED ROUTE GOES THROUGH LODGEPOLE FOREST WITH LOW GROUND COVER OF HUCKLEBERRIES. VERY OPEN

FOREST. PART OF THIS TRAIL GOES THROUGH BIODIVERSITY PLOT OF MCDONALD CREEK BELOW LAKE MCDONALD. (GNPA035)

4 APG LOK TR - APGAR LOOKOUT TRAIL - (W) TRAILHEAD IS ACCESSED BY CROSSING QUARTER CIRCLE BRIDGE, WHERE MCDONALD CREEK AND THE MIDDLE FORK OF THE FLATHEAD CONVERGE. ACCROSS THE CREEK, FOLLOWING THE FLATHEAD RANGER STATION ROAD, ONE CUTS OFF NORTH TO APGAR LOOKOUT APPROX I MILE PAST THE BRIDGE. THIS TRAIL WAS CENSUSED PRIMARILY AT THE LOWER LEVEL, FROM THE TRAILHEAD UP 1.25 MILES. (GNPA061-064)

5 AVALNCH LK - AVALANCHE LAKE - (W/R) EASY HIKE FROM THE TRAIL OF THE CEDARS UP 2+ MILES TO THE LAKE THROUGH CEDAR/HEMLOCK FOREST TO A GLACIAL LAKE. BIRDS WERE CENSUSED ALONG TRAIL AS WE WALKED UP. (GNPA249)

6 BARING CRK - BARING CREEK (UPPER- VALUE FOR NORTHING) - (HA) ACCESSED FROM THE GOING TO THE SUN ROAD AT SUNRIFT GORGE. TRAIL LEADS UP FROM THE ROAD TO SIYEH PASS. BUTTERFLIES AND BIRDS WERE CENSUSED FROM THE POINT WHERE THE TRAIL LEADS OUT OF THE FOREST PAST A ROCKY OUTCROPPING, AND THEN ABOVE THE OUTCROPPING. CENSUSES AT LOWER POINTS WERE CONDUCTED ON BOTH SIDES OF THE TRAIL. (GNPL240-242)

7 BEAR CREEK - BEAR CREEK - (R) ACCESSED FROM RT2 NEAR NIMROD. THERE IS A BEAR CREEK ACCESS POINT ALONG RT 2. FROM THIS POINT WALK SOUTH ALONG THE EAST SIDE OF THE MIDDLE FORK OF THE FLATHEAD RIVER. THIS SITE IS NOT SO EASY TO CENSUS ON THE GRAVEL BARS, BUT IT DID TURN UP THE ONLY VANESSA ATALANTA IN 1987. IT WAS NOT RECENSUSED IN 1988. (GNPL059-060)

8 BELLY R RS - BELLY RIVER RANGER STATION - (MM) 6 MILE HIKE FROM CHIEF MT. INTERNATIONAL HIGHWAY, MOSTLY DOWNHILL. RANGER STATION ITSELF SITS IN A VALLEY AND THE SURROUNDING PASTURES ARE PRIMARILY VEGETATED WITH TIMOTHY. THIS SITE WAS NOT USED AS A BIODIVERSITY PLOT DUE TO THE POTENTIAL UNNATURAL STATE OF THE PASTURES THE TIMOTHY IS REPORTED TO HAVE BEEN PLANTED THERE HISTORICALLY. (GNPA082-085, GNPL041)

9 BELLY R TR - BELLY RIVER TRAIL - (TR) TRAIL FROM CHIEF MT. INTERNATIONAL HIGHWAY DOWNHILL THROUGH FORESTS AND SMALL MEADOWS. PRIMARILY REFERRED TO THE FIRST 3 MILES. TRAIL CENSUSES TURNED UP NEARLY 20 SPECIES IN 1988. (GNPL018)

10 BELY CG CA - BELLY CAMPGROUND CANADA - (R) CAMPGROUND ON WEST SIDE OF CHIEF MT INTERNATIONAL HIGHWAY, JUST AFTER CANADIAN CUSTOMS STATION. BIRD CENSUSING WAS CONDUCTED BY WALKING THE CIRCULAR DRIVE THAT WINDS AROUND AND WITHIN THE CAMPGROUND. IN 1987, THE ROAD FROM THE CAMPGROUND UP TO THE HIGHWAY AND ACROSS THE HIGHWAY WAS CENSUSED. IN 1988 ONLY THE CAMPGROUND WAS CENSUSED. HABITATS INCLUDE ASPEN GROVES, RIPARIAN SHRUBBY AREAS NEAR THE RIVER, OPEN GRASSLANDS AND

CAMPGROUND ITSELF.

11 BELY COSLY - BELLY RIVER TRAIL AND COSLEY LAKE TRAIL - (W/R) CENSUSED BIRDS FROM RIVER, UPHILL ALONG COSLEY LAKE CUTOFF TRAIL FOR APPROX. 1 MILE. HABITATS INCLUDED RIPARIAN, OPEN HILLSIDES, AND DENSE FORESTS. (GNPA084-085)

12 BELY TR CG - BELLY RIVER TRAIL CAMPGROUND - (MM) ACCESSED FROM CHIEF MT INTERNATIONAL HIGHWAY, APPROX. 3 MILES DOWN THE HILL. CAMPGROUND IS VERY CLOSE TO BELLY RIVER. BUTTERFLIES WERE CENSUSED IN THE LARGE MEADOWS JUST NORTH OF THE CAMPGROUND. TOWARDS THE LATTER PART OF THE SUMMER, THESE MEADOWS ARE PRIMARILY COVERED WITH TIMOTHY. IN 1988, A VERY LARGE ORANGE SPEYERIA WAS CAUGHT, BUT IT ESCAPED BEFORE IT COULD BE IDENTIFIED. IT MAY HAVE BEEN AN CYBELE, BUT IT SEEMED TOO LIGHT COLORED. (GNPL275-277)

13 BELY TR MD - BELLY RIVER TRAIL MEADOW - (MM) REFERS TO SMALL MEADOWS AT APPROX 1.5+ MILES FROM CHIEF MT INTERNATIONAL HIGHWAY WHICH LIE ON EITHER SIDE OF THE TRAIL. THESE MEADOWS WERE CENSUSED FOR BUTTERFLIES EXTENSIVELY IN 1987. (GNPL019)

14 BIG PRARIE - BIG PRAIRIE - (XM) THIS SAGEBRUSH PRAIRIE IS SEVERAL MILES LONG, AND ACCESSED FROM GLACIER RT 7. THE AREA WE CENSUSED LIES ON THE WEST SIDE OF THE ROAD AT THE CANOE ACCESS TURNOFF. THIS SITE IS JUST NORTH OF A LANDING STRIP ON THE OPPOSITE SIDE OF THE RIVER. THE SPECIES DIVERSITY OF BUTTERFLIES TENDS TO BE LOW, AS THE AREA IS VERY DRY. (GNPA039, GNPL009)

15 BOULDER PS - BOULDER PASS - (HA) CENSUSED IN 1988 FROM CAMPGROUND, ALONG PASS TO OVERLOOK. THERE ARE SEVERAL SEASONAL PONDS AND WILDFLOWERS ABOUND. UNFORTUNATELY, WE ARRIVED TOO LATE IN THE AFTERNOON TO GET GOOD RESULTS FROM A CENSUS (BUTTERFLIES). (GNPL303)

16 BOWMAN 1.5 - BOWMAN 1.5 -(HM) EARLY STAGE SUCCESSIONAL MEADOW WITH THICK GRASSES AND HIGH WATER CONTENT. ACCESSED FROM THE BOWMAN LAKE ROAD, JUST 1.5 MILES FROM THE TURNOFF FROM GLACIER RT 7. A CHAINED DRIVEWAY CUTS OFF TO THE LEFT, AND THE TRAIL TO THIS MEADOW CUTS OFF TO THE RIGHT OF THIS DRIVEWAY JUST PRIOR TO ARRIVING AT A DUMP SITE. THE TRAIL PASSES AN OLD BUILDING WITH A SIGN "DANGER EXPLOSIVES", THEN OPENS UP INTO THIS MEADOW. ONE CAN BARELY WALK THROUGH THE MEADOW BECAUSE OF THE GRASSES AND THE WET GROUND, BUT THE EDGES ARE MANEUVERABLE. (GNPL028)

17 BOWMN L CG - BOWMAN LAKE CAMPGROUND - (R) AREA CENSUSED FOR BIRDS IN 1987.

18 CAMAS TRAL - CAMAS TRAIL - (TR) WOODED TRAIL FROM GLACIER RT7 TO CHRISTENSEN MEADOW. USUALLY WELL SUNLIT, AND THE

PUDDLE AREA USUALLY SUPPORTS MANY BUTTERFLY SPECIES. (GNPL008)

19 CHRISMEADO - CHRISTENSEN MEADOW - (MM) LARGE MESIC MEADOW (ESPECIALLY WET IN THE SPRING) ACCESSABLE FROM GLACIER RT 7. MEADOW SITS APPROX. 1/4 MILE NE OF ROAD. CENSUSED AREA IS THE FIRST LARGE MEADOW FROM THE ROAD, PRIMARILY CENSUSED ON THE NORTHWEST SIDE OF THE CREEK. (GNPL001-004 GNPA001-003)

20 CLEVELD CR - CLEVELAND CREEK - (R) CENSUSED SMALL MEADOW ALONG CLEVELAND CREEK AT POINT WHERE TRAIL FROM GOATHAUNT CROSSES CREEK AS ONE TRAVELS SOUTHWARD. (GNPL040)

21 COAL CREEK - COAL CREEK - (R) FROM THE NORTH FORK ROAD, THIS RIPARIAN AREA IS ON THE EAST SIDE OF THE ROAD AND ON THE SOUTH SIDE OF COAL CREEK. THE PLOT EXTENDS FROM THE ROAD TO THE CONFLUENCE WITH THE NORTH FORK OF THE FLATHEAD RIVER. (GNPL083)

22 DEER LICK - DEER LICK MEADOW - (MM) SMALL MEADOW THAT EXTENDS ON BOTH SIDES OF GLACIER RT 7, JUST APPROXIMATELY 1 MILE NORTHWEST OF THE DUTCH CREEK CROSSING. THE MEADOW WAS GIVEN THIS NAME BECAUSE OF A SALT LICK THAT CONTINUALLY SUPPORTS A DEER POPULATION. THE BUTTERFLIES APPARENTLY ALSO LIKE THE SALT LICK. (GNPL014)

23 DESANTOS - DESANTOS - (MM) JERRY DESANTOS PROPERTY ON LEE CREEK IN ALBERTA, CA, JUST NORTH OF GLACIER NATIONAL PARK.

24 DRY FORK - DRY FORK - (TR) DRY FORK TRAIL WAS CENSUSED AS TRAIL CENSUS APPROXIMATELY BETWEEN 4 AND 3 MILES EAST OF OLDMAN LAKE IN THE OPEN ALPINE AREA. THERE WERE SEVERAL DRAINAGES VEGETATED WITH HEARTLEAFED ARNICA ABOVE THE TRAIL WHERE THE BUTTERFLIES WERE PLENTIFUL. (GNPL212)

25 DUT CRK NW - DUTCH CREEK NORTHWEST - (MM) MEADOW .5MILES + NORTHWEST OF DUTCH CREEK ON GLACIER RT 7. SMALL IN SIZE - APPROXIMATELY 1/8 MILE WIDE. (GNPL014)

26 DUT CRK SE - DUTCH CREEK SOUTHEAST - (MM) MEADOW JUST SHORT OF 1 MILE SE OF DUTCH CREEK ON GLACIER RT 7, ON THE NORTHEAST SIDE OF THE ROAD SMALL IN SIZE, APPROX. .25 MILES WIDE (GNPL015)

27 FERN CR MD - FERN CREEK MEADOW - (MM) BARELY LARGE ENOUGH TO BE CALLED A MEADOW, THIS 1 ACRE + PLOT IS A CLEARING ON THE EAST SIDE OF GLACIER RT 8 JUST 1/2 MILE SOUTH OF THE POINT WHERE FERN CREEK CROSSES THE ROAD. IT OFTEN HARBORS MANY WILDFLOWERS, SO IT WAS CENSUSED, BUT NOT AS A BIODIVERSITY PLOT DUE TO ITS SMALL SIZE. (GNPL077)

28 FIFTY M SE - FIFTY MOUNTAIN SOUTHEAST - (HA) WALKING NORTH FROM 50 MT CAMPGROUND, THE TRAIL CURVES WESTWARD. THE AREA

CENSUSED IS FOUND BY TRAVELING EASTWARD AND UPHILL APPROX 0.5 MILES TOWARDS THE CONTINENTAL DIVIDE LINE. (GNPL051)

29 FIFTY MT - FIFTY MOUNTAIN - (HA) SAME AS 50 MT NW - CENSUSED AREA NORTHWEST OF TRAIL HEADING NORTH FROM CAMPSITE, AND WESTWARD ALONG TRAIL. BUTTERFLIES SEEM ESPECIALLY DENSE NEAR AND ALONG DRAINAGES. THIS SITE IS NOT EASILY ACCESSIBLE DUE TO THE DISTANCE FROM THE ROAD, AND THE WEATHER IS OFTEN BAD FOR BUTTERFLY CENSUSING ONCE WE ARRIVE THERE. IF HIKED TO IN ONE DAY FROM PACKERS ROOST, ONE CAN ARRIVE BEFORE 4 PM, LEAVING THE ROOST BY 8:30 A.M. OR SO. (GNPL050)

30 FISH LAKE - FISH LAKE - (R) SMALL LAKE APPROX 2+ MILES UP SPERRY TRAIL. NORTH SIDE OF LAKE IS A BOG WITH TWO SPECIES OF SUNDEWS AND ORCHID-LIKE FLOWERS. AREA IS WOODED AND SUPPORTS SEVERAL SPECIES OF DUCKS INCLUDING GOLDEN EYES. A MOOSE WAS SEEN AT THIS SITE IN 1988. (GNPA016)

31 FLTHD FIRE - FLATHEAD FIRE - (D) FLATHEAD RANGER STATION ROAD APPROXIMATELY 1 MILE NORTHEAST FROM THE RANGER STATION. WOODLAND CLEARING IN LODGEPOLE PINE AREA THAT HAS BEEN BURNED, POSSIBLY AFTER LOGGING. CENSUSED FOR BIRDS GNPA079 AND BUTTERFLIES GNPL029. HIGH INFESTATION OF MOSQUITOES.

32 FLTHD RGST - FLATHEAD RANGER STATION - (W) SITUATED AT THE CONFLUENCE OF THE MIDDLE FORK AND NORTH FORK OF THE FLATHEAD RIVER ON A BLUFF ABOVE THE RIVER. ACCESSED BY A NATIONAL FOREST ROAD THAT LEADS SOUTHWEST FROM QUARTER CIRCLE BRIDGE. (GNPL030, GNPA080)

33 FLTHD RS R - FLATHEAD RANGER STATION ROAD - (W) FLATHEAD NATIONAL FOREST ROAD LEADS SOUTHWEST FROM QUARTER CIRCLE BRIDGE AT THE CONFLUENCE OF THE MIDDLE FORK OF THE FLATHEAD RIVER AND MCDONALD CREEK. THIS ROAD WAS CENSUSED AT VARIOUS POINTS FOR BUTTERFLIES AND BIRDS. THE HEAVY HORSE TRAFFIC CREATES HIGH CONCENTRATIONS OF BUTTERFLIES AROUND THE HORSE MANURE.

34 FLTP CG .5 - FLATTOP CAMPGROUND .5 MILES N - (HA) SMALL, NARROW MEADOW ALONG TRAIL 0.5 MILES NORTH OF FLATTOP MOUNTAIN CAMPGROUND ON FLATTOP MT TRAIL. (GNPL049, GNPA092)

35 FLTP MT CR - FLATTOP MOUNTAIN CREEK - (AR) CREEK THAT FOLLOWS FLATTOP MOUNTAIN TRAIL UP THE HILL FROM MINERAL CREEK TO FLATTOP MOUNTAIN CAMPGROUND. BIRDS WERE CENSUSED ALONG THE TRAIL FROM THE CAMPGROUND DOWN TO MINERAL CREEK. SEVERAL WARBLERS INHABIT THE SHRUBBY FOLIAGE ALONG THE TRAIL. (GNPA091-098)

36 FLTP MT LK - FLATTOP LAKE SOUTH, ALSO FLATTIP MT - (AR) INTERMITTENT LAKE ON FLATTOP MOUNTAIN RIDGE ALONG FLATTOP MOUNTAIN TRAIL, APPROXIMATELY 1.5 MILES NORTH WEST FROM

FLATTOP MT CAMPGROUND. THE TRAIL OPENS UP INTO A LARGE MEADOW ON BOTH SIDES. (GNPL046-047, GNPA094,095)

37 FLTP MT RG - FLATTOP MOUNTAIN RIDGE - (HA) AREA ON FLATTOP MOUNTAIN TRAIL APPROX 1.5 MILES NORTH OF FLATTOP MT CAMPGROUND WHERE RIDGE OFFERS A VIEW ACROSS VALLEY TO THE HIGHLINE TRAIL AND 50 MT AREA. THIS OPEN AREA SUPPORTS MANY WILDFLOWERS AND WAS CENSUSED IN TWO PLACES FOR BUTTERFLIES. FINDINGS WERE SLIM AT THE TIME, DESPITE A LACK OF WIND AND A MODERATE COVERING OF WILDFLOWERS SUCH AS ASTER AND YELLOW COMPOSITES. (GNPL052-053)

38 FNF LOGD 8 - FLATHEAD NATIONAL FOREST LOGGED SITE - (D) APPROXIMATELY 2+ MILES FROM THE INTERSECTION OF GLACIER RT 8, FOLLOWING THE NORTH FORK ROAD NORTHWARD THERE IS A SMALL CLEARCUT AREA ON THE WEST SIDE OF THE ROAD (PROBABLY LESS THAN 20 ACRES). THIS AREA WAS CENSUSED FOR BUTTERFLIES, BUT RUNNING WAS DIFFICULT DUE TO THE SLASH PILED ON THE GROUND. (GNPL082)

39 GOAT H TRL - GOATHAUNT TRAIL - (W) TRAIL FROM GOATHAUNT RANGER STATION TO KOOTENAI LAKES AND BEYOND TOWARDS STONEY INDIAN PASS. THIS DENSELY WOODED AREA HAS BEEN CENSUSED ON THE NORTHERN END FOR BIRDS FOR APPROX 3 MILES IN 1987, AND FOR BUTTERFLIES AT THE SOUTHERN END IN 1987 FOR APPROX 3 MILES. BUTTERFLY CENSUSES BEGAN WHERE TRAIL OPENED UP OUT OF THE FOREST AND CONTINUED TO THE STONEY INDIAN CAMPGROUND. (GNPA081)

40 GOATH LK T - GOATHAUNT LAKE TRAIL - (R) TRAIL FROM VISITOR CENTER TO RANGER STATION AND ALONG LAKE, THEN SOUTH TO CLEVELAND CREEK. THIS AREA WAS CENSUSED FOR BUTTERFLIES IN 1988 AND BIRDS IN 1987. (GNPA090)

41 GOATH RF L - GOATHAUNT RAINBOWFALLS LAKE - (R) SMALL LAKE ON EAST SIDE OF TRAIL TO RAINBOW FALLS. THIS SPOT WAS CENSUSED FOR BIRDS IN 1987. (GNPA088)

42 GOATH STBL - GOATHAUNT STABLE - (D) STABLE AREA WEST OF RANGER STATION. WAS CENSUSED IN 1987 FOR BIRDS. (GNPA086)

43 GOATHNT RS - GOATHAUNT RANGER STATION - (R) BIRDS WERE CENSUSED BY MARY MCFADSEN IN 1987 AS SHE WATCHED THE BALD EAGLE NEST ON THE LAKE. BUTTERFLIES WERE CENSUSED IN THIS AREA IN 1988. (GNPA090)

44 GRANITE PK - GRANITE PARK - (HA) SET UP AS A BIODIVERSITY SITE IN 1988, THE AREA DIRECTLY WEST OF THE CHALET WAS CENSUSED FOR BUTTERFLIES AND BIRDS. IT INCLUDES AN OPEN AREA BETWEEN THE CHALET AND THE TRAIL CREW CABIN THAT IS OPEN WITH MANY ROCKY OUTCROPS. THIS AREA COULD NOT BE CENUSED IN 1987 DUE TO BAD WEATHER.

45 GRANITE TR - GRANITE TRAIL - (TR) BUTTERFLIES WERE OFTEN CENSUSED FROM THE LOOP, UP TO GRANITE PARK ALONG THE TRAIL, AS THE WEATHER AT THE PARK ITSELF WAS OFTEN UNPREDICTABLE. THESE CENSUSES OFTEN TURNED UP NEAR 15 SPECIES. (GNPL081)

46 GUNST P TR - GUNSIGHT PASS TRAIL - (TR) CENSUSED BUTTERFLIES FROM 1/2 MILE SOUTHWEST OF FLORENCE FALLS (STARTING AT GOING TO THE SUN ROAD NEAR JACKSON GLACIER OVERLOOK). CENSUS CONTINUED UPHILL ALONG TRAIL UNTIL 1/2 MILE PRIOR TO GUNSIGHT LAKE WHERE TRAIL BECAME DARKER AND THICKER WITH WILLOWS. (GNPL070)

47 HIDDN LAKE - HIDDEN LAKE - (HA) SAME AS HIDN LK ES (HIDDEN LAKE EAST SHORE) IN 1987 CENSUS. STEEP SLOPES OVER NORTHEAST SIDE OF HIDDEN LAKE. USUALLY FULL OF WILDFLOWERS, THIS AREA SUPPORTS MANY BUTTERFLY SPECIES CENSUSING HAS BEEN CONDUCTED QUITE FAR UP THE SLOPES BELOW ROCK OUTCROPPINGS, SO THE MANEUVERING IS NOT ALWAYS EASY. CENSUSING IS USUALLY STARTED FROM A EASTWARD LOOP OF THE TRAIL FROM THE HIDDEN LAKE PASS DOWN TO THE LAKE. (GNPL066-067)

48 HIDDN MEAD - HIDDEN MEADOW - (MM) APPROXIMATELY 1.5 MILES NORTHEAST OF GLACIER RT 7 AT LONE PINE PRAIRIE IS HIDDEN MEADOW. IT IS ACCESSED BY AN OLD, OVERGROWN TRAIL THAT STARTS FROM TWO POSTS ON THE EAST SIDE OF THE ROAD, AND IS RELATIVELY EASY TO FOLLOW. THE AREA WE CHOSE TO CENSUS IS ON THE EAST SIDE OF HIDDEN MEADOW LAKE, AT THE SITE OF AN OLD HOMESTEAD. THIS AREA WAS CENSUSED FOR BUTTERFLIES. BIRDS WERE CENSUSED FROM AN ASPEN GROVE ALONG THE TRAIL WHERE THREE-TOED WOODPECKERS WERE KNOWN TO HAVE NESTED IN YEARS PAST (ACCORDING TO BOWMAN BOB), AND THE CENSUS CONTINUED TO THE LAKE AREA. A SUCCESSIONAL MEADOW WITH MANY SNAGS WAS ALSO CENUSED IN 1988 THIS AREA IS SOUTH OF THE HIDDEN MEADOW LAKE AREA.

49 HIDN LK TR - HIDDEN LAKE TRAIL - (TR) SAME AS HIDN LK OV (HIDDEN LAKE OVERLOOK) IN 1987 CENSUS - BUTTERFLIES ARE OFTEN COLLECTED ALONG THE TRAIL TO HIDDEN LAKE. MANY SPECIES OF LYCEANA RESIDE HERE AMONG THE TALLUS AND WILDFLOWERS

50 HIDN LK WS - HIDDEN LAKE WEST SHORE - (HA) ACTUALLY SOUTHWEST SHORE. OPPOSITE SIDE FROM TRAIL WHERE LARGE BOULDER FIELD IS INTERSPERSED WITH ALPINE FLOWERS. VERY FEW BUTTERFLIES WERE PRESENT ON THE ONE CENSUS. (GNPL068)

51 HOLE N WAL - HOLE IN THE WALL - (HA) THIS AREA WAS UNSUCCESSFULLY CENSUSED FOR BUTTERFLIES IN 1988 DUE TO CLOUDINESS.

52 HOLE TO BR - HOLE IN THE WALL TO BROWN PASS - (TR) THIS TERRAIN WAS CENSUSED IN 1987 AS A TRAIL CENSUS FROM HOLE IN THE WALL TO BROWN PASS. (GNPL078)

53 I WALTN AC - ISSAC WALTON RIVER ACCESS POINT - (R) THIS RIVER BANK WAS CENSUSED IN 1987 FOR BUTTERFLIES ALONG THE COBBLES. FOOTING WAS NOT ALWAYS GOOD. (GNPL061)

54 KOOTENAI L - KOOTENAI LAKE - (R) THIS AREA WAS CENSUSED IN 1987 FOR BUTTERFLIES, BUT WAS NOT REPLICATED IN 1988. (GNPL039)

55 LINCN PASS - LINCOLN PASS - (HA) TRAIL CENSUS FOR BUTTERFLIES FROM 3/4 MILES PRIOR TO PASS TO THE PASS ITSELF, COMING FROM LAKE ELLEN WILSON, AND TRAVELLING WEST. OPEN SCREE SLOPES WITH A FEW ALPINE FLOWERS SUPPORTED MANY SPECIES OF BUTTERFLIES. (GNPL072)

56 LK ELLEN W - LAKE ELLEN WILSON - (HA) ALPINE LAKE JUST BELOW GUNSIGHT PASS. KRUMHOLTZ AND LARGE BOULDERS CHARACTERIZE THIS AREA. GROUND COVER OF GRASSES AND WILDFLOWERS CAN BE QUITE THICK NEAR THE LAKE, BUT DIMINISHES OUT AS ONE WALKS BACK UP TO THE TRAIL. (GNPA115-116, GNPL071 (TRAIL CENSUS))

57 LK MCDNL W - LAKE MCDONALD WEST SHORE - (W/R) TRAIL FOLLOWS LAKE SHORE FROM FISH CREEK CAMPGROUND, NORTHEAST TO ROCKY POINT, APPROX. 2 MILES. BIODIVERSITY QUAD IS JUST 0.5 MILES NE FROM CAMPGROUND. (GNPA017-021)

58 LOG CR RT7 - LOGGING CREEK AT GLACIER RT 7 - (R) THIS AREA WAS CENSUSED FOR BIRDS IN 1987.

59 LOGAN PASS - LOGAN PASS - (HA) BIRDS ARE CENSUSED FROM VISITOR CENTER UP TO HIDDEN LAKE OVERLOOK WHILE BUTTERFLIES ARE CENSUSED ON THE OPPOSITE SIDE OF THE PASS. BUTTERFLIES HAVE BEEN CENSUSED ALONG THE TRAIL FROM HIDDEN LAKE PASS TO THE LAKE, AS WELL AS ON THE SLOPES ON THE EAST SIDE OF THE LAKE (SEE HIDDN LK) (GNPA036-037)

60 LONE PINE - LONE PINE PRAIRIE - (MM) ACCESSED FROM GLACIER RT 7 NORTH OF MUD LAKE. CENSUSED AREA IS ON THE SOUTHWEST SIDE OF THE ROAD. PRAIRIE IS A MESIC MEADOW WITH THICK UMBELLIFORMS TOWARDS THE WEST END. (GNPL007, GNPA040)

61 MCDON CR L - MCDONALD CREEK, LOWER (BELOW LAKE MCDONALD) - (R) CANOED FROM LAKE MCDONALD TO QUARTER CIRCLE BRIDGE, SLOWLY CENSUSING BIRDS ALONG THE WAY. MANY SHRUBS AND WILLOWS ALONG THE WAY HARBOR LITTLE WARBLERS. (GNPA069-072)

62 MCGEE MEAD - MCGEE MEADOW - (HM) THIS LARGE HYDRIC MEADOW IS ACCESSABLE FROM BOTH GLACIER RT 7 AND GLACIER RT 8. THE LARGER PORTION OF THE MEADOW IS ACCESSED AT A MEADOW OVERLOOK ON GLACIER RT 8. VERY WET, IT IS CENSUSED PRIMARILY AT THE EDGES FOR BOTH BIRDS AND BUTTERFLIES. BUTTERFLIES TEND TO PUDDLE IN THE ENTRANCE AREA FROM RT 8 ALONG THE TRAIL. MANY PAPILIO SPECIES AND BOLORIAS WERE FOUND THERE. (GNPL074-076)

63 MED/BIS MT - MEDICINE/BISON MT - (HA) THE PASS AREA BETEEN THESE TWO MOUNTAINS WAS CENSUSED, AS WAS THE TOP OF MEDICINE MOUNTAIN ITSELF, FOR BUTTERFLIES IN 1987. (GNPL 022)

64 MFF MCDONL - MIDDLE FORK OF THE FLATHEAD AT MCDONLD CREEK - (R) RIPARIAN AREA AT QUARTER CIRCLE BRIDGE WHERE LOWER MCDONALD CREEK MEETS THE MIDDLE FORK OF THE FLATHEAD RIVER. WARBLERS ARE ABUNDANT IN THIS AREA BECAUSE OF THE THICKETS AND WILLOWS ALONG THE RIVER. (GNPA074-075)

65 MFF PAOLA - MIDDLE FORK OF THE FLATHEAD RIVER AT THE PAOLA ACCESS POINT FROM RT 2 - (R) BUTTERFLIES WERE CENSUSED ALONG THE RIPARIAN AREA ALONG THE RIVER, BOTH UP RIVER AND DOWNRIVER ALONG SANDBARS. CENSUSING AREAS WERE INTERMITTENTLY SPACED AND DIFFICULT TO RUN ALONG BECAUSE OF ALL THE PEBBLES AND ROCKS. (GNPL057)

66 MFF SLOAN - MIDDLE FORK OF THE FLATHEAD NEAR SLOAN RANCH - (R) CENSUSED BIRDS ALONG RIVERS EDGE AND BUTTERFLIES ALONG THIS AREA ON COBBLY RIVERSIDES AND ISLANDS. (GNPL063)

67 MFF W GLAC - MIDDLE FORK OF THE FLATHEAD AT WEST GLACIER - (R) RIPARIAN AREA FROM WEST GLACIER RESIDENTIAL AREA DOWNRIVER (WEST) APPROXIMATELY ONE MILE AND UPRIVER ALONG BOUNDARY TRAIL TWO MILES (BIRD SURVEYS). BUTTERFLY SURVESYS ARE CONDUCTED BOTH ALONG THE OPEN AREAS EAST FROM WEST GLACIER, OVER OLD BRIDGE, PAST CAMPING AREA TO RAILROAD TRACKS. ON THE NORTH SIDE OF THE RIVER, BUTTERFLIES WERE ALSO CENSUSED IN THE SMALL SHRUBBY MEADOW THAT IS SITUATED EAST ALONG THE TRAIL JUST BEYOND THE OLD BRIDGE. (GNPL231, GNPA031-033, GNPA057-060)

68 MIN CRK DN - MINERAL CREEK DOWN - (TR) FROM MINERAL CREEK TO PACKER'S ROOST. THIS TRAIL WAS CENSUSED FOR BUTTERFLIES WHILE HIKING DOWN FROM FLATTOP MOUNTAIN. (GNPL054)

69 MINERAL CR - MINERAL CREEK - (R) CENSUSED FOR BIRDS JUST EAST OF BRIDGE ON MCDONALD CREEK TRAIL COMING DOWN FROM FLATTOP MOUNTAIN TRAIL. COULD NOT CENSUS EASILY AT THE CREEK ITSELF DUE TO THE NOISE LEVEL OF THE WATER. (GNPA102)

70 MOOSE FLAT - MOOSE FLAT - (R) MOOSE HABITAT NEAR SACRED DANCING CASCADES TRAIL ABOVE THE FALLS. CENSUSED FOR BIRDS.

71 MUD CRK MD - MUD CREEK MEADOW - (HM) WE USED THIS NAME FOR A HYDRIC MEADOW ON THE EAST SIDE OF GLACIER RT 7 JUST SOUTH OF MUD CREEK CAMPGROUND BY APPROX 1/4 MILE. THIS MEADOW IS INTERSPERSED WITH WILLOWS AND OTHER SHRUBS AND SUPPORTS A HIGH DIVERSITY OF BIRDS AND BUTTERFLIES. (GNPL011)

72 MUD LAKE - MUD LAKE - (R) ACCESSED FROM GLACIER RT 7 ABOVE QUARTZ CREEK CAMPGROUND (APPROX 1 MILE) IF TRAVELLING NORTHWEST. LAKE IS ON WEST SIDE OF ROAD. LOONS, WHITE-WINGED

CROSSBILLS AND WARBLERS ARE COMMON THERE. SHORE IS VERY NARROW AND A LIMITED AMOUNT OF AREA IS AVAILABLE FOR CENSUSING. CANOE IS PREFERRED TO HIKING. (GNPA041)

73 NAPI LOWER - NAPI LOWER - (MM) OPEN MEADOW PATCH AT BASE OF NAPI POINT JUST PRIOR TO THE FORK IN THE TRAIL AS ONE TRAVELS DOWN FROM THE POINT. APPROXIMATELY 3 MILES FROM GLACIER RT 3. AN WOODEN OLD BEAR TRAP IS A LANDMARK. (GNPL208)

74 NAPI POINT - NAPI POINT - (HA) CENSUSED THE POINT AREA FOR BUTTERFLIES EARLY IN 1988. SAXIFRAGE AND MANY OTHER LOW ALPINE FLOWERS WERE SCATTERED AROUND THE AREA. THE INTERMITTENT SUN WAS A PROBLEM, HOWEVER IN OBTAINING A GOOD CENSUS. LATER WE FOUND OUT THAT ACCESS WAS LIMITED (BLACKFOOT PROPERTY), SO NOT RECENSUSED. (GNPL207)

75 NFF LANDST - NORTH FORK OF THE FLATHEAD LANDING STRIP - (D) ON WEST SIDE OF THE RIVER ACROSS FROM BIG PRAIRIE IS A SMALL LANDING STRIP. WE ACCESSED THIS AREA FOR BUTTERFLY CENSUSING IN 1987 VIA CANOE. (GNPL079)

76 NFF RIV CG - NORTH FORK OF THE FLATHEAD AT RIVER CAMPGROUND -(XM) THIS AREA WAS CENSUSED FOR BUTTERFLIES IN 1987 ALONG THE GRAVEL BAR ON THE WEST SIDE OF THE RIVER. ACCESSED VIA CANOE. (GNPL080)

77 PACKRS RST - PACKERS ROOST - (W) JUST PRIOR TO THE LOOP IN THE GOING TO THE SUN ROAD, THERE IS A TURN-OFF TO THE WEST THAT LEADS ONE TO PACKER'S ROOST. THIS TRAIL WAS CENSUSED FOR BIRDS AS A BIODIVERSITY QUAD IN 1987 AND 1988. THE DENSE WOODLAND SUPPORTS A WIDE VARIETY OF WARBLERS AND THRUSHES. QUALITATIVE BUTTERFLY SAMPLING (I.E. TRAIL CENSUSING) IS SOMETIMES CONDUCTED ON THE WAY DOWN FROM FLATTOP MOUNTAIN. (GNPA005-007)

78 PPINE RT7 - PONDEROSA PINE STAND ON RT 7 - (W) NORTH FORK INSIDE ROAD, PONDEROSA PINE STAND, 0.8 MILES NORTHWEST OF ANACONDA CREEK. (GNPA009)

79 PRESTON PK - PRESTON PARK - (SA) PARK AREA BELOW SIYEH PASS. THIS AREA WAS CENSUSED IN SEVERAL AREAS IN BOTH 1987 AND 1988. A BIODIVERSITY SITE WAS CREATED THAT INCLUDES 3 MEADOW AREAS ON THE SOUTHWEST SIDE OF THE EASTMOST CREEK CROSSING THE TRAIL. THE FIRST MEADOW FROM THE ROAD IS A SITE WITH A SHALLOW POND ON THE SOUTHEAST SIDE OF THE TRAIL. THE LAST MEADOW INCLUDES THE STREAM CROSSING. THE AREA CENSUSED IS ON THE SOUTH SIDE OF THE TRAIL. (GNPL 034, 036, 037)

80 QRTR CR BR - QUARTER CIRCLE BRIDGE - (R) A WOODEN ARCHED BRIDGE THAT CROSSES OVER MCDONALD CREEK JUST PRIOR TO THE CONFLUENCE WITH THE MIDDLE FORK OF THE FLATHEAD RIVER. ITS

SURROUNDING SHRUBS, WILLOWS, AND THICKETS PROVIDE EXCELLENT WARBLER HABITAT. (GNPA034)

81 QRTZ LK TR - QUARTZ LAKE TRAIL - (TR) WEST LAKES TRAIL FROM BOWMAN LAKE THROUGH DENSE FOREST, ALONG SWITCHBACKS, UP TO TOP OF RIDGE. THIS AREA WAS CENSUSED BY STOPPING EVERY 300 METERS AT 5 POINTS IN 1987. (GNPA022-026)

82 QRTZ PA CB - QUARTZ LAKE PATROL CABIN - SHOULD BE INCORPORATED INTO QUARTZ LAKE TRAIL CENSUS.

83 QUARTZ CG - QUARTZ LAKE - (R) CENSUSED BIRDS AT QUARTZ LAKE FROM A CANOE AT FOUR POINTS IN 1987. THESE INCLUDED THE NORTH SHORE, THE CAMPSITE, THE LOGJAM AREA, AND ANOTHER SOUTH SHORE SITE FURTHER EAST FROM THE LOGJAM. (GNPA065-068)

84 RAINB FALL - RAINBOW FALLS - (R) SMALL FALLS ACCESSED FROM GOATHAUNT RANGER STATION. BIRDS WERE CENSUSED FROM THE RIDGE ABOVE THE FALLS ON RAINBOW FALLS TRAIL IN 1987. ACTIVITY WAS LOW AT THE TIME. (GNPA089)

85 ROCKY KNOB - ROCKY KNOB - (XM) ROCKY OUTCROPPING ALONG FLATHEAD RANGER STATION ROAD, APPROX 2 MILES SW OF QUARTER CIRCLE BRIDGE, OR 1.25 MILES NE OF THE FLATHEAD RANGER STATION. THIS OUTCROPPING AFFORDS A WONDERFUL VIEW OF THE MIDDLE FORK OF THE FLATHEAD RIVER AS IT GOES THROUGH A ROCKY GORGE BELOW. THE BIODIVERSITY QUAD INCLUDES THE HILLSIDE ON THE OPPOSITE SIDE OF THE ROAD AS WELL. THIS AREA IS FULL OF DOGBANE AND INTERMITTENTLY FORESTED DUE TO THE ROCKINESS. IT IS ALSO A HIGH POINT ON THE ROAD. (GNPL029, GNPA079)

86 ROCKY PNT - ROCKY POINT - (XM) WALKING NORTH FROM FISH CREEK CAMPGROUND ALONG THE TRAIL THAT FOLLOWS LAKE MCDONALD'S SHORE, ONE ARRIVES AT ROCKY POINT, A SMALL POINT THAT PROTRUDES INTO LAKE MCDONALD, OFFERING A SPLENDID VIEW. BIRD CENUSING WAS CONDUCTED HERE JUST BEYOND THE LAKE MCDONALD WEST BIODIVERSITY SITE.

87 ROUND PRAR - ROUND PRAIRIE - (XM) LARGE SAGEBRUSH MEADOW ACCESSED FROM THE NORTH FORK ROAD, GLACIER RT 7. THE PRAIRIE LIES ON BOTH SIDES OF THE ROAD, ALMOST 1/4 SQUARE MILE IN SIZE. IT IS USUALLY ACCESSED FROM THE SMALL TURNOFF THAT CUTS NORTHWEST, USED FOR RIVER ACCESS. THIS DRY MEADOW TENDS TO SUPPORT FEW FLOWERS AND CONSEQUENTLY FEW BUTTERFLIES. (GNPL010, GNPA038)

88 RT8 BURNSC - RT8 BURNSCAR - (D) INTERPRETIVE TRAIL ACCESSED VIA GLACIER RT8 JUST PRIOR TO ITS INTERSECTION WITH THE NORTH FORK ROAD. BURNPLOT TRAIL IS A CIRCUIT TRAIL. IT WAS A DIFFICULT PLACE TO CENSUS BUTTERFLIES DUE TO THE FALLEN LOGS AND LACK OF LARGE OPEN SPACES. BIRDS WERE PLENTIFUL IN THE 1988 CENSUS. (GNPA028-029)

89 RT8 THINPL - RT 8 THINPLOT - (D) EXPERIMENTAL TREE-THINNING PLOT IN FLATHEAD NATIONAL FOREST. ACCESSED VIA THE NORTH FORK ROAD. JUST A FEW MILES NORTH OF THE INTERSECTION WITH GLACIER RT 8. LODGEPOLE PINE STAND OF SMALL DIAMETER TREES HAS BEEN THINNED, LEAVING OPEN SPACES AND SOME GROUND COVER. (GNPA030)

90 S.BOUND TR - SOUTH BOUNDARY TRAIL - (R) AS ITS NAME IMPLIES, THIS TRAIL SKIRTS THE SOUTH BOUNDARY OF THE PARK. BIRDS WERE CENSUSED ALONG THIS TRAIL FROM WEST GLACIER, UPRIVER APPROXIMATELY 2-3 MILES TO THE TOP OF A KNOB HILL. THIS TRAIL WAS ALSO USED TO CENSUS BIRDS DOWNRIVER FROM WEST GLACIER TO THE POINT ACROSS FROM SLOAN RANCH. (GNPA058-060)

91 SACR DANCE - SACRED DANCING CASCADES TRAIL - (R) BIRD CENSUSING PLOT THAT IS CENSUSED AT SEVERAL POINTS ALONG TRAIL ON NORTH SIDE OF MCDONALD CREEK AND INCLUDING MCDONALD FALLS. STARTING POINT IS THE FROM MCDONALD RANGER STATION ROAD. HEADING EASTWARD, ONE PASSES THE FALLS, AND CONTINUES TO THE SLOW PART OF THE CREEK NEAR MOOSE COUNTRY. (GNPA051-056)

92 SCENIC PT - SCENIC POINT - (HA) LARGE FLAT PASS AREA. ACCESSED FROM MT HENRY TRAIL STARTING FROM TWO MEDICINE ROAD NEAR TWO MEDICINE LAKE. JUST BEYOND FIRST PASS (NOT SCENIC PT), AROUND THE CORNER THERE IS A ROCKY OUTCROPPING ON THE SIDE OF ANOTHER UNNAMED PEAK, JUST SOUTHWEST OF SCENIC POINT. THIS AREA, AS WELL AS THE SCENIC POINT SOUTH SIDE, WAS CENSUSED FOR BUTTERFLIES IN 1987 AND 1988. (GNPL020-021)

93 SIYEH BEND - SIYEH BEND - (HA) MEADOW ON SIYEH BEND SIDE OF SIYEH PASS TRAIL WHERE STREAM CROSSES TRAIL. CENSUSED IN 1987. (GNPL034)

94 SIYEH CIRQ - SIYEH CIRQUE - (HA) AREA NEAR LAKE BELOW AND WEST FROM SIYEH PASS. ON EAST SHORE BUTTERFLIES WERE CENSUSED IN 1987. THERE WERE SEVERAL WILDFLOWER PATCHES NEAR THE LAKE BEYOND THE KRUMHOLTZ. (GNPL035)

95 SIYEH PASS - SAME AS SIYEH PASS-U (UPPER) IN 1987 CENSUS - (HA) THIS IS THE TRUE PASS AREA, THE AREA FURTHER UP FROM THE LOW PASS, WHERE A VIEW OF SEXTON GLACIER IS POSSIBLE. OFTEN THE WIND IS SO EXTREME THAT IT IS DIFFICULT TO STAND UP, MUCH LESS CENSUS BUTTERFLIES. (GNPL032)

96 SIYEH PS-L - SIYEH PASS LOWER - (HA) THIS IS THE LARGE FLAT AREA SEEN FROM PRESTON PARK AS ONE HIKES UPHILL. MANY LYCENIDS AND COLIAS SPECIES WERE FOUND HERE AND THE WILDFLOWERS ARE PROLIFIC IN EARLY SUMMER. (GNPL033 AND 035)

97 SIYEH/PIEG - SIYEH/PIEGAN PASS - (HA) HIKED FROM SIYEH BEND UP TO THE POINT WHERE PIEGAN PASS CUTS OFF WESTWARD. BUTTERFLIES FOR THIS CENSUS WERE COLLECTED IN A LONGMEADOW

FROM THIS TRAIL INTERSECTION TOWARDS SIYEH CREEK. (GNPL036)

98 SPERRY DWN - LISTING OF SPECIES FOUND ALONG SPERRY TRAIL (IN ONE CASE COMING DOWN FROM SPERRY CHALET) - (TR) THIS WAS A TRAIL CENSUS, AND THEREFORE QUALITATIVE RATHER THAN QUANTITATIVE. MANY HABITATS WERE PASSED THROUGH, INCLUDING CEDAR FOREST, LODGEPOLE FOREST, OPEN FOREST CLEARINGS, AND OTHERS. HORSE SCAT ATTRACTED BUTTERFLIES ALONG THE TRAIL. (GNPL043)

99 SPERRY TR - SPERRY TRAIL - (W) CENSUSED FOR BIRDS ONLY DUE TO LACK OF LIGHT AT LOWER END IN CEDAR-HEMLOCK FOREST. FOLLOWS SNYDER CREEK AND VARRIES IN PROXIMITY TO THE CREEK. AT SOME POINTS IT IS DIFFICULT TO HEAR BIRDS OVER THE RUSHING WATER. (GNPA011-015)

100 SPOT MT - SPOT MOUNTAIN - (AR) ACCESSED FROM RT49 AT LOOKING GLASS HILL. THIS ROAD SKIRTS THE EAST BOUNDARY OF THE PARK THROUGH THE BLACKFEET RESERVATION. APPROXIMATELY 8 MILES NORTH OF EAST GLACIER PARK, THERE IS AN OLD SERVICE ROAD THAT LEADS DIRECTLY WEST FROM THE MAIN HIGHWAY. AFTER CROSSING THE PARK BOUNDARY FROM THE RESERVATION, THE ROAD PEETERS OUT. CONTINUE WEST ALONG A SMALL RIDGE, PASSING A SMALL LAKE, AND WESTWARD TO A LONG, OPEN MEADOW JUST BELOW SPOT MOUNTAIN. THE MEADOW BELOW SPOT MOUNTAIN WAS CENSUSED, AS WAS AN INTERMITTENT DRAINAGE THAT HEADS UP THE MOUNTAIN NORTHWEST FROM THE MEADOWS. THREE BENCHES ON THE EASTFACING SIDE OF THE SOUTH END OF THE MOUNTAIN WERE CENSUSED. THE ACTUAL MOUNTAIN TOP WAS NOT CENSUSED. BEST LUCK WAS FOUND AT THE LOWER MEADOW AND ALONG THE INTERMITTENT DRAINAGE, AS THE UPPER BENCH WAS FULL OF LUPINES AND VERY FEW BUTTERFLIES SEEM TO USE THIS PLANT.

101 ST MARY CG - SAINT MARY CAMPGROUND - (R) THIS AREA WAS CENSUSED AT THE NORTH END OF THE CAMPGROUND NEAR AN OLD FIELD, AT THE SOUTH END OF THE CAMPGROUND NEAR THE SAINT MARY RIVER, AND AT SAINT MARY LAKE FOR BIRDS. (GNPA105 ETC.)

102 ST MARY RS - SAINT MARY RANGER STATION - (MM) THIS AREA IS DISTINGUISHED FROM THE CAMPGROUND FOR THE BUTTERFLY CENSUSING, AS NO BUTTERFLIES WERE CENSUSED IN THE CAMPGROUND. THREE PLOT IN THE MEADOW JUST NORTH OF THE LAKE WERE CENSUSED IN 1988 FOR BUTTERFLIES, AND THE AREA WAS DESIGNATED AS A BIODIVERSITY SITE. SITES DIFFERRED IN THEIR PROXIMITY TO THE LAKE.

103 STONY I CG - STONEY INDIAN CAMPGROUND - (AR) THIS AREA IS CARPETED WITH WILDFLOWERS IN THE SUMMER AND MAKES A PRIME CENSUS SITE FOR BUTTERFLIES BETWEEN THE CAMPGROUND AND THE POINT WHERE THE TRAIL SKIRTS THE SOUTHEAST END OF THE LAKE. (GNPL044)

104 STONY I PS - STONEY INDIAN PASS - (AR) OFTEN FULL OF ALPINE WILDFLOWERS THIS PASS IS ALSO A GOOD PLACE TO CENSUS BUTTERFLIES. BECAUSE OF THE PRECIPITOUS EDGES IT IS NOT ALWAYS EASY TO CAPTURE BUTTERFLIES. WITH AN EARLY START FROM GOATHAUNT THIS AREA CAN BE CENSUSED AS A DAYHIKE. (GNPL043)

105 STONY I TR - STONEY INDIAN TRAIL - (TR) THE TRAIL TO STONEY INDIAN CAMPGROUND FROM WATERTON LAKES TRAIL IS SOMETIMES CENSUSED FOR BUTTERFLIES AS ONE HIKES. THE TRAIL AREA INCLUDED IS THE OPEN TRAIL THAT FOLLOWS PASS CREEK ALONG THE FALLS. (GNPL045)

106 SULLIVAN M - SULLIVAN MEADOW - (MM) LARGE 12 ACRE MEADOW (AREA CENSUSED) ON THE NORTHEAST SIDE OF GLACIER RT 7, A LITTLE MORE THAN A MILE SOUTH OF LOGGING CREEK RANGER STATION. THE MEADOW IS NOT DIRECTLY VISIBLE FROM THE ROAD, AS THERE IS A PATCH OF LODGEPOLE CREATING A VISUAL BUFFER. A GOOD LANDMARK FOR FINDING THE MEADOW IS A YELLOW CAUTION SIGN WITH AN ARROW INDICATING A SHARP CURVE IN THE ROAD (TO THE RIGHT). PARKING NEAR THIS SIGN, THE MEADOW IS A SHORT WALK FROM THE ROAD. THE HISTORIC USE AS AN AGRICULTURAL FIELD IS EVIDENT FROM THE BURNED TREE STUMPS, THE OLD FENCING, AND THE SUGGESTION OF A POND IN YEARS PAST. (GNPL012, GNPA042)

107 SWAN LAKE - SWAN LAKE - (R) LAKE ON JERRY DESANTO'S PROPERTY IN ALBERTA, CA, NORTH OF GLACIER PARK. NAMED FOR THE SWANS THAT NEST ON THIS LAKE.

108 SWIFTCR LK - SWIFTCURRENT LAKE - (R) A CIRCUIT TRAIL SKIRTS THE PERIMETER OF SWIFTCURENT LAKE. THIS TRAIL WAS CENSUSED FOR BUTTERFLIES IN 1988 AS A QUALITATIVE TRAIL CENSUS. (GNPL234)

109 TWO DOG FL - TWO DOG FLATS - (XM) THIS AREA EXISTS JUST OFF OF THE GOING TO THE SUN ROAD NEAR ST MARY LAKE. THE SITE DESIGNATED AS THE BIODIVERSITY SITE IS GNPL056 FROM THE 1987 CENSUS. IT IS APPROXIMATELY 3 MILES FROM THE SAINT MARY VISITOR CENTER. CENSUSES WERE CONDUCTED A GOOD DISTANCE FROM THE ROAD (ON THE WEST SIDE) TO DECREASE THE LIKELIHOOD OF OBSERVATION BY PASSING MOTORIST, ALTHOUGH THIS IS NOT ENTIRELY POSSIBLE TO PREVENT. (GNPL055-056)

110 TWO MED CG - TWO MEDICINE CAMPGROUND - (R) THIS AREA WAS CENSUSED ONE MORNING IN 1987 WHEN WE WERE CAMPING. A THOROUGH CENSUS WAS NOT CONDUCTED THROUGHOUT THE CAMPGROUND. BIRDS IN THE AREA OF THE TENT WERE NOTED AS WE ATE BREAKFAST AND PREPARED FOR THE DAY'S WORK. (GNPA049)

111 WALTN SCAP - WALTON SCAPLOCK - (W) BIRDS WERE CENSUED IN TWO POINTS 1/2 MILE+ UP THE SCAPLOCK LOOKOUT TRAIL FROM ITS INTERSECTION WITH OLE CREEK TRAIL. (GNPA112, 114)

112 WALTON OLE - WALTON OLE CREEK - (W) TWO BIRD CENSUSES WERE CONDUCTED FROM THE INTERSECTION OF OLE CREEK AND SCAPLOCK LOOKOUT TRAIL STOPPING EVERY 300 M WITH THE TRANSECT ROUTINE. (GNPA111,113)

113 WALTON RS - WALTON RANGER STATION - (R) BIRD CENSUSES WERE CONDUCTED HERE IN 1987 AND 1988 FROM THE RANGER STATION, UP THE TRAIL, STOPPING EVERY 300M IN 1987 AND USING A 1 SQ KM SECTION CENSUS IN 1988. BIRDS WERE CENSUSED WITHIN THE DENSE FOREST, AT BRIDGES, AND ALONG THE RIVER. BUTTERFLIES WERE ALSO CENSUSED IN THIS AREA IN 1987 ALONG THE RIVERBANKS. (GNPA106-108, GNPL061-062)

114 WILBUR CR - WILBUR CREEK - (SA) OPEN MEADOWS ALONG WILBUR CREEK AT MANY GLACIER, APPROXIMATELY 1.5 MILES UP ICEBURG LAKE TRAIL. AREA NEAR AN INTERMITTENT ROCKY STREAM BED WAS ESPECIALLY PRODUCTIVE FOR BUTTERFLIES.

APPENDIX B

PRESENCE/ABSENCE MATRICES FOR EACH YEAR

APPENDIX B: PRESENCE/ABSENCE MATRICES FOR EACH YEAR
SPECIES ARE ARRAYED ALONG THE VERTICAL AXIX
SITES ARE ARRAYED ALONG THE HORIZONTAL AXIS

BIRD 1987 DATA

SPECIES CODES	SITE CODES
BLKCP CHIC	MFF W GLAC
PINE SISK	BELY CG CA
AMERI ROBN	MCDON CR L
DARKE JNCO	CHRISMEADO
RBRST NUTH	SACR DANCE
SWAIN THRS	ST MARY CG
NORTH FLIC	LONE PINE
YELBE SAPS	FLTHD RS R
GOLDN KING	MUD LAKE
VARRI THRS	WALTON RS
SONGS SPAR	LK MCDNL E
CEDAR WAXW	SPERRY TR
COMMN RAVN	QRTZ LK TR
YELLO WARB	RT8 BURNSC
GRAY JAY	QUARTZ CG
MCGIL WARB	S.BOUND TR
TREE SWAL	QRTR CR BR
YELRP WARB	GOATHNT RS
WILLO FLYC	FISH LAKE
BARN SWAL	APG LOK TR
REDEY VIRI	BELY COSLY
BANK SWAL	BELY RV CG
RUFUS HUMG	FLTP MT CR
COMON YLTH	BIG PRARIE
AMERI REDS	PACKRS RST
WTCRN SPAR	ANACND .8N
CALIO HUMG	SULLIVAN M
WARBL VIRI	LOG CR RT7
CLIFF SWAL	BELY RV RS
VIOLT SWAL	GOAT H TRL
FOX SPAR	APG BIK TR
BRNHD BLKB	FLTP CG .5
HOUSE WREN	FLTHD RGST
WESTN TANG	LOGAN PASS
ROSY FINC	QRTZ PA CB
NORTH WATR	GOATH RF L
ROUGH SWAL	ROCKY PNT
SAVNA SPAR	ROUND PRAR
BELTD KING	FLTP MT LK
VESPR SPAR	TWO MED CG
WLSON WARB	WALTON RS
HAIRY WDPK	FLTP LK SO

STELR JAY
HAMON FLYC
SOLIT VIRI
WWING CROS
WINTR WREN
GREY CATB
TWNSN WARB
ORGCR WARB
HERMI THRS
CHIPP SPAR
VEERY
MOUNT BLUE
WATER PIPI
PINE GROS
CASSN FINC
WTTHR SPAR
RDWNG BLKB
PILIA WDPK
CLARK NUTC
NORTH ORIO
OLIVS FLYC
AMERI GOLD
BROWN CREP
DUSKY FLYC
BOHEM WAXW
AMERI DIPR

WALTN SCAP
WALTON OLE
FLTP MT CG
SCENC PT T
FLTP MT RG
RAINB FALL
BOWMN L CG
GOATH STBL
GOATH LK T
LK ELLEN W
MINERAL CR

Presence-absence matrix: Birds 1987

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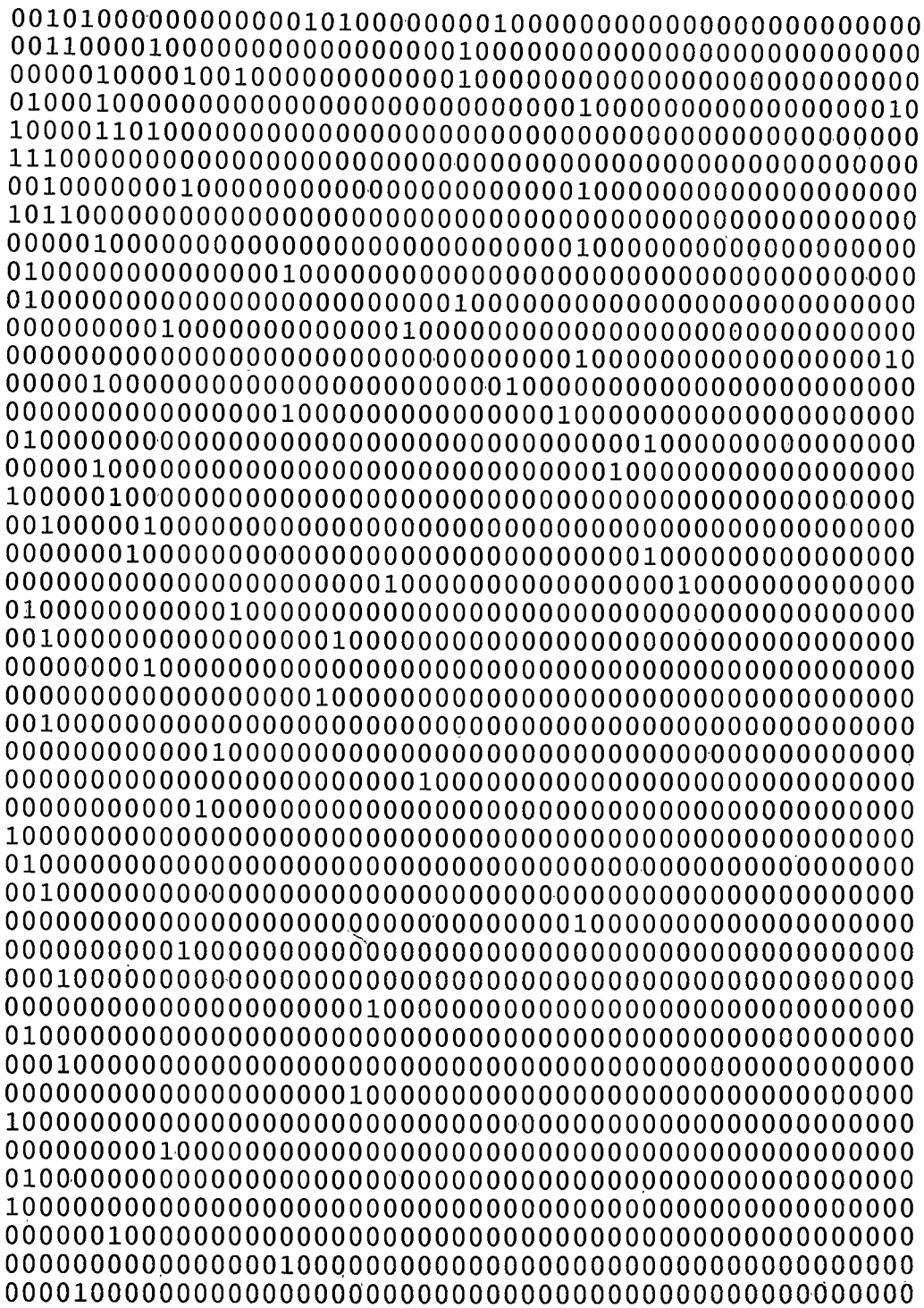

BIRD 1988 DATA

SPECIES CODES	SITE CODES
AMER ROB	HIDDN MD
SWAN THR	DESANTOS
GOLD KNG	RT8 BURN
PINE SIS	FLATH RS
RBRST NT	MFF W GL
N FLICKR	GRANIT P
SONG SPR	BELLY CA
DK JUNCO	LONE PIN
AM REDST	ST MARY
MCGIL WB	SULLIVAN
LST FLYC	LK MCDNL
BLK CHIC	DRY FORK
TREE SWL	SWAN LAK
CED WAXW	QC BRIDG
CHIP SPR	LOGAN PS
YBL SAPS	BELLY RS
YELO WBL	MCGEE MD
MT CHICK	CHRISTNS
YLRMP WB	MUD LAKE
WLO FLYC	APGAR LK
COM RAVN	SPERRY T
TWNS WBL	MOOSE FL
VAR THRS	P PINE 7
RBY KING	PCKR RST
WBL VREO	SACR DNC
W TANAGR	I WALTN
RWG BLKB	BARNG CR
BRHD COW	ROCKY KN
COM YLTH	ANACONDA
WLSON WB	AVALANCH
BARN SWL	BELY/COS
HOUSE WR	MUD CRK
WTCRN SP	FISH LK
CLK NUTC	
CLIF SWL	
WWD PEWE	
OLVS FLY	
WNTR WRN	
BRWR BLK	
PLIA WDP	
N ORIOLE	
YHD BLKB	
SAVN SPR	
HERM THR	
SOL VRIO	
VEERY	
MT BLUEB	
RUF HUMR	

GRAY CAT
GRAY JAY
AM GOLDF
KNGFISHR
CAS FNCH
N WTRTHR
CHES CHC
WTR PIPT
BCHN HUM
RDEY VIR
CALI HUM
AM DIPPR
ROS FNCH
FOX SPAR
STLR JAY
DWNY WDP
E KINGBD
VESP SPR
AMR CROW
VIOL SPR
BLK GROS
WST FLYC
BANK SWL

Presence-absence matrix: Birds 1988

11111111111100011110101001001111 0
10111001011101101110110111110101 0
10111101011001000001111101010100 1
10111011001100011011011010001010 0
10011101011001100011011110000100 0
11101101011110010110001000001000 0
10100110110101011101100100000000 0
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BIRD 1989 DATA

SPECIES CODES	SITE CODES
AMER ROB	LONE PIN
DK JUNCO	HIDDN MD
PINE SIS	SULLIVAN

SWAN THR	MUD CRK
MCGIL WB	DESANTOS
N FLICKR	TWO DOG
RBRST NT	ANACONDA
GOLD KNG	MUD LAKE
RBY KING	RT8 BURN
WBL VREO	LK MCDNL
COM RAVN	CHRISTNS
YLRMP WB	DRY FORK
BLK CHIC	QC BRIDG
AM REDST	MFF W GL
CHIP SPR	ST MARY
CED WAXW	MCGEE MD
TWNS WBL	ROCKY KN
WLSON WB	SPOT MTN
YBL SAPS	I WALTN
FOX SPAR	FLATH RS
GRAY JAY	BELY/COS
BRHD COW	BIG PRAR
WLO FLYC	PCKR RST
HAMN FLY	SPERRY T
SONG SPR	APGAR LK
YELO WBL	SACR DNC
W TANAGR	AVALANCH
OLVS FLY	P PINE 7
CALI HUM	SCENC PT
VAR THRS	LOGNG LK
CLK NUTC	BARNG CR
PLIA WDP	LOGAN PS
WTCRN SP	GRANIT P
COM YLTH	FIFTY MT
N WTRTHR	
MT CHICK	
ORCR WBL	
HAIR WDP	
WWD PEWE	
TREE SWL	
SOL VRIO	
BARN SWL	
RWG BLKB	
WNTR WRN	
LNCN SPR	
LST FLYC	
VIOL SPR	
KNGFISHR	
RUF HUMR	
AMER CRO	
LAZU BNT	
TOWN SOL	
THRE TOE	
YHD BLKB	
AM DIPPR	

BANK SWL
TENN WBL
CLIF SWL
BLK GROS
VEERY
MT BLUEB
DWNY WDP
BRWR BLK
E KINGBD
WTR PIPT
ROS FNCH
GRAY CAT
N ORIOLE
STLR JAY
DUSK FLY
PINE GRS
RWNG SWL
VESP SPR
RDEY VIR
CAS FNCH
HERM THR
AM GOLDF
BRWN CRP
SAVN SPR
HOUS WRN

Presence-absence matrix: Birds 1989

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BUTTERFLIES 1987 DATA

SPECIES CODE	SITE CODES
PLEB ARG	CHRISMEADO
SPEY ATL	SULLIVAN M
NYMP MIL	DEER LICK
CERC OET	BELY TR MD
EUPH ANI	ANACONDA M
SPEY MOR	LONE PINE
COLI EUR	DUT CRK NW
COLI INT	BELLY R TR
LYCN MAR	TWO DOG FL
NYMP CAL	HIDN LK WS
PARN PHO	COAL CREEK
POLY FAU	GUNST P TR
SPEY HYD	CAMAS TRAL
PLEB SAP	I WALTN AC
LIME LOR	DUT CRK SE
COLI PHI	MED/BIS MT
PIER OCI	SCENIC PT
PHYC TAR	SIYEH PS-L
NYMP ANT	GRANITE TR
SPEY ZER	BEAR CREEK
CLOS PAL	MFF PAOLA
LYCN HET	FNF LOGD 8
NYMP VAL	LOGAN PASS
BOLO TIT	STONY I TR
POLY SAT	FLTP MT LK
EPID NIV	HOLE TO BR
BOLO SEL	MUD CRK MD
BOLO EPI	LINCN PASS
CERC PEG	FLTP CG .5
LYCN HEL	STONY I PS
PLEB ACM	BELY TR CG
PHYC CAM	CLEVELD CR
COEN INO	FERN CR MD
PIER RAP	SIYEH BEND
PIER NAP	FLTHD RGST
COLI ALX	SIYEH PS-U
EUPH EDI	SPERRY DWN
COLI MED	STONY I CG
PAPI RUT	STONY I TR
HARK TIT	BOWMAN 1.5
LYCN DOR	ROUND PRAR
PLEB ICA	LK ELLEN W

BOLO ALB	KOOTENAI L
LYCN CUP	ST MARY RS
EVER AMY	FLTHD FIRE
POLY COM	BELLY R RS
LIME WED	NFF LANDST
LYCN HYL	PRESTON PK
VANE ATL	SIYEH/PITA
EUPH GIL	50MT NW
PIER PRO	SIYEH CIRQ
SPEY EDW	NFF RIV CG
SPEY CYB	FLTHD RS R
PARN CLO	BIG PRARIE
POLY ZEP	MCGEE MEAD
COLI NAS	MFF SLOAN
EREB EPI	HIDN LK OV
	FLTP MT RG
	50MT SE
	MUD CR MED
	FLTP LK SO
	MFF MCDONL
	HIDN LK ES

Presence/Absence Matrix: Butterflies 1987

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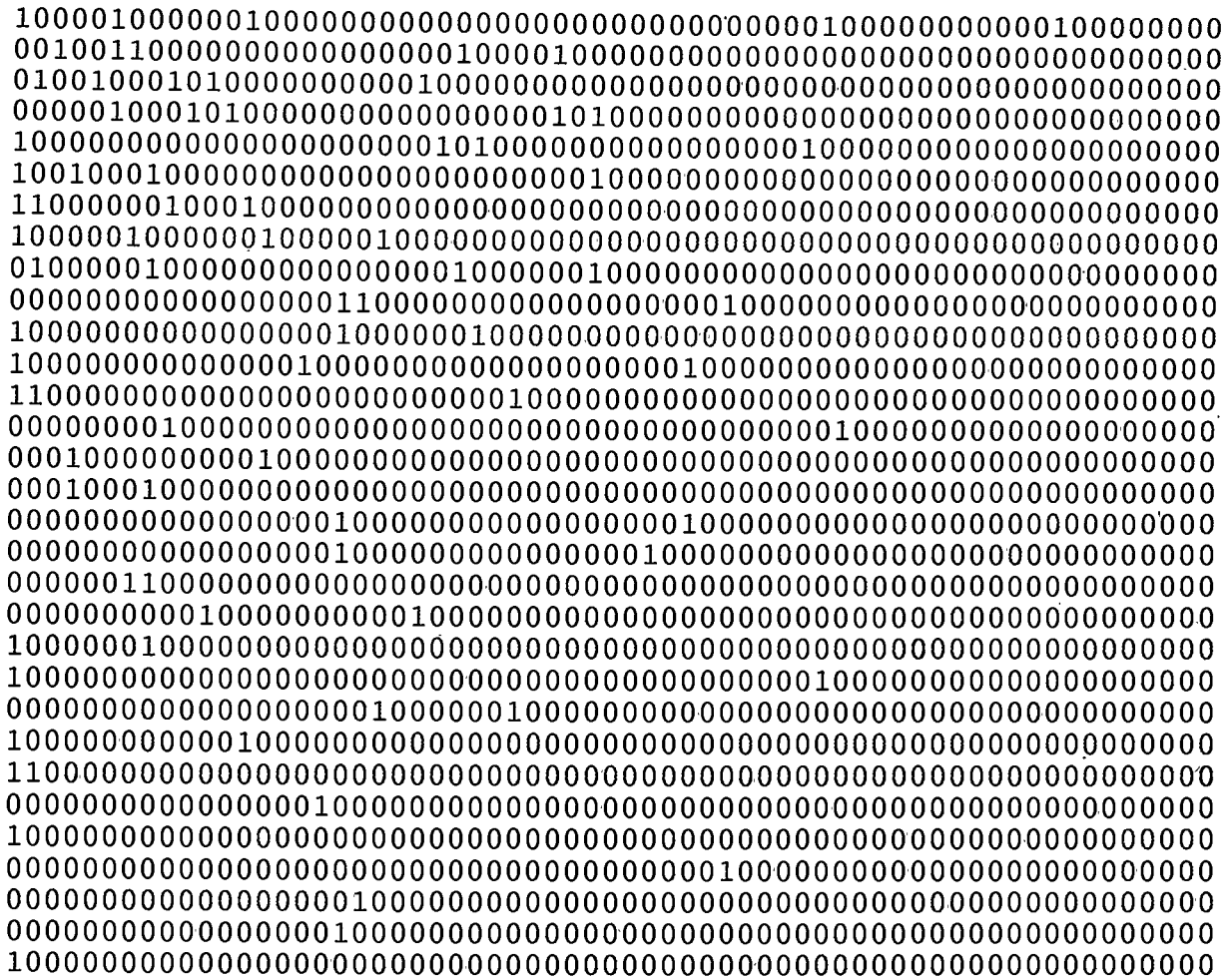

BUTTERFLIES 1988 DATA

SPECIES CODE	HABITAT CODE
COLI INT	SPOT MT
PLEB ARG	CHRISMED
PLEB SAP	HIDDN LK
SPEY MOR	PRESTN P
CERC OET	BELLY CG
NYMP MIL	BARNG CR
EUPH ANI	SULLVN M
PIER OCI	LONE PIN
COEN INO	STONY IN
SPEY ATL	GRANIT P
EREB EPI	HIDDN MD
PARN PHO	WILBR CR
CLOS PAL	TWO DOG
PHYC TAR	BIG PRAR
PHYC CAM	MCGEE MD

PAPI RUT	MFF W GL
VANC CAR	SCENC PT
PIER NAP	FLATTP M
PIER RAP	ROCKY KN
NYMP ANT	DESANTOS
POLY FAU	FIFTY MT
PLEB ACM	RT8 BURN
BOLO EPI	ST MARY
SPEY ZER	ROUND PR
COLI PHI	
LYCN MAR	
LIME LOR	
PAPI EUR	
PAPI ZEL	
PLEB AQL	
NYMP CAL	
POLY SAT	
SPEY HYD	
EUCH AUS	
BOLO SEL	
NYMP VAL	
OENE CHR	
BOLO TIT	
CERC PEG	
CALO ERY	
LYCN HET	
COLI EUR	
VANE ANA	
EUPH GIL	
LYCN CUP	
EUPH EDI	
COLI MED	
POLY ZEP	
OENE UHL	
EVER AMY	
CELA ARG	
LYCN HEL	
PHAD PIA	
SPEY EGL	
EPID NIV	
LIME WED	
LYCN PHL	
VANE ATL	
COLI NAS	
PLEB ICA	
ANTH SAR	
PAPI GLA	
PARN CLO	
CALO SHR	
ANOP ANC	
NEOP MEN	

Presence-absence matrix: Butterflies 1988

```
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BUTTERFLIES 1989 DATA

SPECIES CODE	HABITAT CODES
COLI EUR	CHRISTNS
PIER OCI	LONE PIN
COLI PHI	ST MARY
PHYC CAM	SPOT MTN
COLI INT	HIDDN MD
PAPI RUT	SULLIVAN
PLEB SAP	TWO DOG
CERC OET	BELLY CG
EREB EPI	MCGEE MD
PAPI ZEL	DESANTOS
NYMP MIL	ROUND PR
PHYC TAR	BARNG CR
COEN INO	RT8 BURN
PLEB ICA	SCENC PT
PAPI EUR	ROCKY KN
CALO ERY	WILBR CR
EUPH ANI	BIG PRAR
SPEY ATL	GRANIT P
SPEY MOR	HIDDN LK
BOLO EPI	MUD CRK
NYMP ANT	STONY IN
POLY FAU	PREST PK
CLOS PAL	FIFTY MT
OENE CHR	FLTTP MT
PIER NAP	
PLEB ARG	
PARN PHO	
CERC PEG	
EUCH AUS	
PIER RAP	

LYCN HET
BOLO SEL
PLEB GLN
GLAC LYG
SPEY EGL
PAPI GLA
EUPH EDI
BOLO TIT
LIME ART
VANE CAR
SPEY HYD
LYCN MAR
EUPH GIL
EVER AMY
POLY SAT
HARK TIT
POLY ZEP
VANE ATL
COLI NAS
NYMP VAL
BOLO AST
EPID NIV
SPEY ZER
ANTH SAR
COLI MED
SPEY APH
CALO POL
SPEY CYB
LYCN PHL
SATY SPN
CELA ARG
LYCN HEL
LIME LOR
PLEB ACM
PLEB AQL
NYMP CAL
VANE ANA
LYCN CUP
OENE UHL
CELA ARG
PHAD PIA
LIME WED
PLEB ICA
PAPI GLA
PARN CLO
CALO SHR
ANOP ANC
NEOP MEN

Presence-absence matrix: Butterflies 1989

```
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APPENDIX C

STARCH GEL ELECTROPHORESIS METHODOLOGY

APPENDIX C: Starch Gel Electrophoresis Methodology

A minimum of twenty male individuals was collected from each region and often from each population. After collection, the wings were removed and the bodies placed in ampules and frozen in liquid nitrogen. At the end of the field season, the specimens were returned to the electrophoresis laboratory at Montana State University and stored at -80 C until electrophoresis. Specimens were prepared by crushing the whole body in a centrifuge tube with 0.2 ml of cold buffer (0.05 m Tris-HCL, 0.05 m Tris-Base, with pH adjusted to 7.1 with HCL). They were then centrifuged for five minutes at 12,000 rpm.

Allozyme variation was assayed at 22 structural gene loci using horizontal starch-gel electrophoresis. General methods and staining procedure were similar to those described by May et al. (1979). The enzymes assayed and the buffer systems used to resolve them are listed in Table 23. Buffer "R" is that of Ridgeway et al (1970), and buffer "4" is described in Selander et al. (1971). For "C" the electrode buffer was 0.04 m/dm citric acid adjusted to pH 6.1 with N-(3-amino propyl) morpholine; it was diluted 1:10 for the gel buffer (Clayton and Tretiak 1972). Genotype frequencies were obtained by direct count from the phenotypes observed on the gels, and electromorph (allozyme) frequencies were calculated from the genotype frequencies. Expected genotypic frequencies, fixation indices (F-statistics), and fit to Hardy-Weinberg expectation were calculated by procedures described in Nei (1977). Heterogeneity among populations was tested for significance using the G-test for goodness-of-fit (Sokal and Rohlf 1981). Nei's (1972) measure of genetic distance (D) was used to quantify overall genetic differentiation among populations.

APPENDIX D

1988 DATA

ALLELE FREQUENCIES AND GENETIC VARIABILITY MEASURES

Table 36. Electrophoretic Results: Belly River 1988.

	Locus and sample size								
Allele	AGP-1 21	IDH-1 23	IDH-2 21	GAPDH 23	AAT-1 23	AAT-2 23	PEP-1 23	HBDH1 21	GP-01 23
A	.119	.000	.000	.000	.000	.000	.000	.000	.000
B	.405	.000	.000	.000	.000	.000	.000	1.000	.000
C	.476	.000	.976	1.000	1.000	1.000	1.000	.000	1.000
D	.000	.000	.024	.000	.000	.000	.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000
G	.000	1.000	.000	.000	.000	.000	.000	.000	.000
H	.000	.000	.000	.000	.000	.000	.000	.000	.000
H	.595	.000	.046	.000	.000	.000	.000	.000	.000
H(unb)	.610	.000	.048	.000	.000	.000	.000	.000	.000
H(D.C.)	.619	.000	.048	.000	.000	.000	.000	.000	.000

	Locus and sample size							
Allele	XDH-1 6	SOD-1 23	SOD-2 23	LDH-1 22	PGD-1 23	GPI-1 20	MDH-1 19	MDH-2 23
A	.000	.000	.000	.000	.087	.000	.000	.000
B	.000	.000	1.000	1.000	.739	.000	.000	.000
C	1.000	.000	.000	.000	.174	.975	.000	1.000
D	.000	1.000	.000	.000	.000	.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.974	.000
F	.000	.000	.000	.000	.000	.025	.026	.000
G	.000	.000	.000	.000	.000	.000	.000	.000
H	.000	.000	.000	.000	.000	.000	.000	.000
H	.000	.000	.000	.000	.416	.049	.051	.000
H(unb)	.000	.000	.000	.000	.425	.050	.053	.000
H(D.C.)	.000	.000	.000	.000	.348	.050	.053	.000

	Locus and sample size		
	DIA-1	DIA-2	PGM-1
Allele	23	3	23
A	.000	.000	.000
B	1.000	.000	.000
C	.000	.833	.000
D	.000	.167	.000
E	.000	.000	.000
F	.000	.000	.065
G	.000	.000	.913
H	.000	.000	.022
H	.000	.278	.162
H(unb)	.000	.333	.165
H(D.C.)	.000	.333	.174

Mean heterozygosity per locus (biased estimate) = .080 (S.E. .037)
Mean heterozygosity per locus (unbiased estimate) = .084 (S.E. .038)
Mean heterozygosity per locus (direct-count estimate) = .081 (S.E. .037)

Mean number of alleles per locus = 1.50 (S.E. .17)

Percentage of loci polymorphic (0.95 criterion) = 20.00
Percentage of loci polymorphic (0.99 criterion) = 35.00
Percentage of loci polymorphic (no criterion) = 35.00

****

Table 37. Electrophoretic Results: Christensen Meadow 1988.

	Locus and sample size								
	AGP-1	IDH-1	IDH-2	GAPDH	AAT-1	AAT-2	PEP-1	HBDH1	GP-01
Allele	14	16	15	16	16	16	16	16	16
A	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.250	.000	.000	.000	.000	.000	.000	1.000	.000
C	.750	.000	1.000	1.000	1.000	1.000	1.000	.000	1.000
D	.000	.000	.000	.000	.000	.000	.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000
G	.000	1.000	.000	.000	.000	.000	.000	.000	.000
H	.375	.000	.000	.000	.000	.000	.000	.000	.000
H(unb)	.389	.000	.000	.000	.000	.000	.000	.000	.000
H(D.C.)	.357	.000	.000	.000	.000	.000	.000	.000	.000

	Locus and sample size							
Allele	XDH-1 16	SOD-1 16	SOD-2 16	LDH-1 16	PGD-1 16	GPI-1 16	MDH-1 13	MDH-2 16
A	.000	.000	.000	.000	.250	.000	.000	.000
B	.000	.000	1.000	1.000	.719	.000	.000	.000
C	1.000	.000	.000	.000	.031	1.000	.192	1.000
D	.000	1.000	.000	.000	.000	.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.808	.000
F	.000	.000	.000	.000	.000	.000	.000	.000
G	.000	.000	.000	.000	.000	.000	.000	.000
H	.000	.000	.000	.000	.420	.000	.311	.000
H(unb)	.000	.000	.000	.000	.433	.000	.323	.000
H(D.C.)	.000	.000	.000	.000	.563	.000	.385	.000

	Locus and sample size		
Allele	DIA-1 16	DIA-2 7	PGM-1 16
A	.000	.000	.000
B	1.000	.000	.000
C	.000	.714	.000
D	.000	.286	.000
E	.000	.000	.000
F	.000	.000	.000
G	.000	.000	1.000
H	.000	.408	.000
H(unb)	.000	.440	.000
H(D.C.)	.000	.571	.000

Mean heterozygosity per locus (biased estimate) = .076 (S.E. .035)
Mean heterozygosity per locus (unbiased estimate) = .079 (S.E. .037)
Mean heterozygosity per locus (direct-count estimate) = .094 (S.E. .044)

Mean number of alleles per locus = 1.25 (S.E. .12)

Percentage of loci polymorphic (0.95 criterion) = 20.00
Percentage of loci polymorphic (0.99 criterion) = 20.00
Percentage of loci polymorphic (no criterion) = 20.00

APPENDIX E

1989 DATA

ALLELE FREQUENCIES AND GENETIC VARIABILITY MEASURES

Table 38. Electrophoretic Results: Idaho 1989.

	Locus and sample size								
Allele	AGP-1 20	IDH-1 20	IDH-2 20	GAPDH 20	AAT-1 20	AAT-2 20	PEP-1 19	HBDH1 20	GP-01 20
B	.000	.000	1.000	.000	.000	.000	.000	1.000	.000
C	.000	.000	.000	1.000	1.000	.000	1.000	.000	1.000
D	.100	.000	.000	.000	.000	1.000	.000	.000	.000
E	.900	.000	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000
G	.000	1.000	.000	.000	.000	.000	.000	.000	.000
H	.000	.000	.000	.000	.000	.000	.000	.000	.000
H	.180	.000	.000	.000	.000	.000	.000	.000	.000
H(unb)	.185	.000	.000	.000	.000	.000	.000	.000	.000
H(D.C.)	.200	.000	.000	.000	.000	.000	.000	.000	.000

	Locus and sample size								
Allele	XDH-1 19	MPI-1 20	SOD-1 20	SOD-2 20	PGM-1 19	LDH-1 20	G6PDH 20	PGD-1 20	GPI-1 20
B	.000	.400	.000	1.000	.000	1.000	.000	.950	.025
C	1.000	.600	.000	.000	.000	.000	1.000	.050	.975
D	.000	.000	1.000	.000	.000	.000	.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000
G	.000	.000	.000	.000	.921	.000	.000	.000	.000
H	.000	.000	.000	.000	.079	.000	.000	.000	.000
H	.000	.480	.000	.000	.145	.000	.000	.095	.049
H(unb)	.000	.492	.000	.000	.149	.000	.000	.097	.050
H(D.C.)	.000	.400	.000	.000	.158	.000	.000	.100	.050

	Locus and sample size				
Allele	MDH-1 20	MDH-2 20	DIA-1 20	GK-01 20	GK-02 20
B	.000	.000	1.000	.000	.000
C	.000	1.000	.000	1.000	1.000
D	.100	.000	.000	.000	.000
E	.900	.000	.000	.000	.000
F	.000	.000	.000	.000	.000
G	.000	.000	.000	.000	.000
H	.000	.000	.000	.000	.000
H	.180	.000	.000	.000	.000
H(unb)	.185	.000	.000	.000	.000
H(D.C.)	.200	.000	.000	.000	.000

Mean heterozygosity per locus (biased estimate) = .049 (S.E. .023)
Mean heterozygosity per locus (unbiased estimate) = .050 (S.E. .024)
Mean heterozygosity per locus (direct-count estimate) = .048 (S.E. .021)

Mean number of alleles per locus = 1.26 (S.E. .09)

Percentage of loci polymorphic (0.95 criterion) = 21.74
Percentage of loci polymorphic (0.99 criterion) = 26.09
Percentage of loci polymorphic (no criterion) = 26.09

Table 39. Electrophoretic Results: Belly River 1989.

	Locus and sample size								
Allele	AGP-1 7	IDH-1 9	IDH-2 9	GAPDH 9	AAT-1 9	AAT-2 9	PEP-1 9	HBDH1 9	GP-01 9
A	.429	.000	.000	.000	.000	.000	.000	.000	.000
B	.571	.000	1.000	.000	.000	.000	.000	1.000	.000
C	.000	.000	.000	1.000	1.000	.000	1.000	.000	1.000
D	.000	.000	.000	.000	.000	1.000	.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000
G	.000	1.000	.000	.000	.000	.000	.000	.000	.000
H	.490	.000	.000	.000	.000	.000	.000	.000	.000
H(unb)	.527	.000	.000	.000	.000	.000	.000	.000	.000
H(D.C.)	.571	.000	.000	.000	.000	.000	.000	.000	.000

	Locus and sample size								
Allele	XDH-1 9	MPI-1 9	SOD-1 9	SOD-2 9	PGM-1 9	LDH-1 9	G6PDH 9	PGD-1 1	GPI-1 7
A	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.111	.000	1.000	.000	1.000	.000	1.000	.000
C	1.000	.889	.000	.000	.000	.000	1.000	.000	1.000
D	.000	.000	1.000	.000	.000	.000	.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000
G	.000	.000	.000	.000	1.000	.000	.000	.000	.000
H	.000	.198	.000	.000	.000	.000	.000	.000	.000
H(unb)	.000	.209	.000	.000	.000	.000	.000	.000	.000
H(D.C.)	.000	.222	.000	.000	.000	.000	.000	.000	.000

	Locus and sample size				
Allele	MDH-1 7	MDH-2 7	DIA-1 7	GK-01 9	GK-02 9
A	.000	.000	.000	.000	.000
B	.000	.000	1.000	.000	.000
C	.000	1.000	.000	1.000	1.000
D	.000	.000	.000	.000	.000
E	1.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000
G	.000	.000	.000	.000	.000
H	.000	.000	.000	.000	.000
H(unb)	.000	.000	.000	.000	.000
H(D.C.)	.000	.000	.000	.000	.000

Mean heterozygosity per locus (biased estimate) = .030 (S.E. .023)
Mean heterozygosity per locus (unbiased estimate) = .032 (S.E. .024)
Mean heterozygosity per locus (direct-count estimate) = .035 (S.E. .026)

Mean number of alleles per locus = 1.09 (S.E. .06)

Percentage of loci polymorphic (0.95 criterion) = 8.70
Percentage of loci polymorphic (0.99 criterion) = 8.70
Percentage of loci polymorphic (no criterion) = 8.70

Table 40. Electrophoretic Results: Red Meadow 1989.

	Locus and sample size								
Allele	AGP-1 25	IDH-1 25	IDH-2 25	GAPDH 23	AAT-1 25	AAT-2 25	PEP-1 23	HBDH1 25	GP-01 25
A	.500	.000	.000	.000	.000	.000	.000	.000	.000
B	.500	.000	1.000	.000	.000	.000	.000	1.000	.000
C	.000	.000	.000	1.000	1.000	.000	1.000	.000	1.000
D	.000	.000	.000	.000	.000	1.000	.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000
G	.000	1.000	.000	.000	.000	.000	.000	.000	.000
H	.500	.000	.000	.000	.000	.000	.000	.000	.000
H(unb)	.510	.000	.000	.000	.000	.000	.000	.000	.000
H(D.C.)	.360	.000	.000	.000	.000	.000	.000	.000	.000

	Locus and sample size								
Allele	XDH-1 25	MPI-1 25	SOD-1 25	SOD-2 25	PGM-1 22	LDH-1 25	G6PDH 25	PGD-1 1	GPI-1 25
A	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.760	.000	1.000	.000	1.000	.000	1.000	.000
C	1.000	.240	.000	.000	.000	.000	1.000	.000	.940
D	.000	.000	1.000	.000	.000	.000	.000	.000	.060
E	.000	.000	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000
G	.000	.000	.000	.000	1.000	.000	.000	.000	.000
H	.000	.365	.000	.000	.000	.000	.000	.000	.113
H(unb)	.000	.372	.000	.000	.000	.000	.000	.000	.115
H(D.C.)	.000	.240	.000	.000	.000	.000	.000	.000	.120

	Locus and sample size				
	MDH-1	MDH-2	DIA-1	GK-01	GK-02
Allele	25	25	23	20	22
A	.000	.000	.000	.000	.000
B	.000	.040	1.000	.000	.068
C	.000	.960	.000	1.000	.932
D	.020	.000	.000	.000	.000
E	.980	.000	.000	.000	.000
F	.000	.000	.000	.000	.000
G	.000	.000	.000	.000	.000
H	.039	.077	.000	.000	.127
H(unb)	.040	.078	.000	.000	.130
H(D.C.)	.040	.080	.000	.000	.045

Mean heterozygosity per locus (biased estimate) = .053 (S.E. .026)
Mean heterozygosity per locus (unbiased estimate) = .054 (S.E. .027)
Mean heterozygosity per locus (direct-count estimate) = .038 (S.E. .019)

Mean number of alleles per locus = 1.26 (S.E. .09)

Percentage of loci polymorphic (0.95 criterion) = 17.39
Percentage of loci polymorphic (0.99 criterion) = 26.09
Percentage of loci polymorphic (no criterion) = 26.09

Table 41. Electrophoretic Results: Marias Pass 1989.

	Locus and sample size								
	AGP-1	IDH-1	IDH-2	GAPDH	AAT-1	AAT-2	PEP-1	HBDH1	GP-01
Allele	17	21	21	21	21	21	21	21	21
A	.471	.000	.000	.000	.000	.000	.000	.000	.000
B	.529	.000	1.000	.000	.000	.000	.000	1.000	.000
C	.000	.000	.000	1.000	1.000	.000	1.000	.000	1.000
D	.000	.000	.000	.000	.000	1.000	.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000
G	.000	1.000	.000	.000	.000	.000	.000	.000	.000
H	.498	.000	.000	.000	.000	.000	.000	.000	.000
H(unb)	.513	.000	.000	.000	.000	.000	.000	.000	.000
H(D.C.)	.235	.000	.000	.000	.000	.000	.000	.000	.000

	Locus and sample size								
Allele	XDH-1 20	MPI-1 21	SOD-1 21	SOD-2 21	PGM-1 21	LDH-1 21	G6PDH 21	PGD-1 6	GPI-1 21
A	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.071	.000	1.000	.000	1.000	.000	.917	.000
C	1.000	.929	.000	.000	.000	.000	1.000	.083	1.000
D	.000	.000	1.000	.000	.000	.000	.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000
G	.000	.000	.000	.000	1.000	.000	.000	.000	.000
H	.000	.133	.000	.000	.000	.000	.000	.153	.000
H(unb)	.000	.136	.000	.000	.000	.000	.000	.167	.000
H(D.C.)	.000	.143	.000	.000	.000	.000	.000	.167	.000

	Locus and sample size				
Allele	MDH-1 21	MDH-2 21	DIA-1 21	GK-01 19	GK-02 21
A	.000	.000	.000	.000	.000
B	.000	.000	1.000	.000	.000
C	.000	1.000	.000	1.000	1.000
D	.000	.000	.000	.000	.000
E	1.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000
G	.000	.000	.000	.000	.000
H	.000	.000	.000	.000	.000
H(unb)	.000	.000	.000	.000	.000
H(D.C.)	.000	.000	.000	.000	.000

Mean heterozygosity per locus (biased estimate) = .034 (S.E. .023)
Mean heterozygosity per locus (unbiased estimate) = .035 (S.E. .024)
Mean heterozygosity per locus (direct-count estimate) = .024 (S.E. .013)

Mean number of alleles per locus = 1.13 (S.E. .07)

Percentage of loci polymorphic (0.95 criterion) = 13.04
Percentage of loci polymorphic (0.99 criterion) = 13.04
Percentage of loci polymorphic (no criterion) = 13.04

Table 42. Electrophoretic Results: Wyoming 1989.

	Locus and sample size								
Allele	AGP-1 21	IDH-1 22	IDH-2 21	GAPDH 21	AAT-1 22	AAT-2 22	PEP-1 18	HBDH1 22	GP-01 22
A	.095	.000	.000	.000	.000	.000	.000	.000	.000
B	.905	.000	1.000	.000	.000	.000	.000	1.000	.000
C	.000	.000	.000	1.000	1.000	.000	1.000	.000	1.000
D	.000	.000	.000	.000	.000	1.000	.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000
G	.000	1.000	.000	.000	.000	.000	.000	.000	.000
H	.172	.000	.000	.000	.000	.000	.000	.000	.000
H(unb)	.177	.000	.000	.000	.000	.000	.000	.000	.000
H(D.C.)	.095	.000	.000	.000	.000	.000	.000	.000	.000

	Locus and sample size								
Allele	XDH-1 22	MPI-1 20	SOD-1 22	SOD-2 22	PGM-1 21	LDH-1 22	G6PDH 22	PGD-1 22	GPI-1 22
A	.000	.000	.000	.000	.000	.000	.000	.023	.000
B	.000	.000	.000	1.000	.000	1.000	.000	.977	.364
C	1.000	.925	.000	.000	.000	.000	1.000	.000	.636
D	.000	.075	1.000	.000	.000	.000	.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000
G	.000	.000	.000	.000	1.000	.000	.000	.000	.000
H	.000	.139	.000	.000	.000	.000	.000	.044	.463
H(unb)	.000	.142	.000	.000	.000	.000	.000	.045	.474
H(D.C.)	.000	.150	.000	.000	.000	.000	.000	.045	.727

	Locus and sample size				
Allele	MDH-1 22	MDH-2 22	DIA-1 12	GK-01 22	GK-02 22
A	.000	.000	.000	.000	.000
B	.000	.000	1.000	.000	.000
C	.000	1.000	.000	1.000	1.000
D	.341	.000	.000	.000	.000
E	.659	.000	.000	.000	.000
F	.000	.000	.000	.000	.000
G	.000	.000	.000	.000	.000
H	.449	.000	.000	.000	.000
H(unb)	.460	.000	.000	.000	.000
H(D.C.)	.682	.000	.000	.000	.000

Mean heterozygosity per locus (biased estimate) = .055 (S.E. .028)
Mean heterozygosity per locus (unbiased estimate) = .056 (S.E. .029)
Mean heterozygosity per locus (direct-count estimate) = .074 (S.E. .042)

Mean number of alleles per locus = 1.22 (S.E. .09)

Percentage of loci polymorphic (0.95 criterion) = 17.39
Percentage of loci polymorphic (0.99 criterion) = 21.74
Percentage of loci polymorphic (no criterion) = 21.74

Table 43. Electrophoretic Results: All Populations 1989.
(standard errors in parentheses)

Population	Mean sample size per Locus	Mean no. of alleles per locus	Percentage of loci polymorphic*	Mean heterozygosity Direct-count	Mean heterozygosity HdyWbg expected**
1. IDAHO 89	19.9 (.1)	1.3 (.1)	26.1	.048 (.021)	.049 (.023)
2. BELLY RIVER	8.2 (.4)	1.1 (.1)	8.7	.035 (.026)	.030 (.023)
3. RED MEADOW	23.2 (1.1)	1.3 (.1)	26.1	.038 (.019)	.053 (.026)
4. MARIAS PASS	20.0 (.7)	1.1 (.1)	13.0	.024 (.013)	.034 (.023)
5. WYOMING	21.1 (.5)	1.2 (.1)	21.7	.074 (.042)	.055 (.028)

* A locus is considered polymorphic if the frequency of the most common allele does not exceed .99

** Biased estimate (see Nei, 1978)