Technical Report No. 211

THE ECOLOGY OF THE NESTING BIRDS OF PREY OF NORTHEASTERN COLORADO

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ABSTRACT

The potential for long-term raptor research and management in northeastern Colorado is great. This paper includes fundamental data concerning nesting phenologies, general life histories, population densities, biomasses, reproductive performances and food habits of raptors which nest on the shortgrass prairies of Colorado. The data were collected between 1 May 1969 and 1 September 1972. Also included are analyses and/or discussions of the following: 1) field techniques and definitions of nesting parameters, 2) the effects of historical and current activities of man on nesting performances, 3) comparisons of current and past population levels of selected species, 4) the effects of certain weather conditions on nesting phenologies and successes, 5) differential use of summer habitats and nest supports, and 6) the importance of interspecific differences in nesting phenologies. Finally, a thorough, long-term study of population dynamics, management techniques and emergency conservation measures applicable to raptorial birds is outlined in detail. All of this information should benefit ecosystem analysts and/or wildlife managers in their respective endeavors involving grassland birds of prey.

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PREFACE

The following report is an update of U.S. IBP Grassland Biome Technical Report No. 151 (Olendorff, 1972b). As such, some of the same material is repeated herein, but an additional year's data has allowed considerable expansion and more thorough analyses of certain relationships. Differences between this report and Technical Report No. 151 include the following: 1) analysis of a three-year rather than a two-year study period, 2) comparison of breeding densities and productivities on a 414-sq mile "unbroken" grassland study area with the same nesting parameters on a 1,000-sq mile study area which is a composite of unbroken grassland, creek bottom, cliff and cultivated habitats, 3) an in-depth analysis of all data collected on the nesting of grassland raptors at man-created nest sites, 4) a preliminary analysis of predator-prey relationships, and 5) a lengthy and detailed outline of much needed, further raptor research for which northeastern Colorado has unlimited potential. The latter was the subject of a proposal submitted to the National Science Foundation entitled "A Study of Population Dynamics, Management Techniques, and Emergency Conservation Measures Applicable to Raptorial Birds." The inclusion of much of that proposal herewith is justified, since the Colorado Division of Wildlife matched IBP funding in 1972 partially to obtain suggestions for further research.

Virtually all aspects of this report are in various stages of preparation for publication in scientific journals.

The guts of the NSF proposal will be published under the joint authorship of Richard R. Olendorff and John W. Stoddart, Jr. The materials on the dangers of raptor nesting studies is being combined with additional material for joint publication by Richard R. Olendorff and Richard W. Fyfe of the Canadian Wildlife Service. The discussions of nesting parameters will be expanded and published by several workers in the field under joint authorship. Some of the life histories will be published by Richard R. Olendorff and John W. Stoddart, Jr., particularly that of the ferruginous hawk. The section on habitat use and nesting at man-created nest sites by grassland raptors has already been submitted to Wilson Bulletin. The following sections are in their first draft in the present report: 1) "Population Levels and Productivities", 2) "Predator-prey Relationships", and 3) "Further Considerations". Criticism of all parts is welcomed. As a composite of several papers in preparation, a few, brief redundancies will be noted, but these provide continuity within the individual sections.

In light of the potentially detrimental popular interest in raptors, I will continue the precedent of previous studies by not giving exact nesting localities for public record.

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THE PROBLEMS OF RAPTOR RESEARCH PERTINENT TO THIS REPORT

Historically, public interest in birds of prey has been directed toward either indiscriminate destruction or total protection of the birds. A trend toward the latter has developed in the United States during the past 30 years or more. The most recent step in that direction was the signing in 1972 of a new migratory bird treaty between the United States and Mexico which placed all birds of prey under federal jurisdiction. With this jurisdiction also came a responsibility, albeit not explicitly stated, to conduct research into the problems confronting birds of prey in the changed environment created by drastically increased human occupation and development.

Protection of birds of prey as a valued natural resource can never be total or complete; direct and indirect pressures of human interference are relentless. Examples are the eagle poisonings, shootings and electrocutions in Wyoming and Colorado in 1971 (Olendorff, 1972a). Others include increased demand for raptors by falconers and zoological gardens, increased activity of amateur ornithologists and photographers, and shooting of birds of prey by irresponsible hunters and owners of game bird farms. In addition to these immediate or proximate factors, there are several subtle, ultimate causes of raptor population decline such as habitat destruction, continuing global development of intensive agriculture and attendant use of chemicals, and continuing emission of environmental pollutants in general.

All of the above is happening when in fact 1) birds of prey, as end of the food chain organisms, have proven to be important barometers of environmental contamination; 2) most are important components of balanced ecosystems; 3) raptorial birds are aesthetically pleasing to a growing number of people who appreciate birds and wildlife in general; and 4) many birds of prey are declining in numbers, some to the point of being considered rare and endangered species by most authorities. Scientists, naturalists, conservationists and mankind in general all stand to benefit from basic and applied research aimed toward raptor management and conservation, and the evaluation of the role of birds of prey in the ecosystem.

There is, nevertheless, no state or federal wildlife agency in North America which manages a single raptor (excluding the California condor (Gymnogyps californianus)) from a position of adequate knowledge of ecology and population dynamics. It was suggested in 1965 during the conference on peregrine falcon populations at the University of Wisconsin (Hickey, 1969) that one outcome of the conference should be "imaginative research and action...to determine the extent that management of birds of prey is possible" (M. W. Nelson, 1969b, p. 407). With the California condor the only approach is to eliminate all interference and hope for the best. There is little opportunity of doing imaginative research to save this condor. All other North American raptors allow considerably more latitude for manipulation and research, because of higher populations and a higher tolerance of human presence, but there is a fundamental lack of knowing just what to do in the field if the birds are to endure.

In short, the concept of raptor management lacks field tested principles -- principles which wildlife agencies throughout the world urgently need. There is further need of these principles by investigators who are attempting to evaluate whole ecosystems, such as the group studying the structure, function and utilization of grassland ecosystems.

There are many reasons for the pausity of useful information concerning population dynamics, energy utilization and the function (at the ecosystem level) of raptors. Not the least important of these reasons is that most raptor population studies have been seasonal and have not been made over the same area for several seasons, much less several full years. Furthermore, studies of raptor population dynamics have typically involved one or two common and/or spectacular species, often only in their dominant habitat along a cliff line, river or gallery forest. The bulk of substantive raptor studies suffer from these biases, biases resulting from the determination of only ecological densities, as opposed to crude densities in an area representative of the total habitat used by a local population of birds (Odum, 1971). Synthesis of concepts from biased population studies carried out in different years, in widely scattered areas, on one or two species at a time, and with varying techniques is not the most fruitful approach to the problems raised by the urgent need to manage the birds of prey and to evaluate their function in the ecosystem. Raptor population dynamics and predator-prey relationships are much too complex for such piecemeal analysis.

Meaningful conclusions concerning the role of birds of prey as top carnivores are best based on long-term population monitoring. Management of populations can only follow basic research into the principles of raptor ecology and population dynamics. Such basic study must include determination of both crude and ecological nesting densities in large areas, quantification of annual productivity, estimation of mortality rates of the various age classes within the population, estimation of relative population levels during migration and wintering periods, and elucidation of annual and longer-term cycles, climatic effects and other phenomena affecting population dynamics. Additional information such as historical occupancy of nests by individual birds, and intra- and interspecific competition between individually recognized birds (as can be obtained through banding and color marking), adds another level of refinement to studies of population dynamics. Finally, as can be determined by radio tracking, the sizes of nesting and winter territories of birds in the populations under study are useful in evaluating the importance of birds of prey. Many of the above represent specific areas of high priority research involving birds of prey which await adequate interest and funding.

Year-round, areal studies of groups of birds of prey were initiated by John J. and Frank C. Craighead. The most complete and authoritative work on avian predator-prey relationships is their Hawks, Owls and Wildlife (Craighead and Craighead, 1956) which resulted from their field work. The impact of this pioneering investigation was great. The Craigheads were at some disadvantage, however, in that they had to collect an enormous amount of ancillary data on weather conditions, history of the study areas, etc., and their study areas were too small (two 36-square mile areas) to allow accurate extrapolation of their data to larger land areas. A multi-faceted and penetrating approach must be made if quantitative data concerning population dynamics, ecological impact, management and conservation are to be synthesized, and this must involve large land areas.

Another serious problem which is evident from the literature is that quantitative studies of prey population levels usually have not been conducted simultaneously with raptor population studies. The work of the Craigheads is an exception. Other notable exceptions include Hagen's (1969) study of reproduction of birds of prey in relation to microrodent population fluctuations, and the study of the golden eagle in relation to its food supply in Scotland by Brown and Watson (1964). Hamerstrom (1969) noted a close correlation between marsh hawk production in Wisconsin and vole abundance in a three state area including Wisconsin from 1961 to 1965, although vole abundance was not measured specifically on the Wisconsin study area. More recent studies confirm the direct relationship between the success of nesting harriers and the population level of voles on the Buena Vista Marsh in Wisconsin (Hamerstrom, pers. comm.). Lack (1966) analyzed a similar relationship between tawny owls (*Strix aluco*) and several species of rodents.

In general, however, most studies of predator-prey relationships have not been approached at levels which would allow adequate estimates of energy flow from the prey resources through the raptor populations present. To allow such analysis data must be collected to deal with 1) biomass dynamics of both the raptor and the prey populations, and 2) the quantitative and qualitative food requirements of the raptors. Both spatial (density) and temporal considerations must be made with regard to 1) and 2). This report includes information of these types, but further study of most species is warranted.

Craighead and Craighead (1956) went a long way toward demonstrating the role of birds of prey as predators. Perhaps the most significant studies of this type are being done by the faculty and students of the Department of Wildlife Ecology at the University of Wisconsin. A 60-sq mile study area near Rochester, Alberta, is under intensive study by the group. With regard to raptors, emphasis has been on red-tailed hawks (Luttich, Rusch, Meslow and Keith, 1970; Luttich, Keith and Stephanson, 1971), great horned owls (Rusch, Meslow, Doerr and Keith, 1972), and broad-winged hawks (Rusch and Doerr, 1972). In several cases this research team has shown a response of raptor populations to changing prey densities. Their techniques yield data which indicate rates of exploitation of prey by certain of the raptorial birds under study, a virtually unprecedented research approach.

It is this type of study which must form the basis for future research involving predator-prey relationships. Such analyses for several grassland species could be developed along the following line of reasoning. a) There is a determinable number of individual adults of each raptorial species per unit area at any given time (Olendorff, 1972b; Olendorff, this report). b) These birds utilize food equal to a certain percentage of their body weight per day (Brown and Amadon, 1968). c) The adults produce a certain number of young each year (Olendorff, 1972b; Olendorff, this report). d) A quantity of food (in grams) is required to produce a kilogram of hawk through 45 days of age (Olendorff, 1971b). e) This represents a quantity of food removed per unit area of territory size. f) From qualitative dietary information (Olendorff, this report; Marti, 1970) for grassland raptors, the number of each prey species taken per unit area can be calculated. g) Comparisons of these numbers with quantitative prey population data available for the area will show the effects of birds of prey on their prey species (or vice versa). Particularly useful information for the final stage of the analysis outlined above will come from IBP bird studies (Gietzentanner, 1970; Strong and Ryder, 1971; Strong, 1971; Porter and Ryder, in press), small mammal studies (Flake, 1971; Donoho, 1971; Grant, 1972), and insect studies (Van Horn, 1972).

THE POTENTIAL OF RAPTOR RESEARCH IN GRASSLANDS, WITH PARTICULAR REFERENCE TO NORTHEASTERN COLORADO

The Pawnee National Grassland (PNG), administered by the U.S. Forest service, and adjacent, privately-owned lands provide nesting habitat and food for one of the densest populations of raptorial birds in North America. Birds of prey abound in the shortgrass prairie when it is broken by scattered trees, gallery forests along creek bottoms, isolated erosional remnants and major cliff lines. Within any given year, of North America's 30 species of falconiforms, 16 or 17 use this portion of northeastern Colorado; 6 or 7 of this continent's 15 owls are part of the same avifauna (Table 1).

The occurrence of 24 species of raptors in a study area, eleven of which breed there, provides an excellent opportunity to study them as a group of predators, to study their intra- and interspecific relationships, ecological and relative nesting densities, differential utilization of grassland habitats, annual and longer term cycles, predator-prey relationships, migration patterns, and most aspects of their behavior. The opportunity for a complete analysis of the role of a group of birds in an ecosystem is available.

In addition to the above listed basic studies which either have been or could be conducted on the PNG, there are many problems of an applied nature which could be solved simultaneously. Nesting populations of golden eagles, prairie falcons, American kestrels, Swainson's hawks, ferruginous

TABLE 1. Species of birds of prey observed or expected on the Pawnee National Grassland. (F, fall; W, winter; Sp, spring; Su, summer.)

Species	Status
Turkey Vulture (*Cathartes aura*)	Rare FSp
Osprey (*Pandion haliaetus*)	Rare FSp
Bald Eagle (*Haliaeetus leucocephalus*)	Uncommon W
*Marsh Hawk (*Circus cyaneus*)	Common FWSpSu
Northern Goshawk (*Accipiter gentilis*)	Uncommon FWSp
Sharp-shinned Hawk (*Accipiter striatus*)	Uncommon FWSp
Cooper's Hawk (*Accipiter cooperi*)	Uncommon FWSp
*Swainson's Hawk (*Buteo swainsoni*)	Abundant FSpSu
Red-tailed Hawk (*Buteo jamaicensis*)	Common FSp, Uncommon WSu
*Rough-legged Hawk (*Buteo lagopus*)	Abundant W
*Ferruginous Hawk (*Buteo regalis*)	Common FWSpSu
*Golden Eagle (*Aquila chrysaetos*)	Common FWSpSu
*American Kestrel (*Falco sparverius*)	Common FSp, Uncommon WSu
Merlin (*Falco columbarius*)	Uncommon W
*Prairie Falcon (*Falco mexicanus*)	Common FWSpSu
Gyrfalcon (*Falco rusticolus*)	Very Rare W
Peregrine Falcon (*Falco peregrinus*)	Rare FWSp
Barn Owl (*Tyto alba*)	Uncommon FWSpSu
Screech Owl (*Otus asio*)	Rare FWSpSu
*Great Horned Owl (*Bubo virginianus*)	Common FWSpSu
*Burrowing Owl (*Speotyto cunicularia*)	Common FSpSu, Rare W
Long-eared Owl (*Asio otus*)	Uncommon FWSpSu
Short-eared Owl (*Asio flammeus*)	Rare FWSpSu
Snowy Owl (*Nyctea scandia*)	Very Rare W

* Major raptors on the Pawnee National Grassland.

hawks, red-tailed hawks, great horned owls and burrowing owls (scientific names in Table 1) are sufficiently high to allow experimentation with ways to circumvent heretofore unchecked natural and unnatural conditions which lower nesting success, and to test methods of introducing new, captive-bred stock into wild populations. Experiments to increase population levels significantly and to explore many combinations of foster parentage (see below) are also feasible.

That such study should be done in Colorado follows from the forward-looking approach of the Colorado State Division of Wildlife to raptor management and conservation. The Division actively supports study of birds of prey in Colorado, cooperates fully with federally funded golden eagle research, and employs a non-game biologist, Gerald Craig, to deal specifically with birds of prey.

Another important source of logistical and informational support is the U.S. Forest Service, Roosevelt National Forest, which administers the PNG. Local Forest Service personnel have decades of experience with the plant and animal life of grasslands. The presence of the International Biological Program (IBP), Grassland Biome Project, Pawnee Site, and Colorado State University allows highly integrative and more thorough analysis of data than would normally be the case.

The merit of northeastern Colorado as a study area also stems, at least in part, from the rather stable land-use practices of the relatively few current owners. The acquisition of land by the federal government to create a national grassland was a definite stablizing factor but so, too, were the attempts at farming made by the homesteaders of the late 1800's and early 1900's. These early settlers learned by experience that the non-irrigable land of northeastern Colorado was suitable for only two forms of agriculture, namely cattle ranching and dry-land grain production. Barring the development of spectacular irrigation projects and unnatural decimation of the birds of prey of the region, their habitat and nesting populations should remain relatively unchanged. It is possible that raptor populations may tend to improve locally during the next several decades, although slow changes are presenting problems. Nevertheless, the resistance to change which has developed in the ecology of the area is an attribute which will give researchers time to solve some of the basic problems of raptor biology and to field test a number of applied raptor management and conservation techniques.

It is also important to note that, as an area where dry-land farming prevails and forest insect control is not necessary, the historical use of persistent pesticides near the PNG has been lower than in most other areas in the continental United States. The PNG is part of a semi-arid ecosystem in which persistent pesticides do not accumulate or move readily. Thus, with the possible exception of prairie falcons and Swainson's hawks, the adverse effects of pesticides are probably at a minimum. This should be verified by further study, yet the relative lack of pesticide applications is an important attribute of the area making it more appropriate for long-term study than contaminated areas with raptor populations.

Another notable advantage of the study area is that crude nesting densities for large raptors can be determined with accuracy which approaches very closely what might be termed "absolute" nesting densities, because of the ease with which nests can be located in grasslands. For example, nearly 100 per cent of the Swainson's hawks, 88 per cent of the great horned owls, 69 per cent of the ferruginous hawks, and 26 per cent of the golden eagles can be located simply by walking the narrow gallery forests along creek bottoms and visiting isolated trees (Olendorff, 1972b; Olendorff, this report). Nearly all of the prairie falcons and over half of the golden eagles can be found on cliffs which have well defined geographical limits. Even isolated erosional remnants, creek banks and man-made structures can be searched systematically by following the stream courses and visually sighting the small outcroppings, buildings and windmills on which raptors might nest. Furthermore, visibility is complemented by the accessibility provided by an extensive network of section line roads and trails by which ranchers monitor their cattle herds.

Thus, the lack of diversity of nesting habitats, the sparseness of gallery forests, the precise limits on the types and distribution of cliffs, and the visibility of isolated trees, erosional remnants and abandoned farmsteads, allow accurate, systematic determinations of nesting population densities of large raptors in grasslands. One or a number of these advantages are absent in most other eco-systems. Visibility and accessibility are usually problems in coniferous, deciduous or mixed forests, the diversity of habitats not withstanding. Accessibility is a serious problem in desert and tundra biomes.

Virtually no ecosystem in North America other than grasslands allows study of a large enough land area to evaluate adequately the use of that ecosystem by birds of prey. Furthermore, grasslands have relatively simple, sparse avifaunas which allow more complete ecological analyses than other more diverse habitats (Wiens, 1969). Contributions of comprehensive studies of grassland raptors to basic raptor population theory would be great because of the potential depth and accuracy of the collectable data.

There is also considerable background information available from non-IBP sources and IBP sources not mentioned above. Descriptions of the life histories of the birds of prey, surveys of the raptor populations, evaluations of the potential of the area for fruitful research, and research on selected birds of prey of the region have been completed. Study in 1971 and 1972 supported by the American Museum of Natural History, the International Biological Program (Grassland Biome), the Colorado State Division of Wildlife, and Colorado State University has resulted in an adequate understanding of the above listed basic information. Furthermore, considerable raptor research was done in the area prior to 1971 (Bailey and Neidrach, 1933; Webster, 1944; Enderson, 1964; Ryder, 1969 for a synthesis of several previous studies; Craig, 1970; Marti, 1970; Boeker and Ray, 1971). Some studies, such as Boeker's aerial census of golden eagles for the U.S. Bureau of Sport Fisheries and Wildlife, are still in progress.

Research on the birds of prey of the PNG and adjacent areas has and will continue to produce significant results. Such research could culminate in the creation of America's first large-scale raptor management area, in addition to being a model for the conservation of birds of prey in many other parts of the world. The land area and raptor populations on the PNG are large enough to set up experimental and control study areas (see below); the private land owners are amenable to biological research; and the research potential goes far beyond the usual natural history studies. Many rare and endangered raptors would benefit from the techniques developed and the knowledge gained from studies of grassland raptors in northeastern Colorado. All things considered, a "statement of the problem" becomes a "description of the opportunity." Rarely does the research atmosphere (CSU and interagency cooperation) match the potential for significant research (ample raptor populations and study areas) to such a high degree.

OBJECTIVES

The general objectives of the study dealt with in this paper include the following:

1) to document the status and timing of the reproductive cycles of the large birds of prey nesting in northeastern Colorado,
2) to determine crude population densities and productivities of the large birds of prey nesting on a 414-sq mile area of unbroken grassland,
3) to determine crude population densities and productivities of the large birds of prey nesting on a 1,000-sq mile area including four different grassland habitats (creek bottoms, cliffs, planted agricultural land, and unbroken grassland),
4) to calculate and discuss the biomasses of the birds of prey in the two grassland study areas,
5) to provide a preliminary analysis of food habits of the large birds of prey in northeastern Colorado,
6) to evaluate some of the factors, such as man's activities, which influence population densities and nesting habits of birds of prey, and
7) to suggest further raptor research for which there is significant potential in northeastern Colorado and grasslands in general.

METHODS

Recent Raptor Research in Northeastern Colorado; Acknowledgements

The raptorial birds of northeastern Colorado have been studied by several ornithologists and students during the last 10 years (see Ryder, 1969, 1972). Through the coordination of the IBP Grassland Biome Project, and Dr. Ronald A. Ryder of the Department of Fishery and Wildlife Biology, Colorado State University, past studies have been reviewed and evaluated, and limited opportunities for study were provided in 1969 and 1970. Following the initiative of Gerald Craig and myself, funding from the Frank M. Chapman Fund of the American Museum of Natural History and the IBP (through Dr. Ryder) made it possible to carry out more intensive study of these top carnivores in 1971. Subsequent funding from the Colorado Division of Wildlife and IBP provided the opportunity for further study in 1972. This report includes analyses of studies conducted between 1 May 1969 and 1 September 1972.

During the spring of 1969 I sought only enough nests in the area to acquire eggs for my laboratory studies of the growth of ferruginous, red-tailed, and Swainson's hawks (Olendorff, 1971b). During the summer of 1970 Gerald Craig and I, with some assistance from John W. Stoddart, Jr., of Eaton, Colorado, located over 70 raptor nests in northeastern Colorado and banded about 40 young birds in our spare time. We collected a small amount of food habits data, growth data and behavioral observations, but the important input from that summer was the base it established for study in 1971.

Study in 1971 was quite intense. From 15 March through 10 October my full-time work involved all aspects of the biology of the birds of prey of the PNG and adjacent areas as part of a post-doctoral fellowship from the American Museum of Natural History. Emphasis was placed on Swainson's and ferruginous hawks, although considerable data on the other large nesting birds of prey were collected (Olendorff, 1972b). Gerald Craig, then a Master's Degree candidate in wildlife biology, was very helpful during the first half of the study period. Calvin Sandfort of Denver, Colorado, provided much needed field assistance. The inspiration and encouragement of Dr. Dean Amadon, Department of Ornithology, American Museum of Natural History, and of Dr. Ronald A. Ryder, Department of Fishery and Wildlife Biology, Colorado State University, are gratefully acknowledged.

In 1972, with matching funds from the Colorado Division of Wildlife and IBP, I was able to spend the period from 18 March through 1 September in the field while a Field Associate of the Department of Ornithology, American Museum of Natural History. Study in 1972 was essentially the same as in 1971, except for the establishment of a large study area (1,000 sq miles) in which crude nesting densities were determined (see below). Norman A. French of the Natural Resources Ecology Laboratory, Colorado State University, and Gerald Craig, Robert Tully and Wayne Sandfort of the Colorado

Division of Wildlife were instrumental in obtaining funds for the second season of full-time effort. John W. Stoddart, Jr., as a salaried field assistant, provided countless hours of able assistance and stimulating discussions while in the field in 1972. His input to the section of this report on suggestions for further research is significant. Dr. Gustav A. Swanson of the Department of Fishery and Wildlife Biology, Colorado State University, was helpful throughout the course of the present study. The permission to study on the PNG was granted by the administrators of the U.S. Forest Service, Roosevelt National Forest. Dale Wills, wildlife biologist for the Roosevelt National Forest, was particularly helpful. Probably the most important contribution to the project was by the owners of the non-federal lands, who were very amenable to biological research on their property and often provided useful field information.

The Study Areas

Three different study areas will be mentioned in this report. The largest, hereafter called the <u>extensive study area</u>, consists of the northern 34 miles of Weld County, Colorado, excluding the highly populated and farmed area west of Purcell and south of Nunn (Fig. 1). The total land area is approximately 2,000 sq miles (5,180 km^2). All data from the extensive study area cannot be analyzed in terms of raptors per unit area because the eastern half was not systematically and completely searched for nests. The data from both halves

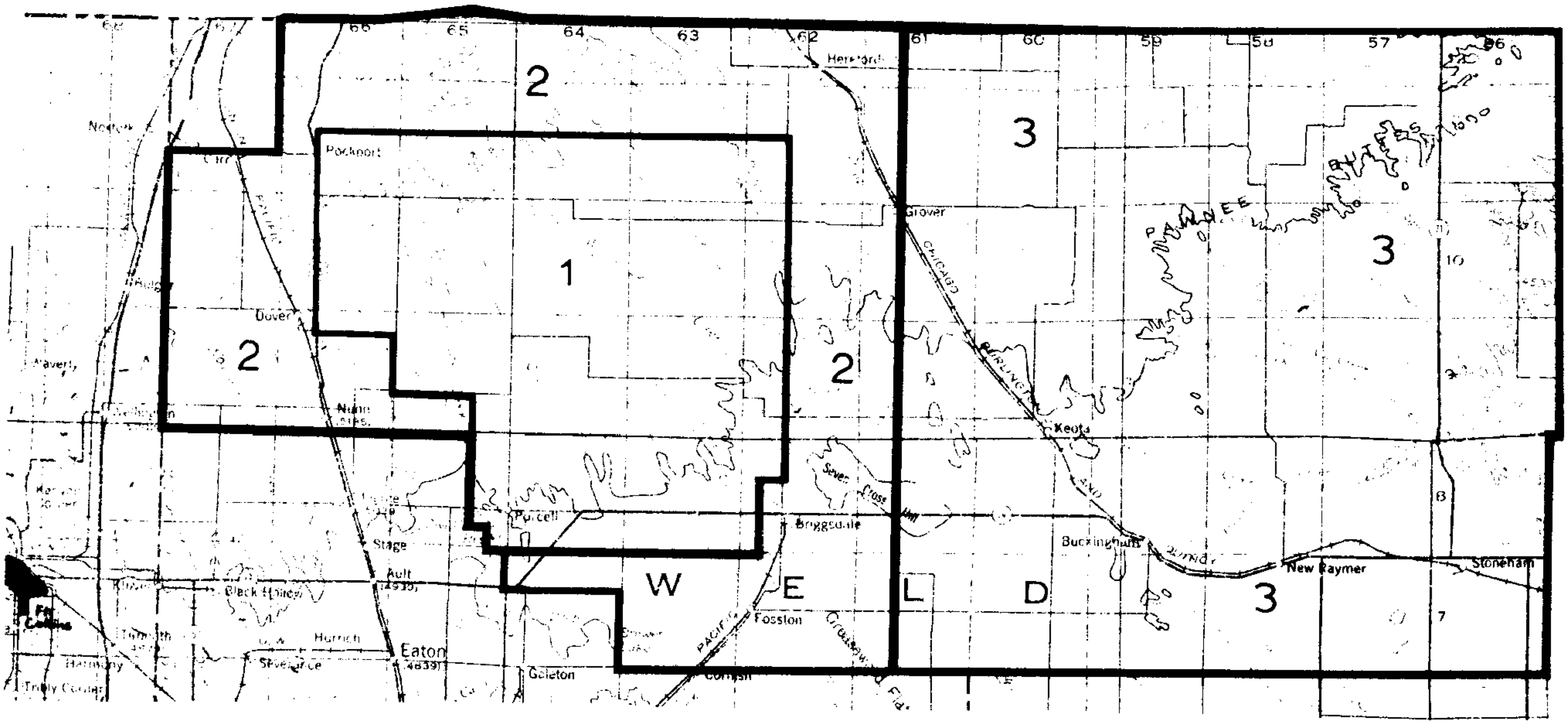

Figure 1. Map showing the relationship between the extensive, 1,000-sq mile and 414-sq mile study areas. 1 = 414-sq mile area. 1 + 2 = 1,000-sq mile area. 1 + 2 + 3 = extensive area.

of the extensive study area are useful for analyzing overall clutch sizes, brood sizes, fledging successes, nest site preferences, etc.

The 1,000-sq mile study area comprises the western half of the extensive study area, including the IBP Pawnee Site, the Central Plains Experimental Range, the entire western portion of the PNG, one large and several smaller creek bottoms, and a major line of cliffs (Fig. 1). This area, a composite of unbroken grassland and grassland interrupted by gallery forests along creek bottoms, cliff lines and tracts of cultivated land, was designed 1) to include sufficient numbers of nesting raptors to allow fruitful study and 2) to eliminate biases introduced by studying small areas not representative of all available nesting habitats. The data from the 1,000-sq mile area could reasonably be used to estimate raptor populations in much of eastern Colorado and Wyoming, and portions of western Nebraska and Kansas.

The 414-sq mile study area includes essentially unbroken grassland, i.e. shortgrass prairie without major cliff lines, creek bottoms and attendant gallery forests, and large tracts of cultivated land. Geographically, this area corresponds to the western portion of the PNG and is included within the 1,000-sq mile and extensive study areas (Fig 1). Analyses of population levels and productivities are made for this area, since it is shortgrass prairie of the type emphasized in IBP studies; it is similar in topography, flora and fauna to the IBP Pawnee Site (Jameson and Bement, 1969).

As the 414-sq mile study area was searched for nests in 1971, each section was classified as being grazing land or cultivated land, and all trees and other potential nest sites were noted (Table 2). Only about 27 sq miles (6.5%) were cultivated, and the largest continuous tract of cultivated land was about 7 sq miles. Of the 414 sections only 79 contained trees suitable for nesting by large birds of prey. Another 8 sections contained creek banks or small erosional remnants which might attract ferruginous hawks to nest, for a total of 87 sections (21.0%) with nest sites. Roughly 50 sections had occupied dwellings, i.e. about one for every 8 sq miles. The remaining 250 sq miles (60.4%) of the study area was grazing land without houses, trees or other suitable nest sites. In all, 387 sq miles (93.5%) was grazing land. All of the land, including the cultivated land, was suitable for use by birds of prey either as hunting or nesting territory with the possible exception of 50 quarter-sections adjacent to occupied dwellings. Thus, about 97% of the land was usable by raptors without much interference from man. Similar analyses of the 1,000-sq mile and extensive study areas have not been undertaken.

The accuracy of the determinations of nesting densities and productivities in areas as large as those involved in the present study would be evident to most people only after personal contact with the study area and the techniques involved. In general, it is reasonably certain that the nests of over 95 per cent of all golden eagles, prairie falcons,

Table 2. Land-use practices on the 414-sq mile (1,073 km^2) study area.

Land-use Practices	Sq Miles	Percent
Cultivated	27	6.5
Grazing		
With occupied houses	50	12.1
With raptor nest sites	87	21.0
Without houses or nest sites	250	60.4
TOTALS	414	100.0

Swainson's hawks, ferruginous hawks and great horned owls were found on the designated study areas. It is possible that all pairs of golden eagles and prairie falcons were located on the intensive study areas in the respective years. Perhaps, some of the nests of the other species (surely not more than 5 per cent) were missed for various reasons: 1) Swainson's hawks were very numerous and, apparently, were the most capable of renesting after nest failure; 2) ferruginous hawks occasionally nested on the ground making it difficult to locate this small segment of the breeding population; and 3) great horned owls began nesting before field study was initiated both in 1971 and 1972.

In general, then, the present report deals with the major raptorial species on the PNG as a group of predators which nest in and exploit the prey base of a number of shortgrass prairie habitats. All of the habitats are included in the areal component of the crude breeding density calculations (see below).

The Dangers of Raptor Nesting Studies

Eggs and nestling birds, since they are tangible and stationary parts of the raptor breeding cycle, have been studied from almost every viewpoint imaginable. Throughout the history of ornithology they have been counted, collected, weighed, measured, photographed and often jeopardized by frequent observation. The determination of clutch size, incubation period, egg coloration, physical and chemical characteristics, and egg collecting for the sake of collecting have too often been done at the expense of the birds. So, too, has some research involving nestlings. Our current, extensive knowledge of nesting birds is, regardless of such detrimental effects, the result of this research.

There is a very poignant sentence which relates to the negative side of this matter in the introductory pages of Francis Heatherley's (1913) book The Peregrine Falcon at the Eyrie: "This book is dedicated to all egg collectors in the hope that someday they will realize that the shell is not the most important part of a bird's egg." A similar sentence could be composed lamenting the fact that countless birds' eggs and young have been accidentally destroyed in the field by contemporary biologists, falconers, bird protectionists and the general public. It is not within the scope of this paper to justify the motives of the four groups listed. Nevertheless, there is often a total lack of both compassion and understanding when a nest is discovered. Clutch size and other egg-related parameters, for example, may be unnecessary parts of an overall study, yet these data are usually collected "just for the record." When a bird watcher finds a nest, he often climbs to it immediately for no valid reason. Unfortunately, some amateur and professional "ornithologists" do not keep in mind that the eggs or young they may place in jeopardy by visiting nests are the means to an end, i.e. to the production of fledglings and, subsequently, new breeding stock.

Twentieth Century research involving birds' eggs and young must not suffer from this disregard for the birds. This is particularly true of those raptors showing population declines. Refined field techniques must reflect a concern for the study material -- a concern which is dependent upon common sense for the most part. Similarly, current researchers must not ignore the voluminous literature dealing with raptor eggs and young (see Olendorff and Olendorff, 1968-1970). There is a lot to be learned before the first step is taken into the field, not to mention the first step up a tree or down a cliff to a nest.

In part, the information presented in this section may seem superfluous to professional ornithologists and naturalists. Hopefully, some professionals will benefit from the introspection stimulated by the ideas presented, inexperienced field biologists will profit from the discussions, and a decrease in raptor nest interference will result.

When a nest is visited: 1) parent hawks may become so vexed that they desert their eggs or young completely; 2) the chances of egg breakage by the parent birds are increased, as are the chances of cooling, overheating, loss of humidity and avian predation (such as by crows and magpies) of eggs; 3) newly hatched birds of prey may be chilled or overheated and even die in the absence of brooding; 4) one or more feedings may be missed; 5) the parents may not return before nightfall if the nest is visited late in the day; 6) older nestlings may fledge prematurely and break bones at the end of a futile first flight or be forced to spend one or several nights on the ground where vulnerability to predation is very high; 7) mishandling may damage feathers, bones and claws; 8) mammalian predators may follow scent trails directly to the eggs or young; 9) the attention of other humans may be attracted; and 10) on cliffs, rocks might inadvertently be knocked onto eggs or young birds. It is not unknown for the weight of a climber to break the limb on which the nest is situated. Fortunately, selection acts very quickly against such incompetent "biologists."

In the following paragraphs each of the above listed problems is discussed. An assessment of the seriousness of each problem and suggestions for minimizing the adverse effects of human disturbance are included.

Accidental Trampling. Parent birds may crush eggs, trample newly hatched young or eject the young from the nest in the excitement of being forced suddenly from a nest. The fact that raptors sit very tightly on a nest during incubation and the early days following hatching complicates the matter considerably. Some birds will not leave a nest until a climber is halfway up the tree or down a cliff (Brown, 1953; Cade, 1960; and many others), particularly at the precise time of hatching. A simple circumstance like the end of a stick popping up after being stepped upon at the opposite end can crack an egg or hurl a young bird out of a nest. The downbeat of hurried wings is another source of trouble.

It is second nature for a person to want to sneak up on an incubating or brooding bird to get a closer look or a photograph. Flushing a bird from a nest by startling it invites disaster. It is much better to let your presence be known long before you are ready to climb. This can be done by whistling, talking or making an approach within sight of the nest. The latter is best, since some raptors respond poorly, if at all, to auditory signs of a human's approach. If you approach the nest tangentially rather than directly, your approach is slowed and the parent can stand before flying off unhurriedly. This is much better than flushing it quickly when you are halfway up the tree. Visual warning is almost unavoidable in grasslands, where our experience does not include a single incident of eggs or young being seriously damaged by adults leaving nests during nest visits.

Cooling, Overheating and Loss of Moisture from Eggs. Overheating is a very serious problem with eggs. Direct sunlight should be strictly avoided. Unattended eggs do not receive the normal transfer of moisture from the brood patch to the eggs and may become somewhat dehydrated in dry air and the heat of the sun. One need not worry about cooling of eggs except in extreme cases.

In the xeric conditions of many grasslands young birds become overheated more easily than in deciduous forests or other biomes. Many nests of Swainson's hawks, ferruginous hawks and golden eagles do not give shade to eggs in the absence of an adult. Ferruginous hawk eggs seem very sensitive to overheating, particularly at hatching (Olendorff, 1972b). When a nest is not shaded, all visits should be restricted to the cooler part of the day, before noon.

Keep visits short, relatively unobtrusive and as timely as possible with regard to weather, sun position and the time of day. If an extended visit is planned, put the eggs into a fur-lined glove or cover them with a cloth to slow down the loss of heat and moisture. Most important of all, be justified in making the nest visit in the first place and avoid, if possible, visiting nests at the precise time of hatching.

Avian Predation. The chance encounter between an avian predator and an undefended nest full of eggs is impossible to interdict, particularly since your presence may have attracted the predator. Most avian predation of eggs probably occurs after nest desertion from other causes.

Desertion. The failure of the parents to return to eggs or young is probably the most serious, and is certainly the most unpredictable, problem. The nest-building, egg-laying and incubation phases are very critical periods during which the slightest disturbance may cause nest abandonment. The most critical time is likely just prior to laying when the female spends many hours sitting on her empty nest (Nethersole-Thompson and Nethersole-Thompson, 1933). There is much variability depending upon the general tolerances of the species, the idiosyncrasies of individuals and the "level of acceptability" of nest sites (Ratcliffe, 1962; Hickey, 1942; and many others).

It has been widespread experience that ferruginous hawks are very prone to nest desertion during the early stages of nesting. In our studies we do not climb to active ferruginous hawk nests until hatching has occurred. In Colorado, Swainson's hawks and prairie falcons rarely desert after a visit during the incubation period. In Saskatchewan, however, Stuart Houston (pers. comm.) maintains a hands-off policy with Swainson's hawks like our policy for ferruginous hawks. We now do the same, not being willing to risk even occasional nest desertion. Ospreys seem to be the most tolerant of all raptors during the early stages of nesting. They can be trapped, banded and color marked at their nests, and will tolerate their eggs being moved from nest to nest without deserting. In our experience great horned owls are about as tolerant. What a boon to ornithologists it would be if all species were as cooperative!

Field experience pays great dividends in avoiding nest desertion. Performance records of particular pairs of birds over the years, the success at specific nest sites and the tolerances of the species involved come into play. Unfortunately, the experiences of the biologists I have talked to have been as diverse as the birds under study.

Some trends are noteworthy, however. 1) All things considered, desertion is less likely the longer incubation is allowed to progress. If at all possible, visits should not be made until all of the eggs have hatched. It is not difficult, given a spotting scope and a little field time, to determine <u>from a distance</u> whether or not hatching has occurred. 2) If a pair (or nest) has been consistently unsuccessful in the past, chances are desertion will occur more readily. Stay away from such birds and nest sites. Enderson (1964) points out that prairie falcons often nest in an eyrie the year after a total failure. 3) Several short visits are better than one lengthy visit. If a blind or other data acquisition equipment must be installed at a nest, spread the work out, with short visits every other day (or even less often if possible). 4) It is very uncommon for raptors to desert a nest after the young have hatched. The intensity of nest defense by most adult raptors increases as the nesting period progresses (coincidental with a decrease in the possibility of desertion). Our routine nest checking for prey items, intensive banding studies and growth research in the field involving nearly 400 nesting attempts by eight species of grassland raptors have not caused a single desertion of nestlings to our knowledge.

Heat Prostration and Chill. As with eggs, young hawks can withstand far more cooling than heating; except when ambient temperature is below about 45^{o} F, no attempts to warm even newly hatched young are necessary during brief nest visits. The young of early nesting great horned owls can withstand even more cooling. In the Arctic, study would surely be hampered by absolute rules concerning temperature and weather; research methods must fit the area under study. The physiological (and psychological) limits of the birds must weigh heavily in all decisions, however.

Young birds have mechanisms, such as panting and crawling to shade, to deal with normal high temperatures in nests.

Intense, direct sunlight, however, can be fatal to young raptors. M. W. Nelson (1969a) recorded several instances of heat-caused death of young golden eagles. Kochert (1972) found that 32 per cent of the mortality of nestling golden eagles along the Snake River in Idaho was probably caused by heat prostration. The outward distress of young raptors exposed to direct sunlight and the shading of young by adults during the heat of the day are indicative of the danger involved.

Missed Feedings. The failure of a young hawk to get one (or even several meals in a row) is not likely to kill it except, perhaps, shortly after hatching. This is another reason not to interfere with nestling birds within one or two days of hatching. Unfortunately, hatching dates are important in establishing the overall timing of the breeding cycle.

Mishandling of Young Birds. If there is no reason to handle a young bird, collect the required data (e.g. brood size, prey items, etc.) and leave promptly. Time spent unnecessarily handling, admiring or photographing birds at a nest can often lead to unfortunate circumstances for the birds. If nestlings must be picked up and examined, age, weight and stage of plumage development must be noted because of the possibility of damage to insufficiently ossified bones and to inadequately developed feathers.

Whenever possible, birds should be picked up with both hands. This is not always possible when one hand is holding a rope or a tree limb. Several methods of handling birds are satisfactory assuming only one hand is free. 1) A very young bird, for example a buteo in the first two weeks, can be cradled in one hand and held firmly with the thumb. 2) During the nest two weeks buteos and other medium-sized raptors should be held firmly by both "drumsticks." Immediately cradle the bird against your body to stablize it on top of your hand. If the bird falls over in your hand, do not try to right it by putting counter-pressure on the legs, as this may sprain joints, pull tendons or break bones. Instead, let the bird go completely upside down, lay it in the nest or your lap on its back and begin again. 3) During the final weeks of nest life it is best to pin a bird to the nest with your free hand and slip the same hand slowly underneath in search of the feet. This is possible, since a bird which is firmly pinned to a nest will usually remain in that position when the pressure is released, at least long enough to grasp the legs. This technique also prevents premature fledging and effectively immobilizes large birds such as eagles to allow the legs to be secured by the other hand if it is free. Doug Whitfield (pers. comm.) suggests that well developed nestlings can sometimes be banded while they lie prone of their own accord. Simply pull a leg out behind the bird and attach the band. 4) A larger bird can also be picked up at the bases of both wings, provided this is done properly. Approach the bird from behind and slip the spread fingers of one hand under the wings. The index finger should pass between the proximal wing bones which are then gripped by the thumb and middle finger. Be sure the hand is underneath all of the major flight feathers. A firm grip temporarily immobilizes the bird in a position which has not, in our experience, led to injuries. This is not a satisfactory method of handling very young birds (with weak bones) or large birds (with superior strength), such as golden eagles. The latter must be handled by the feet and legs, if only to prevent injury to the observer.

The drawbacks of handling birds one-handed by the wings include the possibility of feather damage and the fact that the feet are free to grip the nest. Severe damage to claws, with detachment of the horny sheath, can result if a clinging bird is pulled from the nest or a perch. Each claw should be cleared individually, if necessary, before a bird is lifted.

Premature Fledging. This serious problem is encountered late in the nestling period. As your head appears at the edge of a nest, the birds will usually spread their wings, move quickly to the opposite edge, and lean back in a typical, defensive posture. If they leave the nest before their wings are developed sufficiently to break the fall, death or fracture of legs, feathers, wings and even the keel can result.

We have not had problems with premature fledging in our studies of grassland birds of prey. This probably involves a certain amount of luck and the fact that nests on the prairies are low in general but it also stems in part from our field techniques.

If a bird is about to jump, slowly move a hand toward its feet. Leave your hand and arm flat on the nest rather than reaching at the bird as if to grab its body. Move your hand in an arc rather than straight at the bird. If the bird grabs your hand, so much the better; at least there is reliable contact between you and the bird. A makeshift "poultry hook" is handy in some such situations, but make it lightweight and release it if the bird resists vigorously.

If three or four birds are all threatening to jump, you can retrieve them one at a time by reaching in without ever putting your head above the edge of the nest. Your hand is much less obtrusive than your head, shoulders and both of your arms. Make all movements very slowly and do not hesitate to retreat for the sake of the birds.

If a bird does jump during a nest visit, stop climbing and note where it comes down. Keep in mind that the longer you leave the bird on the ground, the harder it will be to find even in shortgrass prairie. The observer is obligated to check it for injury and return it to the nest. Considerable mortality occurs during the normal post-fledging period and an unnatural hastening of this period of high vulnerability to predation should be avoided.

When wing development is sufficient to allow a bird to glide to the ground, the observer can safely be a little more active at the nest. In general, if a nestling is fully feathered except for down on its head and flanks, it can fly well enough to avoid injury. The age at which this can be done varies and in the same nest there are often birds which can get to the ground safely and birds which cannot. Also, a bird may glide a long distance and then come to grief. The only completely safe thing is not to force birds to fledge prematurely.

Mammalian Predation. Scent trails to bird nests pose a very serious threat to eggs and young. If racoons or other predators are common, special precautions should be made to guard the nests under study. Frances Hamerstrom (1970) describes the proper way to approach a nest, i.e. on a trail tangent to and past the nest with a single in-and-out side trail to the nest or nest tree. If the side trail is then sprinkled with napthalene crystals (moth balls) to destroy the human scent, the chances of predation at the nest are greatly decreased. The use of napthalene crystals as protection for nesting raptors has been more thoroughly discussed by Ray (1968).

Miscellaneous Considerations. There are several other cautions and techniques which can reduce the adverse effects of observer interference during raptor nesting studies. The use of two observers, besides being safer when climbing is involved, saves a significant amount of time. There are some field assignments which just cannot be accomplished by one person within a reasonable amount of time, if at all. The second person becomes the greatest time saver if he is capable of taking good field notes, using a notebook or prepared field forms. To save additional time I use preprinted 5 by 8 inch peripherally punched Unisort Cards (Trade name) of three types: nest visit cards, nest data cards and body measurement cards. Each card lists the parameters to be noted and provides adequate space to write the data. The savings of field time directly benefits the young birds by shortening the visits. The card sorting potential provided by the peripheral punches on the cards saves even more time during the analyses.

If the itinerary is known in advance, field forms can be partially filled out (with nest locations, species, date, etc.) before going to a nest. Data such as parental behavior, prey items, behavior of young birds, weather and time of day can be recorded after leaving the nest, on the way to the next nest. Do this well out of sight of the previously visited nest, however, since many adult raptors keep intruders under close surveillance and will not return to a nest until they are out of sight, vehicle and all. Take only the minimum amount of data at the actual nest site.

Banding on rare occasions can be hazardous to young birds. If banded too early, not only may the band slip off the leg, but as happened to one of our Swainson's hawks, it may slip only part way off and encircle the foot at the bases of the toes. As the young bird tried to move about the nest, it broke its leg above the band. During a subsequent visit the band was removed but the bird was left in the nest. It fledged normally, with only a slight "knot" where the break had healed. This suggests that young birds have a certain resiliency following injury and should be left in the nest if there is any chance of survival.

Another isolated mishap which occurred involved barbed wire slipping between the band and the tarsus of a ferruginous hawk.

Short pieces of wire are sometimes used as nest material by golden eagles and ferruginous hawks. A visit several days after banding revealed about 7 inches of a three-foot piece of wire (including one barb) forced through the band. Although the bird's tarsus was slightly scratched, no bones were broken and it fledged normally.

As a general rule, banding should be done when the birds are about one-half to two-thirds of the way through the nestling period. For the prairie buteos this would be at an age of 20 to 30 days. The tarsus reaches 90 per cent of its growth at 20 to 25 days of age in Swainson's, red-tailed and ferruginous hawks (Olendorff, 1971b). At this time the young birds still are not very mobile in the nest and it is unlikely that they will fledge prematurely. This saves time at the nests in two ways: The ease of handling and the small chance of having to retrieve the birds. For example, banding prairie falcons late in the nesting season on our study area is quite difficult because then the young birds can move to the back of the small holes in which they nest, out of reach of the climber, or they fledge prematurely requiring a second rappell to place them back in the eyrie.

The Nesting Parameters

Many inconsistencies exist in the literature concerning raptorial birds with regard to reporting nesting population information. The major sources of differences between <u>apparently</u> similar nesting parameters as used by two independent researchers include the following: 1) variations in the designs and goals of field studies, 2) differences in field techniques, 3) different temporal relationships between time spent in the field and the phenology of nesting by the birds, and 4) dissimilar analytical procedures. The nesting parameters used in the present study are defined and discussed below.

Breeding Density -- the number of potential breeding pairs per unit area. In the present paper the floating adult population and summering immatures were not included in the calculations of breeding densities. Paired, non-nesting adults which showed territorial affinity for a specific area were included, as were non-nesting single adult birds repeatedly observed in a known (but otherwise unoccupied) territory. In studies where unpaired birds represent a significant portion of the potential (but unrealized) breeding population, the breeding density definition should be qualified.

When defining breeding density it must be clear whether the densities are crude (pairs per unit of total space) or ecological (pairs per unit of suitable habitat space) (Odum, 1971). Historically, raptor research has focused on the high density areas within a given ecosystem. The examples are endless. Studies in the tundra biome are typically biased in favor of birds nesting along major water courses (Cade, 1960; Cade and Fyfe, 1970; Enderson, Roseneau and Swartz, 1968; and others). Raptor studies in prairies are often biased in favor of birds nesting on cliffs or along creek bottoms because the habitat is more or less clearly defined (Enderson, 1964; Fyfe, Campbell, Hayson and Hodson, 1969). Golden eagle studies in the western United States have emphasized foothill and mountain populations (Boeker and Ray, 1971) or river populations (Kochert, 1972).

All of these studies deal with populations of one or two species of raptors in their dominant nesting habitat. Densities (if given) are ecological breeding densities which relate in varying degrees (and often not at all) to total population numbers now in high demand by ecosystem analysts and wildlife managers. This is not a criticism of the above mentioned studies; they are used as examples to make a point and somewhat "out of context," since crude breeding densities were not always within the stated objectives. It is merely suggested here that an effort be made in the future to eliminate, where practical, biases which result from studying birds only in their dominant nesting habitats. There should be an attempt to determine crude nesting densities over large land areas using the fundamental research approach of finding virtually every raptor nest in a study area composed of all available nesting habitats.

Crude breeding density and the number of young produced per unit area (see below) are important parameters for extrapolation of population information to larger areas than those actually under study. The overriding assumption is that the species compositions, relative abundances and reproductive performances, and the habitat compositions, are comparable in the area under study and the area to which the figures are to be extrapolated. Even if the intensive study area consists of a composite of all habitats regionally available to all species, extrapolations must be made with caution. Meaningless results are obtained if ecological breeding densities are used for extrapolations, unless the percentage of suitable nesting habitat is known both on the area under study and on the larger area over which the population figures are projected.

Clutch Size--the number of eggs laid by pairs which lay at least one egg. In the present paper, clutch size is usually given as an average of a large number of clutches. Attempted nestings during which no eggs were laid or during which only eggshell fragments were found by the field workers were not included in calculations of average clutch size. Since clutch size was often determined by counting small nestlings and unhatched eggs, a slight bias which would minimize clutch size was probably introduced. Some unhatched eggs may have been broken by the nestlings. As a rule, nests were not visited until shortly after hatching to avoid the high incidence of parental desertion which often occurs at nests visited during the incubation period.

Maximum Brood Size--the number of young hatched in a single nest. Again, averages are used more often than compilations of maximum brood sizes in individual nests. Non-nesting pairs were not included in the relevant calculations. Instances where eggs were laid but not hatched were included (as zeros) in calculations of average maximum brood sizes. The latter includes a large number of nests at which only eggshell fragments were found. Maximum brood size divided by clutch size represents the probability of an egg hatching. Like clutch size, maximum brood size was determined as soon after hatching as possible.

Fledging Success--the number of young (more often an average) fledged from a nest in which eggs were laid. Non-nesting pairs (those which did not at least produce eggs) were not included (as zeros) in calculations of fledging successes. In some cases, nestlings only three-quarters feathered were counted as fledged without subsequent followup. As a rule, however, fledgling counts were made as late in the nestling period as possible for each species separately. Prairie falcon and ferruginous hawk nests were watched particularly closely as fledging approached. Fledging success divided by maximum brood size represents the probability of fledging if hatched. Fledging success divided by clutch size represents the probability of fledging at the time of egg laying.

Nest Success--the per cent of the total number of nests under study from which young actually fledged. This nesting parameter combines (in a rather nebulous way) the reproductive performances of the birds and the adequacy of the nest sites used. Unless considerable time is spent in the field during the egg laying and incubation phases, the time when most nest failures occur, it is likely that a figure for nest success will be so biased on the high side that it will be useless for interpretive discussion -- and very misleading if reported!

<u>Productivity of Young in Successful Nests</u>--the number of young (usually an average) fledged per nest, including only those nests from which at least one young fledged. Most raptor researchers must utilize this parameter, because their field activities begin so late in the nesting season that early nest failures cannot be detected. In many cases, even failures occurring during the early post-hatching phase escape notice. This parameter is much used by banders who often visit nests only once late in the season.

The interpretive value of the number of young produced per successful nest, in spite of its wide use, is questionable. No distinction is made, for example, between 2.5 young fledged per nest when 10 per cent of the population fails completely, and the same number of young fledged per successful nest when 60 per cent of the total population fails. It is important to have other data input to support or otherwise qualify conclusions drawn using this parameter.

<u>Productivity of Young per Known Pair</u>--the average number of young fledged per potential adult pair. This parameter is one of the best indices of the reproductive performance of bird populations. One does not need to know of all nests in an area to calculate this parameter; all pairs and singles are potential data, provided fledging successes are determined for all pairs (and singles) included. An error of varying magnitude is introduced, however, if all the known pairs used in the calculations nest in the dominant nesting habitat for the species, since many species tend to be more successful in

such situations. As with the other nesting parameters, it is best to include data for all birds in a large area containing all habitats suitable for nesting.

Productivity of Young per Unit Area--the average number of young fledged per unit area. This parameter is a crude density figure for young birds at the time of fledging. Nestlings which did not fledge, regardless of the reason, were not included in the relevant calculations. For the present report the areal units employed were 100 sq miles and 100 sq kilometers simply to place the decimal point logically. Conversion to sq miles and sq kilometers are straight forward. To convert to young per acre divide the number of young per 100 sq miles by 6.4. To convert to young produced per hectare (ha) divide the number of young per 100 sq kilometers by 10,000 (i.e. 10^4).

Biomass of Adults (and Young)--the weight of adults present (or young produced) per unit area. Biomasses, both that represented by the adults and that produced by the adults during the breeding season, are commonly used by ecosystem analysts for comparisons of populations and productivities. Biomass is a common denominator which gets around definitions of "individuals," "populations," "breeding pairs," etc. Because of the continuity provided, calculations of biomasses should be encouraged wherever possible, although the fact that populations are composed of individuals must not be buried completely during the analyses. In the present paper the units employed are g/km^2 (i.e. g/100 ha) wet weight.

GENERAL CONSIDERATIONS

The birds of prey which occur on the PNG and the relative status of each are listed in Table 1. Those which figure strongly in summer nesting populations include the Swainson's hawk, ferruginous hawk, great horned owl, golden eagle and prairie falcon. The American kestrel and the burrowing owl are common nesting species, but their small size and less obvious nest sites do not allow fruitful study on large land areas. The marsh hawk and the red-tailed hawk also occur regularly, particularly during the migration periods. Red-tailed hawks (for certain) and marsh hawks (probably) nest on the study area in low numbers. The rough-legged buzzard replaces the Swainson's hawk as the most common buteo in the winter. The latter species migrates to South America for the winter, primarily to the pampas of Argentina.

The other species listed in Table 1 occur as fall and spring migrants or as winter residents in small numbers. The status and timing of the life cycles of the major nesting species as they relate to northeastern Colorado will be discussed more fully below, beginning with the more important grassland buteos.

Swainson's Hawk

This is the smallest buteo which occurs on the PNG, and it is the most common of the large birds of prey during the breeding season and fall migration period. Craighead and Craighead (1956) list weights of males as 908 g (average of 5 individuals) and females as 1,069 g (7 individuals). Twenty young Swainson's hawks fledged on our study area in 1971 averaged 796 g per bird.

The species' breeding range (Fig. 2) includes most of the arid regions of North America west of the Mississippi River from northwest Mexico and Baja California, to the Seward Peninsula in Alaska excluding the Pacific Coast north of Los Angeles, California (Brown and Amadon, 1968). The wintering range of the Swainson's Hawk is quite distant from the breeding range (Fig. 2). A few winter in Florida, but most migrate to Argentina. The Swainson's Hawk is by far the most migratory of the large birds of prey of the PNG.

The food habits of this species make such a lengthy migration desirable, if not necessary. Swainson's Hawks are considerably more insectivorous than the other large birds of prey on the Pawnee. Although their nestlings are fed mostly fledgling birds and small mammals, a large portion of the species' food for the remainder of the year is insects, primarily grasshoppers. The northern pocket gopher (*Thomomys talpoides*), thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), and cottontail rabbit (*Sylvilagus* sp.) are important mammalian prey. During the breeding season, fledgling lark buntings (*Calamospiza melanocorys*), horned larks (*Eremophila alpestris*), and western meadowlarks (*Sturnella neglecta*) are important avian prey. Food habits of Swainson's hawks are considered in more detail elsewhere in this report.

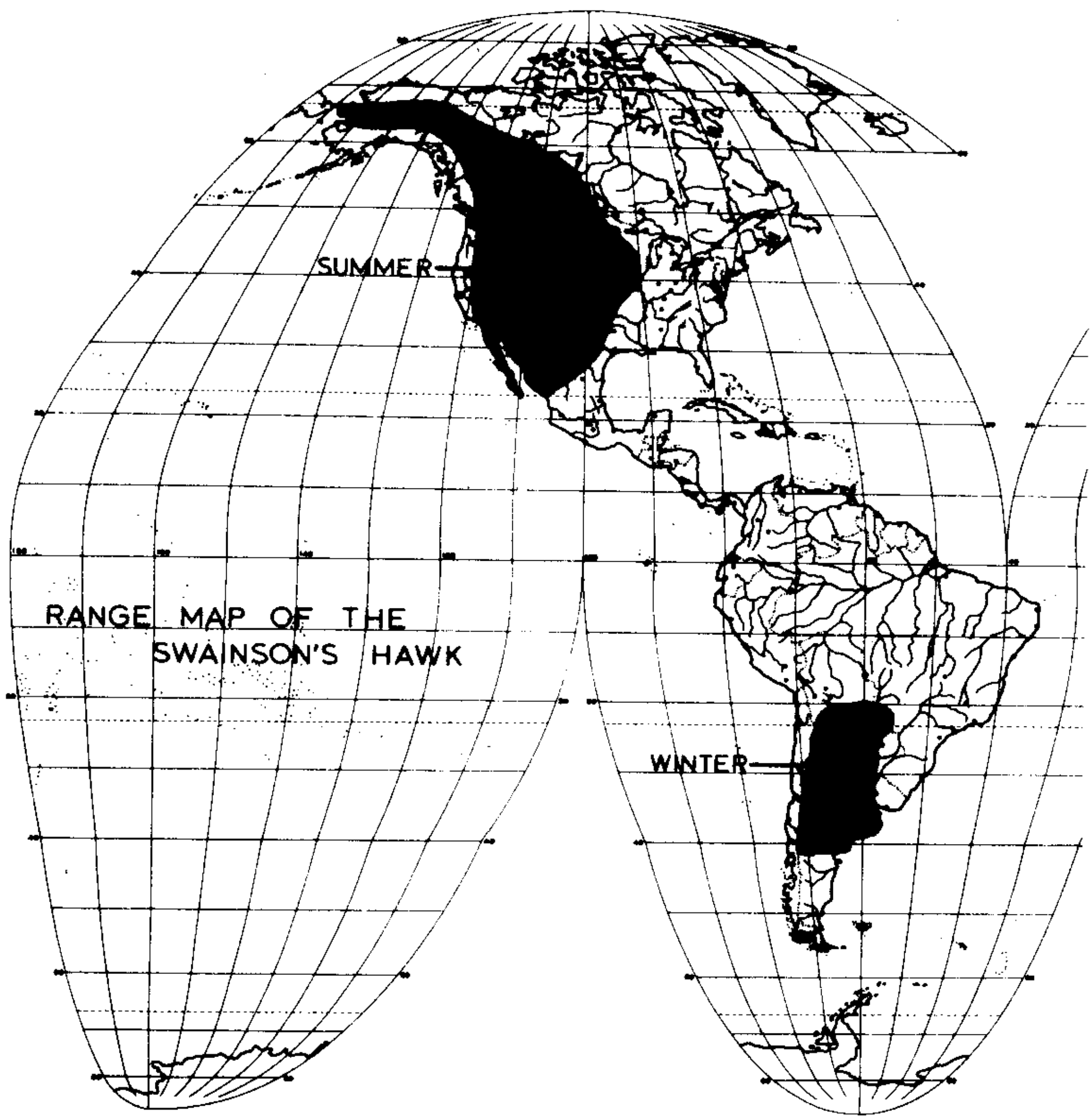

Figure 2.

Swainson's hawks arrive on the breeding grounds in northeastern Colorado from mid-April through early May and, apparently, move straight to their nesting territories. Very few Swainson's hawks were ever observed away from breeding territories in early spring. The first observation of this species in 1971 was on 13 April (Ronald A. Ryder, pers. comm.). On that date a pair was seen sitting in a lone tree with a nest from which young were fledged successfully every year from 1970 through 1972. The same pair was on territory by 11 April 1972. Nearly all Swainson's hawk territories were filled by 5 May each year. Courtship flights were observed on 24 April 1971 and 3 May 1972, but neither resulted in copulation.

Copulation of Swainson's hawks was observed on 15 May, 26 May and 11 June 1971, and on 6 May and 9 May 1972. On three occasions the actual mating occurred on fence posts; twice it took place in trees. The observation of 11 June 1971 involved a very late arriving pair or (more likely) a renesting attempt, because most birds were on eggs by that time. Some already had young.

Although the Swainson's hawk is a common breeding species on the prairies of the western United States, its courtship display has rarely, if ever, been described. Swainson's hawks are relatively tame and confiding hawks, and are not strong, aggressive fliers like some buteos. Nevertheless, their courtship display is vigorous and acrobatic.

On 24 April 1971 I observed a courtship flight of this species. Both birds of a pair soared separately for several minutes within a half mile of a tree containing a nest. The paths of the birds roughly described quarter-mile circles at increasing altitudes to about 300 feet. The birds did not beat their wings for minutes at a time. Then one soared to a position directly over the nest at that altitude, set its wings in a slightly bent attitude and glided in a direct path away from the nest. It lost about 200 feet of altitude in about three-quarters of a mile and again began a leisurely ringing soar as described above.

Once when one of the birds, presumably the male, was over the nest, it began a rapid, flapping flight, followed by closure of its wings and a 20- to 30-foot dive. After the dive the bird continued the vigorous, flapping flight in a circular path (perhaps 25 feet in diameter), climbed sharply a few feet, stalled and dove again. This occurred twice in rapid succession and led to a 15-foot nearly vertical climb to another stall. During this climb even the axis of the bird's body was nearly vertical. The climb was launched from horizontal flight in a tight circle, not as the follow-through of a dive.

This rather acrobatic maneuver and stall was followed by a long dive which described a parabolic path, at the bottom of which the bird lit very gently on the edge of the nest. Between the beginning of the rapid, flapping flight and arrival at the nest, 55 seconds elapsed. Within another 20 seconds the female lit about 5 feet from the nest. The display did not lead to copulation. To the contrary, no posturing, vocalization or other courtship behavior followed. The male flew off shortly. The female hopped to the nest before she, too, flew off. They began soaring again and escorted a third buteo across their territory and out of sight without direct conflict with it. A similar flight (which did not end at the nest) was observed on 3 May 1972.

By extrapolating back from fledging or hatching using a fledging period of 38 days (as determined during this study) and an incubation period of 35 days, it was calculated that the earliest eggs were deposited about 3 May in 1971 and 6 May in 1972 (Fig. 3). Egg laying continued throughout the month of May, with 72 per cent (26 of 36) of the clutches for which adequate data are available being laid during the last three weeks of May (1971 and 1972 data combined). In 1972 all egg laying by Swainson's hawks was bracketed by the same dates shown for 1971, although there were several clutches laid between 4 June and 9 June. These "late" clutches were probably renestings. Those clutches laid in the last week of May could be renestings or may be a late arriving group of birds. More data are needed to evaluate the significance of the weeklong gap in laying between 20 May and 26 May each year.

The eggs of Swainson's Hawks are variously colored, ranging from almost immaculate off-white to extensively

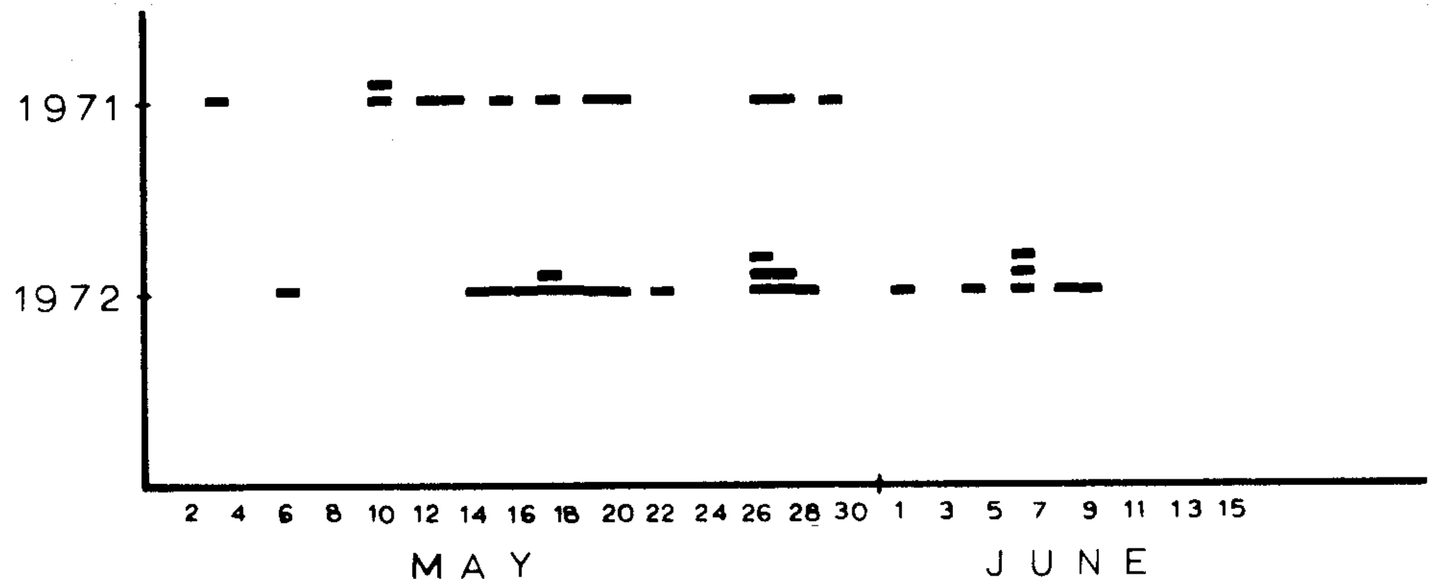

Figure 3. Dates of egg laying of Swainson's hawks. 1971 -- 13 clutches. 1972 -- 23 clutches. (Data points are approximations of the average laying date for all eggs in each clutch.)

splotched with dark brown or chestnut. A single clutch may contain very differently colored eggs. The base color is often a pale cream with a tinge of blue-gray. The size of 50 eggs (measured in 1969 and 1970) ranged from 41.5 to 47.4 mm in diameter and 53.7 to 60.8 mm in length. The average size was 44.9 x 57.6 mm. The weights of seven eggs at various stages of incubation averaged 54.9 g. Clutch size ranged from one to four eggs, usually two or three (Table 3).

Hatching occurred primarily between 14 June and 3 July in 1971 and 1972. To calculate hatching dates, add 35 days to the laying dates. The earliest hatching was about 7 June in 1971 and 10 June in 1972. One "late" clutch known to be a renesting hatched on 18 July 1971. If these birds had been raised, they would not have fledged until 25 August. They did not survive. Most Swainson's hawks fledged between 22 July and 1 August in 1971. To calculate fledging dates add 73 days to laying dates or 38 days to hatching dates. The earliest brood fledged about 12 July and the latest about 10 August 1971. In 1972 many birds fledged later in August (some as late as 21 August) due, apparently, to a high success of "late" nests, i.e. those nests in which eggs were not laid until after 1 June (Fig. 3).

A complete breakdown of the number of young Swainson's hawks hatched per nest showed that broods of 2 or 3 were most common (Table 4). The overall average (including nests in which no eggs hatched) was 1.74 young hatched per nest. Disregarding those nests in which no birds hatched, in the

Table 3. Clutch sizes of large birds of prey on the Pawnee National Grassland (1970, 1971 and 1972 combined).[a]

Species	No. of Eggs						Average
	1	2	3	4	5	6	
Swainson's Hawk	13	39	41	2	0	0	2.34
Ferruginous Hawk	1	10	18	12	3	0	3.14
Great Horned Owl	2	10	7	0	0	0	2.26
Golden Eagle	13	25	0	0	0	0	1.66
Prairie Falcon[b]	0	0	3	9	11	1	4.42

[a] Clutch size equals the maximum number of eggs observed in a nest, fertile and infertile.

[b] Data from 1971 and 1972 only.

Table 4. Maximum brood sizes of large birds of prey on the Pawnee National Grassland (1970, 1971 and 1972 combined).[a]

Species	No. of Young						Overall Average	Average Excluding Nests Where No Eggs Hatched
	0	1	2	3	4	5		
Swainson's Hawk	23	10	32	29	1	0	1.74	2.32
Ferruginous Hawk	11	7	10	17	7	1	2.09	2.64
Great Horned Owl[b]	5	2	15	5	0	0	1.74	2.14
Golden Eagle	10	15	17	0	0	0	1.17	1.53
Prairie Falcon[b]	0	0	3	3	14	7	3.93	3.93

a/ Maximum brood size equals the maximum number of young observed in a nest, whether all were reared or not. Those nests in which only broken eggshells were found are included.

b/ Data from 1971 and 1972 only.

remaining 71 nests an average of 2.32 young per nest were hatched. This corresponds very closely to the clutch size (2.34) of Swainson's hawks (Table 2). In otherwords, the major mortality of Swainson's hawk eggs is not failure to hatch. Rather, outside factors (presumably) which cause total nest failure are at fault. This follows from the 25 per cent decrease in the average maximum brood size if total failures are included (i.e., (2.32 - 1.74) ÷ 2.32 x 100 = 25.0 per cent). As will be shown below, failure to hatch <u>is</u> a significant mortality factor of ferruginous hawk eggs.

The timing of the major events of the breeding cycle for the population of Swainson's hawks as a whole relative to several other species is shown in Figure 4. The period from egg laying through fledging lasted about 73 days in a single nest and 99 days (1971) to 110 days (1972) for the entire population.

As with all birds of prey, the post-fledging period is a learning period for Swainson's Hawks. Apparently, the young spend 3 to 4 weeks in the general vicinity of the nest, sitting in the trees and seeking small rodents and insects, primarily the latter, as food. The adults and young birds then begin to form flocks of 10 to 30 at first and then flocks of hundreds, occasionally thousands. They stop where food is abundant and remain until the weather turns bad before their spectacular migration commences. Such flocks congregate southeast of Briggsdale, Colorado, almost yearly. The peak occurred from 24-28 September in 1971; over 200 of these hawks

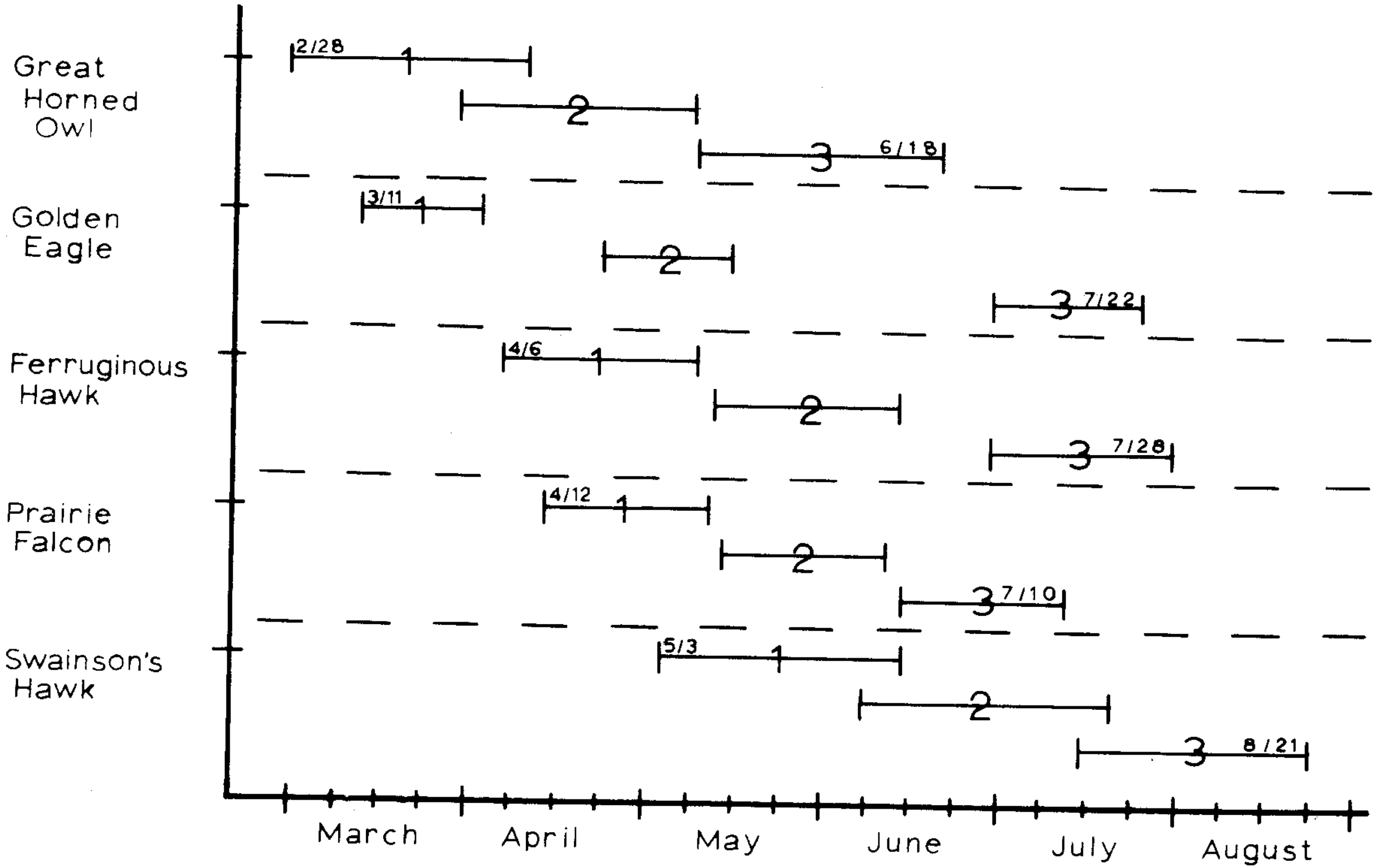

Figure 4. The phenology of nesting by five large raptors in northeastern Colorado. 1 = egg laying period. 2 = hatching period. 3 = fledging period. Dates on which the first eggs were laid and the last young fledged (1970-72) are shown.

were observed on 28 September in about a 10-sq mile area. All had departed by 4 October. Swainson's Hawks are totally absent from northeastern Colorado from early October through mid-April. Two Swainson's hawks banded on the Pawnee, one in 1970 and another in 1971, were recovered in Argentina during the following winter. Another banded in 1971 was recovered 27 August 1972 near Felt, Oklahoma.

Ferruginous Hawk

The ferruginous hawk is one of the least studied birds of prey in North America. Until recently (Weston, 1969; Powers, research now in progress; Olendorff, this report), little substantive information was available on this interesting and, in many ways, peculiar species.

Among the more important aspects of the biology of the ferruginous hawk are the following: 1) it has a smaller overall breeding range than any other buteo which breeds in North America. This includes the semi-arid regions of the western United States and the extreme southern portion of the Canadian prairie provinces, a combined area of about one-fifth the size of the entire United States (Fig. 5). Most ferruginous hawks apparently undergo only short winter movements to the southwest into Baja California, south to the northern states of Mexico and southeast as far as Louisiana. No other North American buteo is as sedentary.

2) Throughout their breeding range, ferruginous hawks occur sympatrically with two congeneric species, namely

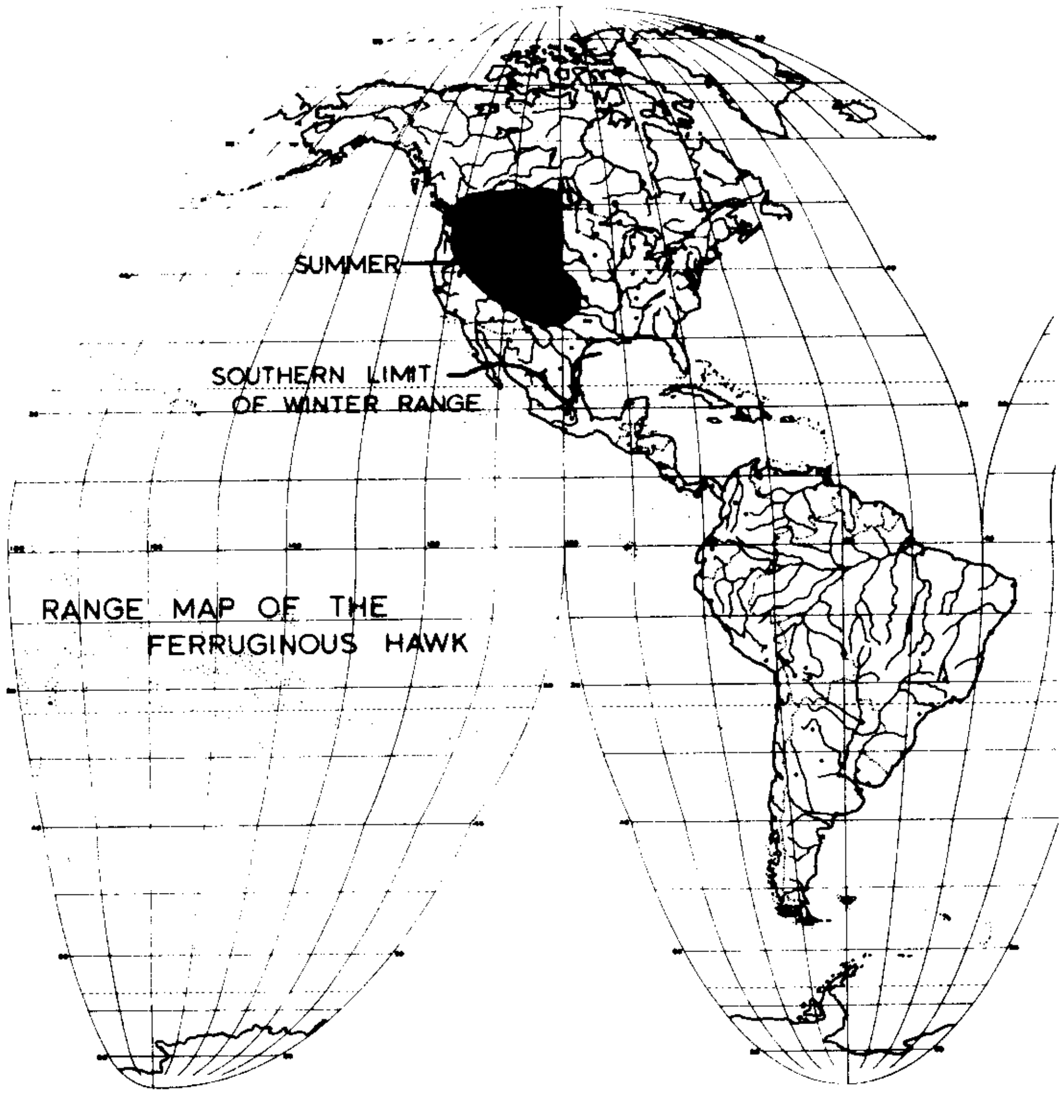
SUMMER
SOUTHERN LIMIT
OF WINTER RANGE
RANGE MAP OF THE
FERRUGINOUS HAWK

Figure 5.

red-tailed hawks and Swainson's hawks. The red-tailed hawk is generally considered to be a forest dweller, while the Swainson's hawk is a major species in arid grassland. The apparently harmonious cohabitation of the three species occurs with some loss of the general habitat identity just mentioned and presents excellent opportunity for the study of intrageneric relationships.

3) As might be expected where sympatric species are involved, ferruginous hawks utilize their breeding range in subtlely different ways than the other buteos. For example, ferruginous hawks have a less diverse diet resulting, at least in part, from a loss of agility due to their size. On the other hand, ferruginous hawks are more versatile nesters than the other buteos in that they use a variety of nesting situations (see Table 17). This allows them to nest in virtually unbroken grassland, a habitat unavailable to the other buteos for nesting. In spite of this, ferruginous hawks occur only in relatively low numbers in the absence of some discontinuity of habitat such as a tree, creek bank, cliff or isolated outcropping. There is far more habitat for ferruginous hawks to nest than is being used due to the limited desirability of certain situations.

4) Ferruginous hawks possess several traits which provide variety and challenge in the field. There are different color phases, including a black phase which occurs in about 3 per cent of the adults in northeastern Colorado. Ferruginous hawks abandon their nests readily if molested by man during

the egg period, yet over the decades since the 1920's man has had a positive effect on the species by providing trees as nest sites at now abandoned farmsteads (see Tables 18 and 19). Ferruginous hawks are almost totally eliminated as a nesting species where cultivation is allowed, however.

5) The extent to which ferruginous hawks utilize man-created nest sites indicates a high potential for planned management, a new concept with regard to raptorial birds born (or at least revitalized) in the wake of global declines in numbers of many of our avian predators (see below). Ferruginous hawks need management.

Imler (1937) lists the weights of adult male ferruginous hawks as 1,237 g (two individuals) and of adult females as 1,983 g (three individuals). The average fledging weight of 17 ferruginous hawks studied on the PNG in 1971 was 1,296 g.

The ferruginous hawk is a year-long resident of the Pawnee, but at much lower population levels than Swainson's hawks in the summer (see Tables 10 and 13) or rough-legged buzzards in the winter. On a drive across the Pawnee one can expect to see 2 to 5 ferruginous hawks per 100 miles almost any time of the year, but rarely more than that unless nest sites are visited. For contrast, Mathisen and Mathisen (1968) reported seeing only 9 Ferruginous hawks in 53,347 miles of driving (1 per 5,927 miles) in all seasons in the Nebraska Panhandle from 1957-59. This is a strikingly low number.

The food of the ferruginous hawk includes most small mammals up to the size of jackrabbits and many small birds, the latter at least as fledglings. Of particular importance on the PNG are the thirteen-lined ground squirrel, northern pocket gopher, cottontail rabbits, jackrabbits (Lepus californicus and L. townsendi), and the same species of birds as mentioned above for the Swainson's hawk. Unfortunately, the food habits of the ferruginous hawk are little known outside the breeding season. Food habits of nestling ferruginous hawks will be considered in more detail elsewhere in this report.

It is difficult to determine the date when ferruginous hawks move to their nesting territories, since they are resident birds. Our first day in the field in 1971 was 17 March. On that day a ferruginous hawk was observed near a nest used in 1970. Another pair was observed sitting in a 1970 nest tree on 21 March 1971, and this and other pairs were seen at nests from that time on. The same dates hold for early observations in 1972, when 18 March was the first day in the field. Pending further study, the earliest nesting activity on the Pawnee will be stated as 10 March with most territories filled by 1 April. Weston (1969) observed nesting activity of ferruginous hawks in the Cedar Valley of Utah as early as 25 February 1968 and 6 March 1967.

Ferruginous hawks, unlike Swainson's hawks, apparently spend considerable time choosing their actual nest site and may repair two or three nests before laying eggs in one of them. This depends, of course, on the availability of nest sites and, in the absence of numerous potential nest sites, may be a limiting factor of ferruginous hawk populations. In several instances pairs of ferruginous hawks were seen repairing nests 1 to 5 miles from where they apparently nested. In one case the subsequently unused territory was defended by the female from the incursions of migrating red-tailed hawks.

No courtship flights of ferruginous hawks were observed in 1971 and 1972, nor have such flights been described in the literature to my knowledge. Although more thorough behavioral studies are needed, our observations suggest that nest site selection and nest building may be more important to ferruginous hawks than courtship flights. Ferruginous hawks build large, sturdy nests during a complex and lengthy nest building period. The opposite is true of Swainson's hawks which, apparently, have evolved spectacular courtship flights, but build small, loose-knit nests very rapidly. These observations are consistent with the considerable differences in the nesting phenologies of the two species. The ferruginous hawk, a relatively sedentary species, has more time available for breeding than does the Swainson's hawk, a highly migratory species. This is supported by the fact that Swainson's hawks return directly to nesting territories at the end of their spring migration.

Copulation by ferruginous hawks was observed on 10 March 1971. The female flew out of a nest which was used by Swainson's hawks in 1969 (and later in 1971) and lit on a fence post. The male flew in from a nearby fence post and returned to another fence post after copulation took place. This was 3 miles from the nearest successful nesting of ferruginous hawks that year, but only about 500 yards from a successful great horned owl nest.

The timing of the major events of the breeding season of ferruginous hawks is shown in Figure 4. Egg-laying began in mid-April 1971, 16 April being the earliest laying date as determined by using an incubation period of 35 days and extrapolating back from hatching (Fig. 6). The Pawnee birds began laying at the time the Utah birds studied by Weston in 1967 and 1968 stopped laying. Egg-laying continued for 12 days and ceased in 1971. This resulted in a compression of egg-laying (and hatching and fledging) of ferruginous hawks, relative to the same periods of Swainson's hawks. In other words, the reproductive sequence of the ferruginous hawk, a resident species, was more precisely timed than that of the Swainson's hawk, a migratory species.

In 1972 the breeding season of ferruginous hawks was less precisely timed (Fig. 6). At least, there were several late nests in which eggs were not laid until late April (even as late as 8 May). Most ferruginous hawks laid eggs between 6 April and 17 April in 1972, about 10 days earlier than in 1971. The late clutches were probably re-nestings. This is supported, at least circumstantially, by a high rate of nest failure in 1972 (35.4 per cent compared with 15.4 per cent nest failure in 1971). Apparently, if ferruginous hawks (as a population) are generally less successful early in a given year, they have

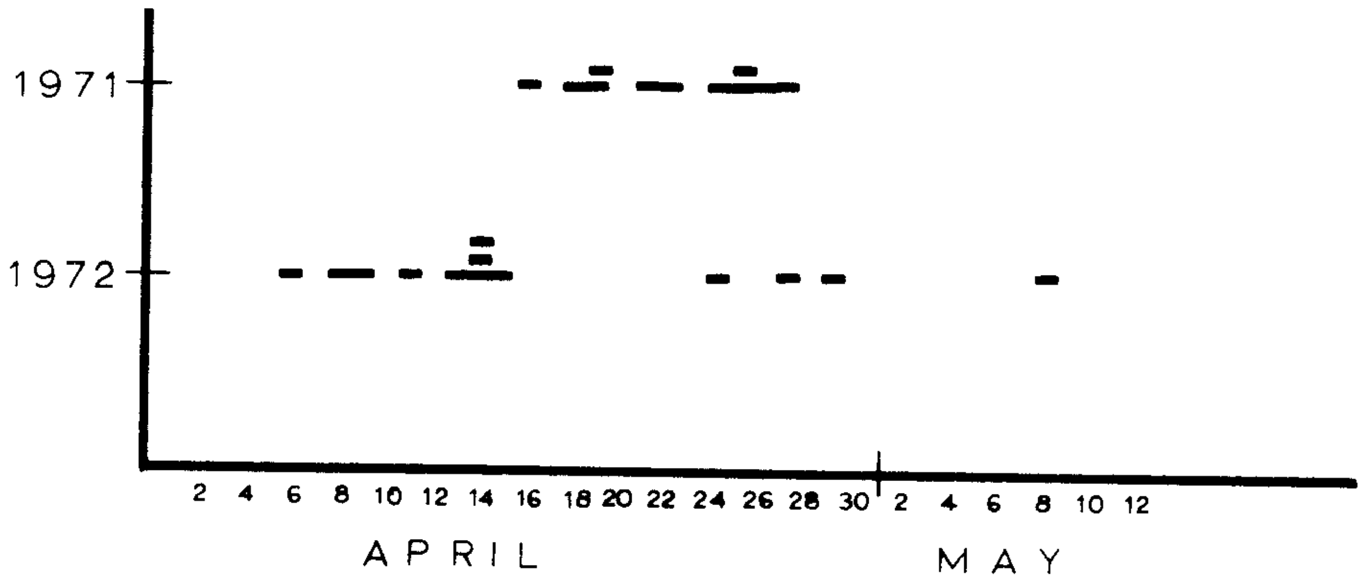

Figure 6. Dates of egg laying of ferruginous hawks. 1971 -- 11 clutches. 1972 -- 14 clutches. (Data points are approximations of the average laying date for all eggs in each clutch.)

the capacity to renest, thereby masking (as in 1972) the usual synchrony of breeding (as in 1971).

Ferruginous Hawk eggs are beautifully colored with splotches of several different browns on a cream base color. Considerable variation may occur in a single clutch, making a full set of eggs extremely attractive. Twenty eggs (measured in 1969 and 1970) were from 45.8 to 50.5 mm in diameter and from 58.5 to 64.9 mm in length. The average size was 48.2 x 61.7 mm. The weights of three eggs at various stages of incubation averaged 73.4 g. The latter compares with an average of 66.1 g for five eggs in late stages of incubation under artificial conditions (Olendorff, 1971b). Clutch size varied from one to five eggs with clutches of 3 most common (Table 3).

Ferruginous hawks typically used three types of nest on the Pawnee: 1) on the ground either on a creek bank, at the crest of a hill, or on an erosional remnant, 2) low in a short tree, usually a stunted, introduced variety, and 3) high in a tall cottonwood tree along a creek bottom. The latter situation was often encountered if the nest was anywhere near plowed land. Large stick nests were constructed of all available materials, including plastic bags, cardboard and other litter. The lining was almost invariably dried cow dung, particularly during incubation. Ground nests at the crests of hills typically had a low profile.

Hatching began about 21 May 1971 and continued through 11 June. Add 35 days to laying dates to calculate hatching dates. The young birds fledged between 6 July and 17 July in 1971 after an average of 46 days (range 42 to 48 days) in the nest. In 1972 ferruginous hawks began fledging about 26 June and continued to do so through about 28 July. The mid-points (not necessarily peaks) of egg-laying, hatching, and fledging in 1971 were 21 April, 27 May, and 11 July, respectively. Similar dates for 1972 were 13 April, 19 May and 3 July, respectively, disregarding the late nests. For a single pair of ferruginous hawks, egg-laying through the fledging of their young lasted about 81 days. Egg-laying through fledging lasted 92 days (1971) and 113 days (1972) for the entire population.

An analysis of clutch size (3.14 from Table 3) and brood size in nests where at least one egg hatches (2.64 from Table 4) revealed a discrepancy of 15.9 per cent. A similar comparison for Swainson's hawks revealed virtually no difference. The difference for ferruginous hawks indicates either a level of infertility or a failure of incubation (or both) in the breeding cycle of ferruginous hawks. There is some evidence suggesting both of these circumstances, although a failure of incubation is apparently the major cause of the difference between the two parameters in question.

Young ferruginous hawks apparently move away from the actual nest site sooner after fledging than do Swainson's Hawks. Study of the post-fledging period must be more intense before this can be stated with certainty, however. One ferruginous hawk banded on the Pawnee during the summer of 1970 was recovered in northern Mexico the following winter.

Red-tailed Hawk

The red-tailed hawk is intermediate in size between the Swainson's and ferruginous hawks. Craighead and Craighead (1956) list the average weight of 108 males as 1028 g and of 100 females as 1224 g. Esten (1931), Norris and Johnston (1958) and Stewart and Skinner (1967) presented weights for immature red-tailed hawks. The average of 5 males was 915 g and that of 9 females was 1166 g.

The red-tailed hawk has the largest overall breeding range of the three buteos which breed on the PNG (Fig. 7). There are many recognized races of red-tails. Their composite range includes southcentral and southeastern Alaska, most of Canada, the continental United States, Baja California, northern and central Mexico, a few of the West Indies and an isolated population in Central America. The race of red-tail which nests on the PNG, *Buteo jamaicensis calurus*, has a breeding range extending from the Yukon Territory on the north to Baja California on the south, west to Texas, the Oklahoma Panhandle, western Kansas, Nebraska, South Dakota, North Dakota and Saskatchewan (Brown and Amadon, 1968).

The winter range of *B. j. calurus* is difficult to describe, since the winter ranges of many races of red-tails overlap. The species is uncommon in northeastern Colorado during the winter months. Most birds of the western race winter further south, probably as far south as northern Nicaragua (Brown and Amadon, 1968).

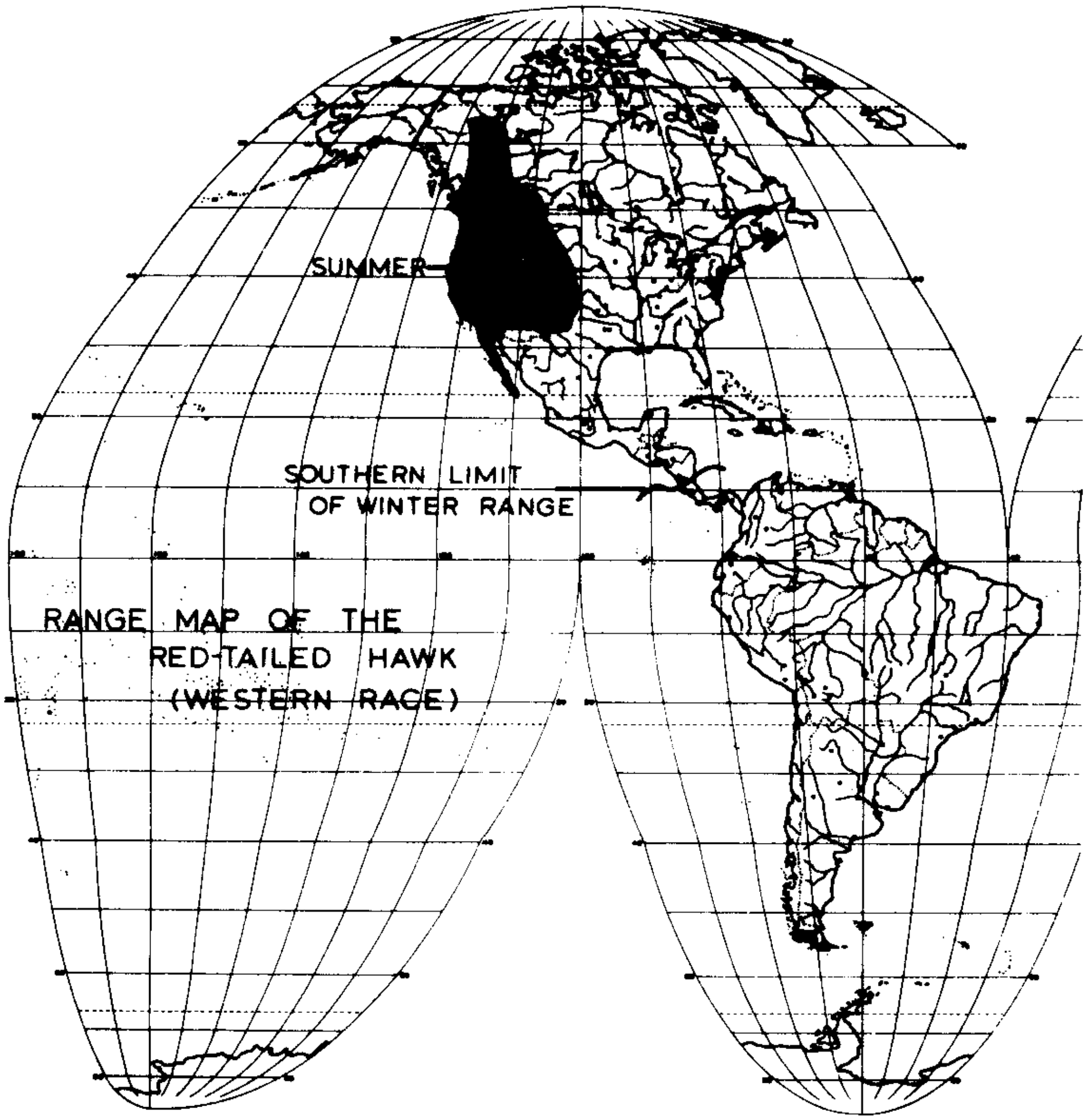
SUMMER
SOUTHERN LIMIT
OF WINTER RANGE
RANGE MAP OF THE
RED-TAILED HAWK
(WESTERN RACE)

Figure 7.

Since the red-tailed hawk is an uncommon nester on the PNG, little detailed information was collected during the present study. Of 8 pairs present in 1972, 5 nested in trees along major creek bottoms and 3 nested on cliffs. Many more red-tails nest in the gallery forest along the South Platte River about 20 miles south of the study area and in the foothills of the Rocky Mountains which begin about 15 miles west of the study area. The phenology of nesting is yet to be described.

The red-tailed hawk is most common on the PNG during the spring and fall migration. During the spring migration adults are most often observed as pairs along the major north-south creek bottoms which, apparently, they use as leading lines. On 26 March 1971, for example, 6 adults were observed along a two-mile stretch of Crow Creek. None were seen in 50 miles of driving in the agricultural land southeast of Briggsdale the same morning.

Golden Eagle

The golden eagle, the largest nesting raptor on the PNG, is present year-round. It is unclear if the nesting birds remain or if they are replaced in winter by individuals from further north. The breeding range of the golden eagle includes the western United States and Canada, northern Canada and Alaska, much of Europe and Asia, and extreme northwest Africa. The populations of the western United States remain quite stable (Boeker and Ray, 1971). The average weight of 7 male golden eagles is listed as 3,924 g and that of 4 females as

4,692 g by Brown and Amadon (1968). The weights of all large birds of prey, particularly the eagles, need further documentation.

The food of nesting golden eagles on the Pawnee is mostly cottontails, jackrabbits, thirteen-lined ground squirrels and, on occasion, ring-necked pheasants (Phasianus colchicus), long-tailed weasels (Mustela frenata), and black-billed magpies (Pica pica). An analysis of available data on food consumption by golden eagles is included elsewhere in this report.

Many golden eagles were at eyries by the time study began in 1971 and 1972. Stoddart (pers. comm.) saw several eagles near eyries on 15 March 1972, but nest building had not begun at one eyrie checked closely. Eggs were laid in that eyrie about 2 April. Most golden eagles already had eggs by that time, the earliest clutch being laid about 11 March (Fig. 8). The overall timing of the breeding cycle of golden eagles is shown in Figure 4.

The eggs of golden eagles range from completely cream-colored to extensively splotched with brown. The average size of 3 eggs was 57.8 x 76.6 mm. The average weight of 2 eggs about half incubated was 122.8 g. Clutch size was 1 or 2, more often 2, with an average of 1.66 eggs per clutch (Table 3). The incubation period of golden eagles is variously reported in the literature as between 35 and 45 days in length. I have used 41 days which is consistent with most European literature and with Camenzind (1969) for golden eagles in Utah.

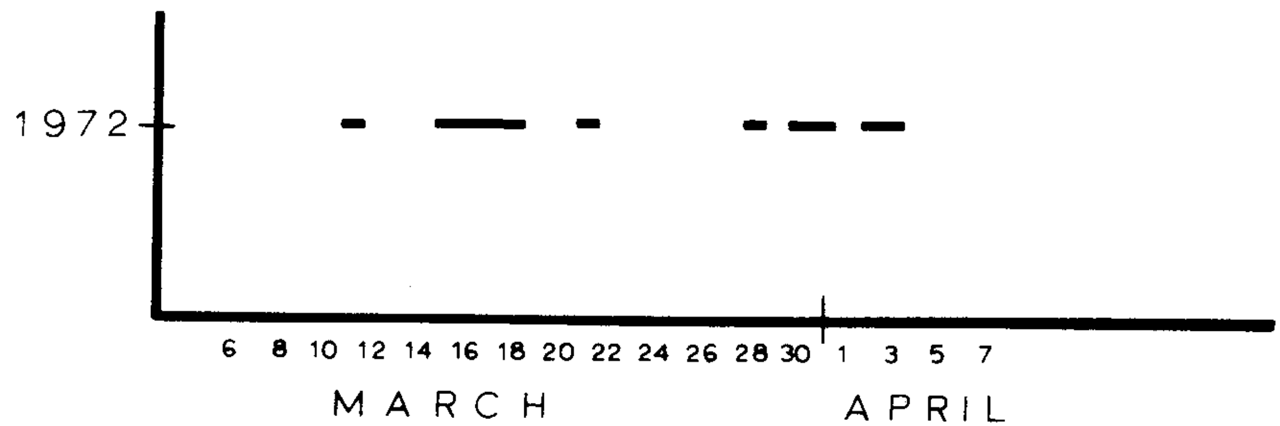

Figure 8. Dates of egg laying of golden eagles. 1972 only -- 11 clutches.

Courtship flights of golden eagles sometimes continue after egg laying. On 30 March 1972 a female, which had been incubating about two weeks, engaged in the typical "roller coaster" courtship flight within minutes after being relieved at the nest by the male. After gaining considerable altitude she gathered her wings in a four-fifths fold and dove at an angle of 50 to 55°. At the bottom of the dive she broke into a vigorous flapping flight for a powered ascent to the height possessed before the dive. This was followed immediately by another fold and dive. The undulating flight continued for about 4 minutes and involved 30 or more undulations.

Copulation was observed near a different eyrie on 31 March 1972. It occurred on the ground about one hour after a kill and at the end of a 40-minute session of nest building. The male left the nest tree and flew to the female, landing next to her on the ground. He then jumped onto her back and copulation took place. This was followed by a lengthy period with both birds perched on the ground, occasionally preening.

Both birds participated in the nest building and brought sticks up to 1½ feet in length, all collected in the creek bed within 100 feet of the nest tree. On at least 10 different occasions in 40 minutes one or both of the birds dove from the tree in a gentle swoop to the ground. Their actions in leaving the growing nest structure were stereotyped, a slow thrust forward, a distinct folding of the wings, a drop of 20 feet and a wide spread of the wings to brake for the landing, all within 8 to 10 seconds. The approach to the nest with a stick was also performed in a monotonous manner, always from the same direction -- into the wind -- and always to the same perch near the nest. At least 3 times the female nearly knocked the male out of the tree upon landing with a large stick trailing behind her. On one occasion, as the male returned to the nest, the female stood in the nest, head almost buried in the cup and turned from side to side as if arranging nest material. The male dropped the stick he brought on that occasion.

In 1972 all observed golden eagles in northeastern Colorado hatched between 21 April and 13 May, and fledged between 30 June and 22 July (assuming that all birds took 10 weeks after hatching to fledge) (see Fig. 4). Actual fledging dates at 3 eyries were 30 June, 4 July and 6 July 1972. The entire length of the breeding season from egg laying through fledging for an individual pair was about 111 days (estimated using an incubation period of 41 days and a fledging period of 10 weeks). For the entire population, eggs and young of golden eagles were in nests for about 135 days.

Maximum brood size in all nests in 1971 and 1972 was 1.17 (Table 4). Brood size in nests where at least one egg hatched (1.53) was only 7.8 per cent less than the average clutch size (1.66), indicating that hatchability of eggs was high where the entire clutch was not destroyed or deserted (or, uncommonly, infertile). As will be shown elsewhere, however, the overall probability of hatching of a golden eagle egg was lower than for any other large raptor of northeastern Colorado, except the ferruginous hawk.

Prairie Falcon

This is the only large falcon which nests on the PNG. It is present throughout the year. Enderson (1964) in the most thorough life history of the species lists weights as follows: 15 adult males -- 554 g, 31 adult females -- 863 g, 5 immature males -- 539 g and 12 immature females -- 824 g.

Prairie falcons breed throughout the western United States, Baja California, northern Mexico and the southern portions of the prairie provinces of Canada (Brown and Amadon, 1968). The species is generally thought to nest only in arid country, but the Rocky Mountain foothills and plateaus (surrounded by cliffs), and some high mountain areas over 11,000 feet support nesting prairie falcons. Excluded from the species' breeding range is a strip along the west coast of the United States.

The prairie falcon is somewhat migratory. Many nestlings banded in California move northeast across the continental divide within three months of fledging. Young from Colorado and Wyoming move generally north and northeast into Montana, the Dakotas and the prairie provinces of Canada for 3 to 5 months after fledging. This is apparently followed 5 to 8 months after fledging by southern movements through the mid-west from North Dakota to Oklahoma (occasionally as far east as Missouri, Iowa and Illinois) (see Figure 4 in Enderson, 1964).

No quantitative food habits study of the prairie falcon has been published to my knowledge. Verland Ogden (pers. comm.) of the Idaho Cooperative Wildlife Research Unit found that mammalian prey, particularly the Townsend's ground squirrel (*Spermophilus townsendi*), was the most common food of prairie falcons along the Snake River in southwestern Idaho. Horned larks, western meadowlarks and western whiptail lizards were also take. Enderson (1964) found that horned larks and Richardson's ground squirrels (*Spermophilus richardsoni*) were brought to nests most often in Wyoming and Colorado (including the PNG and adjacent areas). Enderson adds that the remains of thirteen-lined ground squirrels were found infrequently.

Food habit analysis during the present study was qualitative. Thirteen-lined ground squirrels, lark buntings, horned larks and western meadowlarks were commonly found in prairie falcon nests. McCown's longspurs (*Rhynchophanes mccownii*) and an American coot (*Fulica americana*) were also preyed upon. Although it is quite easy to identify parts of prey in prairie falcon nests, it is very difficult to separate the remains of individual prey items. Eyries are often littered with feathers, bird feet and ground squirrel tails, requiring one to sift the sand (literally) of the nest scrape to retrieve remains. It will require a very specific effort to study prairie falcon food habits quantitatively.

Prairie falcons apparently move to their eyries in very late February and early March (Enderson, 1964), but egg laying does not occur until 5 to 7 weeks later. Most pairs were on territory before the present study began each year. Nest scraping was observed at one eyrie on 8 April 1972, about one week before the first egg was laid. Mean laying dates of clutches ranged from 12 April through 10 May 1972, the only year for which numerous data are available (Fig. 9). These dates coincide almost exactly with the total variation found during Enderson's (1964) entire three-year study period. Most clutches were laid during the second and third week of April in 1972, while 4 clutches in 1971 were laid during the fourth week of April. This suggests, as with ferruginous hawks, that most prairie falcons nested earlier in 1972 than in 1971, but the population as a whole had a prolonged breeding season.

An incubation period of 30 days was used during the present study for extrapolations back to egg laying. A fledging period of 31 days was used. The latter is 5 to 10 days less than reported by Enderson (1964), implying higher rates of growth and development in 1972. Three fledging periods were determined in 1972; they were 29, 32, and 33 days. Although there are several sources of error in such determinations, fledging periods were shorter in 1972 (or on the low side of the range given by Enderson) than in 1960-62. This possibly was the result of the warm dry conditions from February through May 1972.

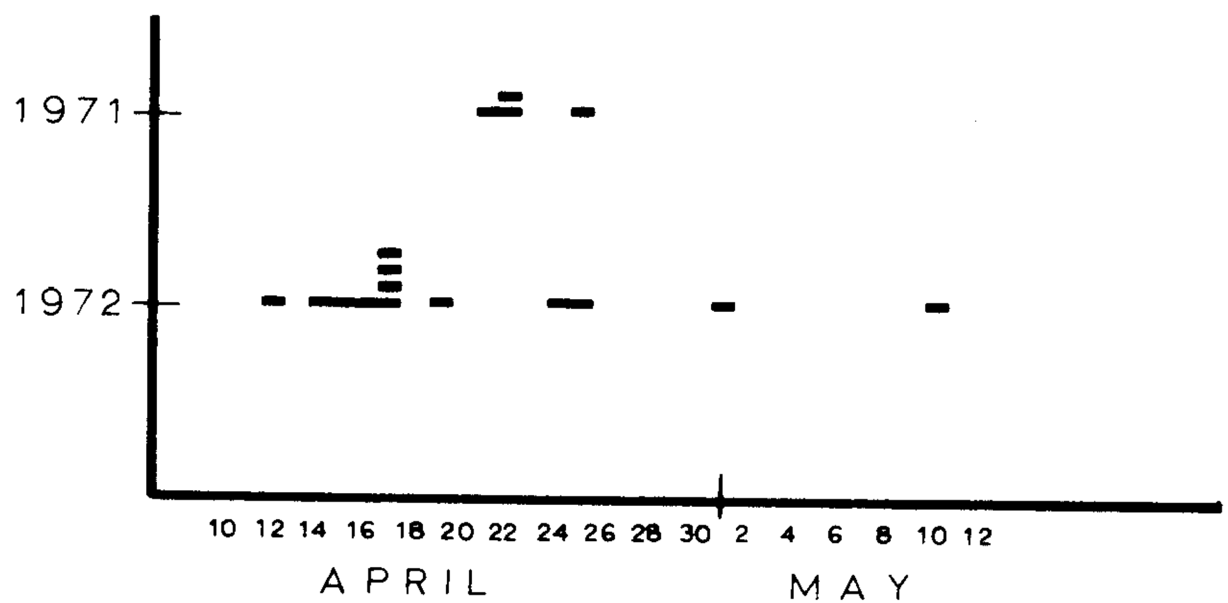

Figure 9. Dates of egg laying of prairie falcons. 1971 -- 4 clutches. 1972 -- 13 clutches. (Data points are approximations of the average laying date for all eggs in each clutch.)

Prairie falcons hatched between 12 May and 10 June 1972, principally from 12 to 19 May. Most fledged between 13 and 19 June, but the young in one very late nest did not fledge until 10 July. The complete phenology of nesting is shown in Figure 4.

Clutch size in 24 eyries in 1971 and 1972 averaged 4.42 eggs (range 3 to 6) (Table 3). Modal clutch size was 5. At least 2 eggs hatched in every active eyrie under study. Clutch size during Enderson's 1960-62 study averaged 4.5 eggs, while Ogden (pers. comm.) found 4.41 eggs per site along the Snake River from 1970-72. Maximum brood size during the present study was 3.93 young overall (range 2 to 5) (Table 4). Fledging success (see below for details) was 3.41 young per eyrie. Ogden (pers. comm.) found 3.1 young fledged per occupied territory from 1970 to 1972. Enderson's (1964) finding of 1.1 young fledged per pair studied (extremely low) is inexplicable.

Great Horned Owl

This resident species is the dominant large strigiform, and contributes significantly to the raptor biomass of northeastern Colorado. Craighead and Craighead (1956) list the average weight of 895 males as 1,304 g and of 772 females as 1,706 g, almost as much as ferruginous hawks. (There is some question as to whether these weights are for different owls or for multiple weighings of a smaller number of owls.)

The breeding range of the great horned owl includes all of North America south of the Brooks Range in Alaska and the Arctic Circle across Canada, and all of Central and South America. The great horned owl is probably the most sedentary raptor which breeds on the PNG.

The food of great horned owls in northeastern Colorado was analyzed by Marti (1970). All important prey species were mammals, including jackrabbits, cottontails, deer mice (Peromyscus sp.), prairie voles (Microtus ochrogaster), and northern pocket gophers. Birds made up less than 5 per cent of the prey items (1.5 to 6.8 per cent of the wet-weight biomass of prey over a three-year period).

Most potential great horned owl territories can be located in late December, as has been indicated by comparisons of the Pawnee Site Christmas birds counts and subsequent nesting records. The date of the onset of courtship was not determined during this study, but the egg laying period was calculated as 4 March through 15 March for 6 clutches in 1971. Four clutches in 1972 for which precise data are available were laid around 28 February, 2 March, 9 March and 9 April. An incubation period of 28 days was used for extrapolations back from hatching to determine laying dates. As with ferruginous hawks, the egg-laying period of great horned owls was more precisely timed in 1971 than in 1972. A widespread failure of nesting by great horned owls in 1972 (see below) apparently resulted in considerable asynchrony of nesting.

Great horned owl eggs are immaculate white. The sizes of 9 eggs (measured in 1969 and 1970) ranged from 45.2 to 48.1 mm in diameter and 50.6 to 58.7 mm in length. The average size was 46.3 x 56.3 mm. Clutch size (2.26) and maximum brood size in nests where at least one egg hatched (2.14) were quite similar (Tables 3 and 4).

Hatching of 6 clutches in 1971 occurred between 1 April and 12 April; the birds fledged between 13 May and 24 May after an average period of 42 days in the nest (Fig. 4). This was 9 weeks earlier than Swainson's hawks and 7½ weeks earlier than ferruginous hawks. In 1972 hatching occurred as early as 27 March and as late as 7 May. The young fledged between 8 May and 18 June. The length of the breeding season from egg laying through fledging of a single brood was 70 days. On a population basis, great horned owls had eggs or young in the nest for 81 days and 110 days in 1971 and 1972, respectively.

The post-fledging period of great horned owls is long. Details of this part of the species' natural history were studied by Dunstan (1970). On the Pawnee, as on Dunstan's study area in South Dakota, young owls were observed near their nests for many months after they fledged, although Dunstan noted a mid-winter dispersal of young great horned owls, and Houstan's (pers. comm.) banding data documents a southern movement of immature birds out of Saskatchewan during the winter.

Burrowing Owl

The first attempt to study burrowing owls in 1972 was quite unsuccessful for several reasons. In particular, manpower was inadequate; another team of two researchers would be needed just to study burrowing owls and American kestrels on the 1,000-sq mile study area. The fossorial habits of the owls, the cavity nesting habit of the kestrels and the small size of both species make observation very time-consuming. The owls present the added problem of locating pairs which nest in holes of badgers (*Taxidea taxus*) and other medium-sized mammals, independent of black-tailed prairie dog (*Cynomys ludovicianus*) towns. In spite of the problems, however, certain qualitative statements can be made.

Burrowing owls are present in northeastern Colorado from early to mid-April through mid-October. The range of the species includes most of North America west of the Mississippi River and north to the prairies of southern Canada. Southwardly, burrowing owls are found through much of Mexico, Central America and South America, excluding tropical areas such as the watershed of the Amazon River (Grossman and Hamlet, 1964). Locally, burrowing owls are not common in cultivated land.

These small owls may be more numerous than any of the large raptors which nest in northeastern Colorado, but in terms of biomass (g/km^2) they are apparently less important. Thomsen (1971) gives the following weights for the species in

California: 12 males--172.0 g (range 145.0-191.3) and 10 females--168.0 g (range 125.6-210.0). He noted that weights of females increased near egg laying time and decreased when dependent young were in the burrows.

Assuming, for example, that burrowing owls were as common as Swainson's hawks on the 1,000-sq mile study area in 1972 (68 pairs per 1,000 sq miles from Table 13 below), their biomass would be about 5.0 per cent of the raptor biomass (American kestrels excluded) of the area. Assuming also that the biomass of a predatory species reflects its ecological impact, burrowing owls, red-tailed hawks and prairie falcons probably have about the same, relatively low impact. The energy utilized during the summer of 1972 by Swainson's hawks, ferruginous hawks, great horned owls or golden eagles (each species considered separately) was 4 to 6 times greater than that which would be used by 68 pairs of burrowing owls.

The figure of 68 pairs per 1,000 sq miles was not chosen in the total absence of population information. It is meant as a <u>minimum</u> estimate, however. Eleven black-tailed prairie dog towns were located on the 1,000-sq mile study area in 1972. None was on the federal land of the western portion of the Pawnee National Grassland. Counts of owls at these towns varied considerably (from 0 to 32), with most seen very early in the morning on sunny days in late July and early August (after the young had fledged, but before emigration). I would estimate that there was a <u>minimum</u> average of 4 pairs of owls per prairie dog town (or 44 pairs). Individual owls were noted on a map throughout the season. This accounted for about another 15 pairs (for a total of 59). It must be stressed, however, that the total population could easily have been 2 or 3 times that number. No area was systematically searched for isolated pairs. Even population levels determined for prairie dog towns are suspect because of the nesting habits and daily activity patterns of the owls.

There is a definite dependence of burrowing owls in northeastern Colorado upon priarie dogs for nest hole "starts". Whether the apparent gregarious habits of the owls involve true social affinity or whether clumping of the owl population near prairie dog towns is related only to the availability of nest sites is an open question. There is considerable evidence in favor of the latter, however.

First, the occurrence of isolated owl pairs at badger holes suggests that social interaction is not an absolute requirement for breeding. Although the extent to which badger holes are used by burrowing owls is unknown, it has been observed many times. Second, burrowing owls are territorial during the breeding season, with territories up to 4.0 acres in size (Thomsen, 1971; Coulombe, 1971). Many social birds have smaller territories and less complex repertoires of territorial behavior than are indicated for burrowing owls.

Third, burrowing owls are mainly dependent upon mammals of the genera Spermophilus and Cynomys for nest site "starts". The badger digs many holes, but not in the numbers dug by large populations of prairie dogs and spermophiles. The hard, shallow and often gravelly soils of the PNG preclude extensive digging by the owls themselves. In California, burrowing owls use the holes of California ground squirrels (Spermophilus beecheyi), a colonial species which Burt and Grossenheider (1964) list as being 9-11 inches long excluding the tail. The thirteen-lined ground squirrel, the common spermophile on the Pawnee, is only 4½ to 6½ inches in length from the nose to the base of the tail. Very few, if any, burrows of the latter species are large enough to provide an adequate "start" for a burrowing owl nest site. Black-tailed prairie dogs (11-13 inches in length) are the only small mammals in northeastern Colorado which provide numerous, closely spaced holes in which burrowing owls can nest. Thus, the owl population is clumped where these holes are available.

Burrowing owls in northeastern Colorado are dependent for nest sites upon species of mammals which suffer from widespread persecution and extermination. If these mammals are extirpated from the region, the burrowing owl may follow. It is possible that the owls may linger for several years in prairie dog towns which are poisoned out. This is not a long-term solution, however. I visited a prairie dog town on the 1,000-sq mile study area in 1972 which had been poisoned in 1968. All dogs were killed. Burrowing owls were common there in 1968 according to the land owner. In 1972 not a single owl or active burrow was found after visiting every mound and dirt patch in the town. A small number of burrows were still kept open, presumably by cottontail rabbits or badgers.

Protective measures are in order. The re-establishment and protection of evenly spaced, size-controlled prairie dog towns, in spite of the dislike of prairie dogs by ranchers, should be undertaken. One person could eliminate virtually every prairie dog on the 1,000-sq mile study area in a week. Likewise, many of the towns should be posted with signs stating that only the prairie dogs are legal targets. I have found adult burrowing owls laying dead at the entrances of burrows. Prairie dogs usually take refuge at the sight of a car stopped near the town, but burrowing owls do not and are easy targets for indiscrimanent shooters.

American Kestrel

The range of the American kestrel or sparrow hawk, actually a small falcon, includes most of North and South America and the West Indes, excluding the treeless Arctic, much of Mexico and Central America, and east central South America (Amazonia). Most of the southern exclusions are heavily forested areas (Brown and Amadon, 1968).

The American kestrel occurs in northeastern Colorado during all seasons, although wintering birds (few in number) probably immigrate from more northern latitudes. Kestrels are most conspicuous on the Pawnee just prior to fall migration and during both the spring and fall migrations. In late August several family groups (apparently) often join in flocks of up to 75 or 100 birds before migrating. Craig (1970) found peak migration periods during the first 2 weeks of September 1969 and the last 10 days of April 1970.

The total number of nesting kestrels was not determined during the present study, although the numbers can be estimated. There are about 76 linear miles of creeks with apparently adequate trees for kestrel nests on the 1,000-sq mile study area. These are usually dead cottonwood trees with loose bark, making climbing dangerous or impossible. The major portion of this 76 miles of creeks includes about 44 miles of Crow Creek and 17 miles of Lone Tree Creek (see Fig. 1).

Along the southern portion of Crow Creek, the best kestrel nesting habitat, about three pairs per mile were encountered in six miles of gallery forest. Extrapolating this ecological nesting density to all apparently adequate creek bottom nesting habitat on the 1,000-sq mile study area, and taking into account that 1) all 76 miles of creeks may not have suitable dead trees, 2) the gallery forest along Crow Creek has many short gaps (up to one mile), and 3) certain of the large raptors may competitively exclude kestrels from otherwise suitable nest sites, the population of this small falcon could be set at about 180 pairs per 1,000 sq miles. A few kestrels nested in the cliffs on the study area, but these probably involved only a small percentage of the entire population.

The accuracy of this estimate must be established by further study. Unlike with burrowing owls, however, it is very doubtful that the kestrel population was higher than here estimated; it could be 20 per cent less depending on the accuracy of the qualified extrapolation of 3 pairs per linear mile of habitat.

POPULATION LEVELS AND PRODUCTIVITIES

The Extensive Study Area

Clutch Size, Maximum Brood Size and Fledging Success. Table 5 is a compilation of these nesting parameters for the five important nesting species on the PNG. Data from 1970, 1971 and 1972 are treated separately and collectively. Averages of 1971 and 1972 data are also presented, since in those years field efforts were of adequate extent. A nesting attempt must have at least produced eggs to be included in these calculations; non-nesting pairs and single birds were ignored, although they were included in the analyses of breeding densities and productivities on the 414- and 1,000-sq mile study areas (see Tables 10-15). If observer interference was a possible cause of nest failure, the suspect data were discarded. The nests from which clutch size data were obtained may or may not be the same nests from which maximum brood sizes or fledging successes were obtained and vice versa.

Clutch size of Swainson's hawks was quite stable from year to year, ranging from 2.31 to 2.41. Maximum brood size ranged from 1.50 to 1.86 young per nest. Fledging success was comparable in 1970 and 1971 (about 1.12), but higher in 1972 (1.24 young fledged per nest). Apparently, the low fledging success of Swainson's hawks in 1970 was due to a higher than average mortality of hatched young, since clutch size and maximum brood size were above or near the overall averages. The low fledging success of Swainson's hawks in 1971 resulted from a lower than average maximum brood size.

Table 5. A compilation of clutch sizes, maximum brood sizes and fledging successes of large raptors in northeastern Colorado--1970-1972. Sample sizes are in parentheses.

Species and Years	Clutch Size	Maximum Brood Size	Fledging Success
Swainson's Hawk			
1970	2.41(22)	1.72(18)	1.11(19)
1971	2.32(28)	1.50(26)	1.13(30)
1972	2.31(45)	1.86(51)	1.24(70)
1971-72	2.31(73)	1.74(77)	1.21(100)
Overall	2.34(95)	1.74(95)	1.19(119)
Ferruginous Hawk			
1970	2.50(6)	1.22(9)	1.22(9)
1971	3.00(14)	2.15(13)	2.08(13)
1972	3.38(24)	2.32(31)	1.87(31)
1971-72	3.24(38)	2.27(44)	1.93(44)
Overall	3.14(44)	2.09(53)	1.81(53)
Golden Eagle			
1970	1.86(7)	1.62(8)	1.50(8)
1971	1.56(18)	1.11(19)	1.00(18)
1972	1.69(13)	1.00(15)	0.93(15)
1971-72	1.61(31)	1.06(34)	0.97(33)
Overall	1.66(38)	1.17(42)	1.07(40)
Prairie Falcon			
1971	4.67(6)	3.90(10)	3.78(9)
1972	4.33(18)	3.94(17)	3.24(17)
1971-72	4.42(24)	3.93(27)	3.42(26)
Great Horned Owl			
1971	2.25(8)	1.64(14)	1.64(14)
1972	2.27(11)	1.85(13)	1.46(13)
1971-72	2.26(19)	1.74(27)	1.56(27)

Ferruginous hawks apparently had a poor year in 1970, although the sample size was small due to the lack of intensive field effort that year. Fledging success in 1970 was only 63 per cent of that in 1971 and 1972 combined apparently because of lower than average clutch and maximum brood sizes. A check of all 1970 nest visit data dismissed the notion that, perhaps, the failure to hatch was caused by observer interference. The highest fledging success of ferruginous hawks occurred in 1971, a year of considerable mortality of eggs, but very little nestling mortality. The lower fledging success in 1972 (compared to 1971) followed more mortality of young birds, not low clutch or brood sizes which were highest in 1972. Overall and 1972 fledging successes on the Pawnee agree almost exactly with 1972 fledging success on a large study area in Utah and Idaho (Leon Powers, pers. comm.), but is somewhat higher than the 1.52 young fledged per nest in 1967 and 1968 in the Cedar Valley of Utah (Weston, 1969).

Clutch size, maximum brood size and fledging success of golden eagles averaged (for the three years combined) 1.66, 1.17 and 1.07, respectively. In 1970 all three of these nesting parameters, particularly the figures for maximum brood size and fledging success, were higher than in 1971 and 1972. This does not represent a real decrease in the success of golden eagles. In 1970 no early nest failures by golden eagles were detected, since field work did not begin until late April and the field effort was not intense. In 1971 and 1972 many early nest failures were detected (see the section on habitat use and nesting at man-created nest sites). In view of this, data collected in 1971 and 1972 are probably more realistic for the shortgrass prairie population under study. The 1971-72 averages for clutch size, maximum brood size and fledging success were 1.61, 1.06 and 0.97, respectively. In the arid, shrub-covered hills surrounding the Cedar Valley of Utah, and in the valley itself, Camenzind (1969) found that golden eagles fledged 0.84 young per nest in 1967 and 1968. A comparison of Pawnee data with other golden eagle population data is included in the section on habitat use and nesting at man-created nest sites (see below).

Prairie falcon productivity was remarkably high in 1971 and 1972. An average of 4.42 eggs were laid per nest of which an average of 3.93 hatched. Fledging success, 3.42 young per eyrie, was slightly more than triple what Enderson (1964) reported for 82 nestings of prairie falcons in northeastern Colorado and Wyoming from 1960 through 1962, exactly ten years earlier. Ogden (pers. comm.) found a mean clutch size of 4.41 eggs and a fledging success of 3.1 young per occupied territory between 1970 and 1972 at 110 eyries along the Snake River in southwestern Idaho. The slightly lower success of prairie falcons on the Pawnee in 1972 resulted more from nestling mortality than lower clutch size, since maximum brood sizes were comparable in the two years.

The success of great horned owls which at least laid eggs was comparable in 1971 and 1972. Clutch size, maximum brood size and fledging success averaged 2.26, 1.74 and 1.56, respectively, for the two years. This compares favorably with Smith's (1969) finding that 1.64 young owls fledged per nest in 1967 and 1968 in the Cedar Valley of Utah. Although fewer great horned owls hatched per nest in 1971 than in 1972 on the Pawnee, considerable mortality of nestlings occurred in 1972. At the same time, great horned owls were in the throes of a serious, nearly population-wide nesting failure. Only 30 per cent of all pairs present fledged young on the 414- and 1,000-sq mile study areas in 1972, compared with 83 per cent on the 414-sq mile area in 1971 (see below) and 79 per cent of all known nests in 1971.

Variation in Nesting Parameters. Year-to-year variations in nesting parameters (Table 6) are useful in ascertaining 1) problem areas within life histories of individual species and, in some cases, 2) portions of the nesting sequence which set the level of productivity of a population within a given year. Year-to-year comparisons are more meaningful on a long-term basis, although two-year comparisons may alert researchers to look for specific problems during subsequent study. The presence of large numbers of non-nesting adult pairs (as was the situation with great horned owls on the Pawnee in 1972), the phenology of nesting and other factors must qualify conclusions drawn from analyses of variations in nesting parameters, particularly when the parameters include data only from pairs which produce eggs.

Clutch size of Swainson's hawks was relatively constant (0.4 per cent variation from the 1971-72 average between

Table 6. 1971 to 1972 variation in nesting parameters from the 1971-72 averages. Values are per cents. Underlined per cents indicate lower values in 1972 than in 1971.

Species	Variation in Clutch Size	Variation in Maximum Brood Size	Variation in Fledging Success
Swainson's Hawk	0.4	13.8	6.6
Ferruginous Hawk	7.4	5.3	7.8
Golden Eagle	5.0	5.7	4.1
Prairie Falcon	5.7	0.8	10.5
Great Horned Owl	0.4	6.3	6.4

**Per cent variation = (1971 value-1972 value) ÷ 1971-72 Average x 100.

1971 and 1972), but maximum brood size varied considerably (13.8 per cent; see Table 6). The causes of the latter variation and subsequent differing rates of nestling mortality resulted in only a moderate variation of 6.6 per cent in fledging success. Thus, in 1971 low mortality of young Swainson's hawks followed high hatching failure (and vice versa in 1970 and 1972) (see Table 5).

It is doubtful that this "compensation" always occurs in Swainson's hawk populations. Future researchers on the Pawnee should anticipate years when mortality of both eggs and young of Swainson's hawks are high, with a resulting fledging success significantly less than 1.11-1.13.

Clutch sizes of the resident falconiform species varied most, while clutch size of the principal migrant (Swainson's hawk) was nearly identical in 1971 and 1972. The resident species are exposed to local weather conditions for longer periods of time than migratory species. Weather conditions were extremely different in 1971 and 1972, with 1972 being relatively warmer and drier from February through May (see Further Discussions). This is suggestive that clutch size is affected by weather conditions. Clutch sizes of ferruginous hawks and golden eagles were larger in 1972 than in 1971. The opposite was true of prairie falcons. If weather was the only factor involved, one would expect a priori that the changes in the different species would be parallel.

Although clutch sizes of ferruginous hawks and golden eagles were greater in 1972, fledging successes were smaller

(Tables 5 or 6). In fact, fledging successes of all resident species were lower in 1972. Swainson's hawks produced many more young in 1972.

Probabilities of Hatching and Fledging. From the overall averages of clutch size, maximum brood size and fledging success in Table 6, the following probabilities were calculated: 1) of hatching, 2) of fledging if hatched and 3) of fledging at egg laying (Table 7). With the exception of ferruginous hawks, the probability of hatching decreased in the same order as clutch size, brood size and fledging success. This was determined by ranking the overall averages in Table 6 and comparison with Table 7. In otherwords, the more eggs laid, the higher the probability of hatching. The low hatching rate of ferruginous hawk eggs is discussed elsewhere (Olendorff, 1972b; Olendorff, this report).

The probability of a Swainson's hawk egg hatching was 0.746, but the probability of fledging if hatched was considerably lower than for all other species (0.688 as opposed to 0.865 - 0.941 for the other species). This resulted in the lowest overall probability of fledging (0.513). Just slightly over half of all Swainson's hawk eggs laid resulted in a fledged young. Prairie falcons hatched a higher percentage of their eggs than any other species and were reasonably successful at fledging young, resulting in the highest probability of a freshly laid egg culminating in a fledged young (0.774).

Table 7. Probabilities of hatching and fledging of large raptors on the Pawnee National Grassland--1970-72.

Species	Probability of Hatching		Probability of Fledging if Hatched		Overall Probability of Fledging at Egg Laying
Prairie Falcon	0.889	X	0.870	=	0.774
Ferruginous Hawk	0.666	X	0.865	=	0.576
Great Horned Owl	0.770	X	0.896	=	0.690
Swainson's Hawk	0.746	X	0.688	=	0.513
Golden Eagle	0.705	X	0.941	=	0.662

With the exception of prairie falcons, the overall probability of fledging at egg laying was lower the later in the season egg laying commenced (compare Fig. 4 and Table 7). There apparently was a premium on nesting early as discussed in the section on nesting phenologies (see Further Discussions).

Golden eagles were more successful at fledging young once the eggs hatched than any of the other species. Over 94 per cent of the hatchlings fledged.

Nest Success. Prairie falcons had the highest nest success (fledged at least one young) of the large birds of prey on the PNG between 1970 and 1972 (88.8 per cent) (Table 8). Ferruginous hawks and golden eagles had nearly equal nest successes (70.4 and 69.7 per cent, respectively). As with the overall probability of fledging, species which nested earlier in the season had a higher nest success, prairie falcons excepted (Table 8).

If nest success of ferruginous hawks and great horned owls was less than 70 per cent, Swainson's hawk nest success was greater than 50 per cent. The converse was also true. This strongly suggests that Swainson's hawk productivity was directly affected by the success of the earlier nesters (see Further Discussions).

Productivity of Young in Successful Nests. This analysis is included here to show that grossly incorrect conclusions can be drawn using the number of young produced per successful nest as the sole analytical tool. From the figures in Table 9 the following conclusions could be reached: 1)

Table 8. Nest successes of the large raptors on the Pawnee National Grassland--1970-72.

Species and Years	Nests	Successful	Per Cent
Swainson's Hawk			
1970	19	10	52.6
1971	30	14	46.7
1972	70	41	58.6
Overall	119	65	54.6
1971-72	100	55	55.0
Ferruginous Hawk			
1970	9	6	66.7
1971	13	11	84.6
1972	31	20	64.6
Overall	53	37	69.8
1971-72	44	31	70.4
Golden Eagle			
1970	8	7	87.4
1971	18	13	72.2
1972	15	10	66.7
Overall	41	30	73.1
1971-72	33	23	69.7
Prairie Falcon			
1971	9	9	100.0
1972	18	15	83.4
1971-72	27	24	88.8
Great Horned Owl			
1971	14	11	78.5
1972	13	9	69.3
1971-72	27	20	74.0

Table 9. Productivity of young in successful nests of large raptors on the Pawnee National Grassland--1970-72.

Species and Years	Young Fledged	Successful Nests	Productivity of Young in Successful Nests
Swainson's Hawk			
1970	21	10	2.10
1971	34	14	2.43
1972	87	41	2.12
Overall	142	65	2.18
Ferruginous Hawk			
1970	11	6	1.83
1971	27	11	2.45
1972	58	20	2.90
Overall	96	37	2.59
Golden Eagle			
1970	12	7	1.72
1971	18	13	1.38
1972	14	10	1.40
Overall	44	30	1.47
Prairie Falcon			
1971	34	9	3.78
1972	55	15	3.66
Overall	89	24	3.71
Great Horned Owl			
1971	23	11	2.09
1972	19	9	2.11
Overall	42	20	2.10

Swainson's hawks had a better year in 1971 than in 1972; 2) ferruginous hawks had a better year in 1972; and 3) golden eagles, prairie falcons and great horned owls had comparable successes in 1971 and 1972.

The data presented in Table 5 show that conclusions 1) and 2) above are opposite from actual fact. This will be sub-stantiated by breeding density and productivity figures presented below (see Tables 10-15). Golden eagles actually experienced a 7.0 per cent decrease in fledging success from 1971 to 1972, yet the number of young fledged per successful nest increased by 1.4 per cent (a negligible change). Like-wise, fledging success of prairie falcons was 14.3 per cent less in 1972 than in 1971, while the number of young fledged per successful nest was only 3.2 per cent less.

The conclusion that great horned owls had comparable success in 1971 and 1972 is very inaccurate. Fledging suc-cess was 11.0 per cent lower in 1972 than in 1971 but, of more importance, about 70 per cent of the great horned owls did not produce eggs in 1972! Unfortunately, this fact is not adequately reflected in the figures of Table 5 for clutch size, maximum brood size and fledging success or in Table 9.

The suggestion which must be made is that if young per successful nest is the only parameter available, report it, but be very careful of the conclusions drawn. At a time when some raptor populations are decreasing, inaccuracies in analyses of trends in population levels cannot be tolerated.

Although a decrease in the number of young per successful nest may occur in pesticide ridden populations, the same probably will not occur in a population being extirpated by human encroachment on nesting habitat. The definitions of clutch size, brood size and fledging success used in the present report allow reasonably accurate analyses, only when conclusions are qualified by other nesting information (e.g. unusually high numbers of non-nesting pairs). Breeding density and productivity of young per unit area are much more meaningful nesting parameters than any of the above. If energetics of the populations are of concern, biomasses should be calculated. The remaining considerations of population levels and productivities utilize the latter three nesting parameters.

The 414-sq Mile Study Area

Breeding density, productivity and biomass data for the 414-sq mile study area in 1971 and 1972 are presented in Tables 10, 11 and 12, respectively. In 1971 experimental nests (one of each for Swainson's and ferruginous hawks) and nests with unknown outcome (two Swainson's hawk nests) were compensated for by taking into account the overall nest failure rates and the modal brood sizes for those species concerned. In 1972 no nests were considered experimental and nests with unknown outcome (a very small number) were simply omitted from calculations of nest successes and productivities.

<u>Breeding Densities and Productivities</u>. Totals of 42 and 50.5 pairs of large birds of prey were observed on the area in 1971 and 1972, respectively (Table 10). In 1971, 37 pairs were known to have nested. Thus, 42.5 per cent of the 87 sections with potential nest sites (Table 2) were occupied. In 1972 45 pairs nested and used 51.8 per cent of the available nest sites.

The number of young Swainson's hawks produced per 100 sq miles in 1972 (11.85) was 258 per cent higher than in 1971 (4.59) (Table 11). This resulted from 1) nearly 50 per cent more pairs in 1972, 2) 70.6 per cent nest success (compared with 33.3 per cent in 1971), and 3) 82 per cent more young produced per pair with known production (Tables 10 and 11). This high production occurred in spite of a lower number of young per successful nest in 1972 (2.12 as opposed to 2.43 in 1971 from Table 9).

The circumstances which led to such high production of Swainson's hawks include at least the following: 1) <u>There was a lower breeding density of ferruginous hawks in 1972 than in 1971, and their nest success and productivity of young were lower</u>. The number of young produced per 100 sq miles was 50 per cent lower. In 1971 nearly all of the young ferruginous hawks on the 414-sq mile study area were measured periodically during intensive growth studies. No young were abandoned, but it is suspected that the adults moved their nesting activity to other locations (mostly off of the 414-sq mile area) in 1972. The lower nest success of ferruginous hawks was

Table 10. Breeding densities and nest successes of the large birds of prey on a 414-sq mile (1,073 km^2) shortgrass prairie study area consisting of essentially unbroken grassland--1971-72.

Species	Number of Pairs		Pairs per 100 Sq Miles		Pairs per 100 Km^2		Successful Pairs (Nest Success)	
	1971	1972	1971	1972	1971	1972	1971	1972
Swainson's Hawk	24	35*	5.80	8.45	2.24	3.26	8(33.3%)	24(70.6%)*
Ferruginous Hawk	10	6	2.41	1.45	0.93	0.56	7(70.0%)	3(50.0%)
Great Horned Owl	6	6.5	1.45	1.57	0.56	0.61	5(83.3%)	2(30.8%)
Golden Eagle	2	3	0.48	0.72	0.19	0.28	0(00.0%)	1(33.3%)
All Species	42	50.5	10.14	12.19	3.92	4.71	20(47.6%)	30(60.6%)

*Outcome of one nest unknown. Nest success calculated on basis of 24 out of 34 successful.

Table 11. Productivity of raptorial birds on the 414-sq mile (1,073 Km^2) study area--1971-72.

Species	Young Produced		Young per Pair with Known Production		Young Produced per 100 sq Miles		Young Produced per 100 Km^2	
	1971	1972	1971	1972	1971	1972	1971	1972
Swainson's Hawk	19	49*	0.79	1.44	4.59	11.85	1.77	4.56
Ferruginous Hawk	16	8	1.60	1.33	3.86	1.93	1.49	0.75
Great Horned Owl	10	4	1.67	0.62	2.42	0.97	0.93	0.37
Golden Eagle	0	2	0.00	0.67	0.00	0.48	0.00	0.19
All Species	45	63	1.07	1.27	10.87	14.73	4.19	5.69

* Young produced in 34 nests.

caused by destruction (probably by humans) of 4 young in one nest, very early nest failure in another, and one non-nesting pair. 2) Although there were about the same number of adult great horned owls present in each of the two years, nest success and productivity of young were very low in 1972 due to the presence of 2½ non-nesting pairs, human destruction of 2 nearly fledged young, and one nest failure of unknown cause.

The apparent result of 1) and 2) above was a relatively low level of interspecific competition between the early nesters and the late arriving Swainson's hawks, as the latter set up territories. Swainson's hawks filled a void made available by different nest site choices and general nesting failure of the potentially competitive species. These relationships are discussed further in the section on nesting phenologies (see Further Discussions). It is clear that a relatively "good" year for one species can be a relatively "bad" year for another.

Biomass Considerations. The following analysis (Table 12) has several inherent assumptions: 1) all nesting and non-nesting pairs on the prescribed area were located; 2) the biomass of adult raptors remained stable (there was no mortality) throughout the breeding season; and 3) only fledged young contributed to the biomass of the population. Calculations of adult biomass before the onset of egg-laying and biomass of the young after fledging (and the combination of the two) were calculated. Species were considered separately and collectively. Calculations are made in detail below for

Table 12. Biomasses of adult and young raptors on the 414-sq mile (1,073 Km^2) study area at the end of the breeding season in 1971 and 1972. The units are g/km^2 wet weight followed by percentages (in parentheses) of the total of all species combined (of each column).

Species	Adults		Young After Fledging		Adults and Young	
	1971	1972	1971	1972	1971	1972
Swainson's Hawks*	44.2(41.3%)	64.5(51.7%)	14.1(31.4%)	36.3(63.7%)	58.3(38.4%)	100.8(55.4%)
Ferruginous Hawks	30.0(28.0%)	18.0(14.4%)	19.3(43.0%)	9.7(17.0%)	49.3(32.4%)	27.7(15.2%)
Great Horned Owl	16.8(15.7%)	18.2(14.6%)	11.5(25.6%)	4.6(8.1%)	28.3(18.6%)	22.8(12.6%)
Golden Eagle	16.1(15.0%)	24.1(19.3%)	0.0(0.0%)	6.4(11.2%)	16.1(10.6%)	30.5(16.8%)
All Species	107.1	124.8	44.9	57.0	152.0	181.8

*Outcome of one Swainson's hawk nest unknown in 1972.

biomasses on the 414-sq mile study area in 1971. Biomasses for other years and for the 1,000-sq mile study area were calculated identically. Metric figures are given, although the names of the study areas mention sq miles.

Six pairs of great horned owls were present on the 414-sq mile study area in 1971 representing a mass of 3,010 g/pair or 18,060 g. This calculated to a biomass of 16.8 g/km^2. (Table 12). The six pairs of adults fledged 10 young owls with weights of approximately 1,235 g each (average of only two individuals), i.e., 12,350 g. This reduced to 11.5 g/km^2. The combined biomass of great horned owls, adults and young, was 28.3 g/km^2 after all birds had fledged, i.e., after late May and before appreciable mortality or emigration occurred.

Ten pairs of ferruginous hawks were present on the area in 1971. At 3,220 g/pair this amounted to 32,200 g or 30.0 g/km^2. These 10 pairs fledged 15 young at an average weight of 1,296 g each or a total of 19,440 g. This was 18.1 g/km^2. The total biomass of ferruginous hawks on about July 17 and after (assuming no mortality of adults) was 48.1 g/km^2.

Twenty-four pairs of Swainson's hawks nested in the area in 1971 with a total mass of 47,448 g and biomass of 44.2 g/km^2. These birds fledged 20 young at an average of 796 g each, representing a mass of 15,920 g, i.e. 14.8 g/km^2. Total biomass of Swainson's hawks after mid-August (assuming no adult mortality) was 59.0 g/km^2.

Two pairs of golden eagles were present. Neither reared young. Mass of the two pairs was approximately 17,252 g and biomass was 16.1 g/km^2 throughout the spring and summer.

At the end of the breeding season (again assuming no mortality of adults or of young during the post-fledging periods of the early nesters) the total biomass of all large raptors on the 414-sq mile study area was 151.5 g/km^2.

Weights used in further calculations include young golden eagles--3,450 g, adult pair of prairie falcons--1,417 g, young prairie falcons 682 g, adult pair of red-tailed hawks--2,252 g and young red-tailed hawks--1,075 g.

Biomasses of adult and young raptors at the end of the breeding season on the 414-sq mile study area were greater or less in 1972 than in 1971 by the following percentages: Swainson's hawks--73 per cent greater, golden eagles--89 per cent greater, great horned owls--19 per cent less, and ferruginous hawks--44 per cent less. For all species combined, biomass was about 20 per cent greater in 1972 than in 1971. Biomass averaged 166.9 g/km^2 for the two years including an average of 116.0 g/km^2 for adults and a biomass production of young of 50.9 g/km^2. The biomass of young produced was less than half (43.9 per cent) of the biomass of the adults present.

The biomass figures, both for adults and young, were dominated by Swainson's hawks, although ferruginous hawks ran a close second in 1971. The total biomass of adults and young was proportioned as follows in 1972: Swainson's hawks--

55.4 per cent, ferruginous hawks--15.2 per cent, great horned owls--12.6 per cent and golden eagles--16.8 per cent. These percentages will be compared below with similar figures for the 1,000-sq mile study area (Table 15).

The 1,000-sq Mile Study Area

In IBP Technical Report 151 (Olendorff, 1972b), crude nesting densities were estimated on a 2,266-sq mile area which included all nesting species and all potential nesting habitats in northeastern Colorado. Limitations of manpower and financial support precluded actual determinations of crude nesting densities on more than 1,000 sq miles, so the 1,000-sq mile study area was designed as representative of most of northeastern Colorado (see Methods above). All future raptor research in the area should place the highest priority on yearly determinations of crude nesting densities and productivities on the 1,000-sq mile study area, a large (but accomplishable) task for two researchers.

Breeding Densities and Productivities. In 1972 the large raptor population on this area consisted of 42.8 per cent Swainson's hawks, 16.4 per cent ferruginous hawks, 19.3 per cent great horned owls, 7.6 per cent golden eagles, 8.8 per cent prairie falcons and 5.1 per cent red-tailed hawks. All species considered, there were 15.85 pairs of large raptors for every 100 sq miles, or 1 pair for every 6.3 sq miles. Only about half (53.3 per cent) produced at least one young (red-tailed hawks not included in this statistic).

Comparisons between 1972 data for pairs per 100 sq miles on the 414-sq mile study area (Table 10) and on the 1,000-sq mile study area (Table 13) revealed quite different population levels, particularly when the species were considered individually. In essentially unbroken grassland (the 414-sq mile study area) there were 24 per cent more Swainson's hawks, 44 per cent fewer ferruginous hawks, 49 per cent fewer great horned owls and 40 per cent fewer golden eagles than in a combination of shortgrass prairie habitats (1,000-sq mile study area). Prairie falcons and red-tailed hawks nested on the 1,000-sq mile area, but not the 414-sq mile area.

One would expect <u>more</u> ferruginous and <u>fewer</u> Swainson's hawks to nest on the 414-sq mile study area (unbroken grassland). Ferruginous hawks nested in unbroken grassland nearly two-thirds of the time (see Table 16 below). Similarly, Swainson's hawks nested in creek bottoms two-thirds of the time. Several factors may be responsible for the deviation from expected results. 1) Essentially unbroken grassland on the PNG has been periodically interrupted by farmsteads, now abandoned and used by hawks as nest sites (see below). Swainson's hawks have taken advantage of these man-created sites. 2) As noted above, most young ferruginous hawks on the 414-sq mile area were measured periodically in 1971; the adults apparently moved into the surrounding area (the 1,000-sq mile area) to nest in 1972. 3) Great horned owls and ferruginous hawks experienced a general nesting failure in

Table 13. Breeding densities and nest successes (1972 only) of the large birds of prey on a 1,000-sq mile (2,598 Km^2) shortgrass prairie study area consisting of unbroken grassland and grassland interrupted by gallery forests along creek bottoms, cliff lines, and tracts of cultivated land.

Species	Number of Pairs	Pairs per 100 sq Miles	Pairs per 100 Km^2	Successful Pairs
Swainson's Hawk	68 1/	6.80	2.62	38(56.8%)
Ferruginous Hawk	26	2.60	1.00	16(61.6%)
Great Horned Owl	30.5 1/	3.05	1.17	8(29.1%)
Golden Eagle	12	1.20	0.46	5(41.6%)
Prairie Falcon	14	1.40	0.54	11(78.6%)
Red-tailed Hawk 1/	8 2/	0.80	0.31	? ? ? ?
All Species	158.5	15.85	6.10	78(53.3%)

1/ Outcome of one Swainson's hawk and three great horned owl nests unknown.

2/ Number of adult pairs is accurate, but productivity data for red-tailed hawks were not collected.

1972, leaving a void of interspecific conflict when the late nesting Swainson's hawks arrived. There were nearly 50 per cent more Swainson's hawks on the 414-sq mile area in 1972 than in 1971 (Table 10). 4) Cursory habitat analysis of the 1,000-sq mile area showed that more sq miles of cliffs, grasslands without trees and cultivated land (poor or unsuitable nesting habitat for Swainson's hawks) were added to expand the 414-sq mile area to 1,000 sq miles. Cliffs and grasslands without trees are suitable nesting habitat for ferruginous hawks (Table 17 below).

All species with the exception of Swainson's hawks produced more young per 100 sq miles on the 1,000-sq mile study area than on the 414-sq mile area (Tables 14 and 11). This corresponds with the differences in breeding population densities. For all species combined, 201 young were produced or 20.1 per 100 sq miles (36.5 per cent greater than on the 414-sq mile area). That was 1.37 young per pair with known production. Most of the greater production of young on the 1,000-sq mile area was attributable to the high production of prairie falcons. The red-tailed hawk data are included for completeness. The estimated productivity figures should be fairly realistic.

Biomass Considerations. For all species and age classes combined, the biomass of all large raptors was 252.8 g/km^2 at the end of the 1972 breeding season, or 39.0 per cent greater than on the 414-sq mile area (Table 15). Biomass of the

Table 14. Productivity of raptorial birds on the 1,000-sq mile (2,598 Km^2) study area--1972.

Species	Young Produced	Young per Pair With Known Production	Young Produced per 100 Sq Miles	Young Produced per 100 Km^2
Swainson's Hawk	80	1.19	8.00	3.08
Ferruginous Hawk	48	1.85	4.80	1.85
Great Horned Owl	18	0.65	1.80	0.69
Golden Eagle	6	0.50	0.60	0.23
Prairie Falcon 1/	41	2.93	4.10	1.58
Red-tailed Hawk 2/	(8)	(1.00)	(0.80)	(0.31)
All Species	201	1.37	20.10	7.74

1/ One pair which fledged at least 2 young could have fledged 3 or 4. Used 2 fledged in this analysis.

2/ All productivity data for red-tailed hawks is estimated. It is assumed that 6 of 8 nests fledged a total of 8 young. Only 2 nests were followed up and each apparently fledged 2 young.

Table 15. Biomasses of adult and young raptors on the 1,000-sq mile (2,598 Km^2) study area at the end of the breeding season in 1972. The units are g/Km^2 wet weight followed by percentages (in parentheses) of the total of all species combined (of each column).

Species	Adults	Young After Fledging	Adults and Young
Swainson's Hawk	51.7 (29.8%)	24.5 (30.9%)	76.2 (30.1%)
Ferruginous Hawk	32.2 (18.5%)	24.0 (30.3%)	56.2 (22.2%)
Great Horned Owl	35.4 (20.4%)	8.6 (10.9%)	44.0 (17.4%)
Golden Eagle	39.8 (22.9%)	8.0 (10.0%)	47.8 (18.9%)
Prairie Falcon	7.6 (4.4%)	10.8 (13.7%)	18.4 (7.3%)
Red-tailed Hawk1/	6.9 (4.0%)	3.3 (4.2%)	10.2 (4.1%)
All Species	173.6	79.2	252.8

1/ Data for young red-tailed hawks after hatching are estimated.

young was 79.2 g/km^2 or only 45.6 per cent greater than adult biomass. For each species individually, biomasses were increased by the following percentages: Swainson's hawk--47.4, ferruginous hawk--74.6, great horned owl--24.3, golden eagle--20.1, prairie falcon--142.2 and red-tailed hawk--47.8 (estimated). Variations in such figures (from species to species) is dependent upon the number of young produced and the nest success of each species. Percentage increase in biomass, a very sensitive measure of productivity, is one of the best indicators of overall reproductive performance and should be used wherever year-to-year comparisons are possible. Future data collection should be aimed toward such comparisons.

One cannot state the relative impacts of the species with certainty from these data, but the order of their biomass percentages is a good estimate. Swainson's hawks were most important (30.1 per cent of the biomass). Energetically, the Swainson's hawk has even greater impact, since it is the smallest species which accounts for more than 10 per cent of the biomass, and smaller animals generally consume more food per gram of body weight than larger animals. It is inefficient to be small, in general. Ferruginous hawks, great horned owls and golden eagles each accounted for about 20 per cent of the 1972 biomass (58.5 per cent collectively). Prairie falcons and red-tailed hawks together accounted for only 11.4 per cent of the biomass.

The percentages of the total biomasses for the two areas in 1972 (from Tables 12 and 15) are displayed below 1) to illustrate the dangers of considering a small, unrepresentative area during a nesting study and 2) to compare an area of essentially unbroken grassland with an area consisting of all available nesting habitats.

	414-sq Mile	1,000-sq Mile
Swainson's Hawk	55.4%	30.1%
Ferruginous Hawk	15.2%	22.2%
Great Horned Owl	12.6%	17.4%
Golden Eagle	16.8%	18.9%
Prairie Falcon	0.0%	7.3%
Red-tailed Hawk	0.0%	4.1%

Only golden eagles occurred in comparable proportions of the total populations of large raptors on the two areas. Prairie falcons and red-tailed hawks (which were absent from the smaller area) accounted for 11.4 per cent of the population on the 1,000-sq mile area. Swainson's hawk biomass was over 25 per cent of the total less on the 1,000-sq mile area.

There were also large differences between population levels based on density (individuals per unit area) and those based on biomasses (weight per unit area). A comparison of percentages of the total population of adults and young in 1972 is shown below.

	Density	Biomass
Swainson's Hawk	41.7%	30.1%
Ferruginous Hawk	19.3%	22.2%
Great Horned Owl	15.3%	17.4%
Golden Eagle	5.8%	18.9%
Prairie Falcon	13.3%	7.3%
Red-tailed Hawk	4.6%	4.1%

Golden eagles accounted for a much smaller percentage of total density than of total biomass. Red-tailed hawk, great horned owl and ferruginous hawk percentages were about comparable, while Swainson's hawk and prairie falcon percentages of total density were greater than percentages of total biomass.

HABITAT USE AND NESTING AT MAN-CREATED NEST SITES BY GRASSLAND RAPTORS

Man has been an important factor in the distribution of nesting birds of prey on the Pawnee National Grassland and adjacent areas in northeastern Colorado. Before man came to this large, shortgrass prairie, trees were restricted primarily to gallery forests along creek bottoms and to small groves near natural springs. The homesteaders of the late 1800's and early 1900's planted native and exotic trees near their houses and windmills, thereby unknowingly but substantially changing the future habitat composition of the area. Most of the homesteaders were driven from the area between 1915 and 1933 by drought conditions. Today the trees at the abandoned farmsteads are used extensively by birds of prey as nest sites.

In addition, volunteer cottonwood trees have grown along abandoned ditches where elaborate, but unsuccessful, attempts at irrigation were made by the early settlers. An analogous situation developed where ranchers dammed usually dry stream beds to collect infrequent, torrential runoff in ponds for their cattle. Quantification of these examples of inadvertent management of wild raptor populations is the main topic of this paper. However, a thorough development of this concept must be preceded by considerations of differential utilization of habitats and actual nest site selection by the birds in question, since these aspects of nesting have direct bearing on the potential of the species to adapt to nesting in man-created situations. Such considerations are included below.

For the purposes of the following analysis the grassland ecosystem was divided into four habitats. These include 1) well defined cliff lines, 2) creek bottoms with scattered trees or nearly continuous gallery forests, 3) large tracts of cultivated land, and 4) grasslands unbroken by cliffs, creeks with trees, or cultivation. The latter will be called "unbroken grasslands" henceforth, although man has artificially interrupted those monotonous expanses of prairie with houses (now mostly abandoned), wind breaks, windmills, roads, power and telephone lines, etc. In addition, hillocks and small erosional remnants often occur in what are here called unbroken grasslands.

Assignment of nests to one of the four habitats was quite arbitrary in a few instances and was done using the following criteria. Bluff lines posed no definition problems. All nests in cultivated land were in trees surrounded by or adjacent to large tracts of winter wheat fields. The distinction between tree nests in creek bottoms and pure grassland was made on the basis of the suspected origin of the tree or trees. Lone or small groups of trees away from a stream bed and surrounded by grazing land were considered to be in pure grassland. This includes trees near windmills, homesteads, and along abandoned irrigation ditches. All of these man-made structures are quite common on the Pawnee National Grassland. Other nests in pure grassland occurred on the ground, erosional remnants, abandoned stone houses, and in trees near ponds (both natural and man-made). In all cases they were surrounded by grazing land.

Creek bottom nests had to be along well-defined stream beds, both large and small. A few such nests were on creek banks, but the majority were in trees. Nests in single trees along stream beds but surrounded by grazing land were also considered as creek bottom nests. This introduced some overlap of creek bottom and pure grassland habitats, but it does not seriously affect trends in the data. An active nest is defined as one in which an adult was observed actively incubating or in which eggs were deposited. Only pairs which produced eggs were included in calculations of productivities. A nest site was counted each year it was used. With regard to observer interference, those few cases where it is suspected that our activities may have caused nest failure are eliminated from the calculations.

The productivity figures herein presented (actually fledging successes as used elsewhere in this paper) will appear low in many cases compared to other published information. This is not to be taken as a sign of increased nesting failure due to environmental contamination or human interference. Rather, this follows from certain habits of the birds, the timing of field study, and the analytical methods used. For example, since this study was begun on about 15 March each year, many early nest failures were noted. Many other studies do not take early nest failures into account.

In the case of Swainson's hawks, which often renest when a clutch of eggs is destroyed early in incubation, the fledging successes per nesting attempt herein calculated are probably slightly less than could be determined on a per adult pair basis. These productivities are <u>much</u> lower than those calculable using only successful nests. This follows from a high rate of nest failure due, primarily, to wind-caused destruction of nests, eggs and/or young of Swainson's hawks (Olendorff, 1972b).

All of the tables included in this section are similarly constructed. Several species are listed and under the species name are two lines. The first line gives percentages followed by sample sizes in parentheses. The nature of the percentages vary according to the subject matter of the table. The second line shows the fledging successes of nests found in the categories tabulated followed, again, by sample sizes in parentheses. Sample sizes for the productivity information will usually be slightly lower than those on which the percentages are based, because the outcomes of a few nests in each case were not determined.

Differential Utilization of Habitats

Each of the four nesting habitats was used differently by each of the five species of raptors (Table 16). Such a statement is trivial, perhaps, in reference to the prairie falcon, which nests only on cliffs. More diverse utilization of nesting habitats was apparent for Swainson's hawks, ferruginous hawks, golden eagles, and great horned owls.

About 63 per cent (or 95 of 150) of the nestings of Swainson's hawks occurred in creek bottoms; exactly 30 per cent nested in unbroken grasslands and a few pairs fledged

Table 16. Differential utilization of shortgrass prairie habitats by nesting birds of prey -- northeastern Colorado, 1970-1972.

	Unbroken Grasslands	Creek Bottoms	Cliffs	Cultivated Land
Swainson's Hawk				
Per Cent Use	30.0% (45)	63.3% (95)	- - - - -	6.7% (10)
Fledglings/Nest	1.19 (37)	0.90 (83)	- - - - -	1.10 (10)
Ferruginous Hawk				
Per Cent Use	57.8% (41)	35.2% (25)	5.6% (4)	1.4% (1)
Fledglings/Nest	1.73 (33)	1.33 (21)	3.00 (2)	4.00 (1)
Golden Eagle				
Per Cent Use	14.5% (8)	32.7% (18)	52.8% (29)	- - - - -
Fledglings/Nest	0.88 (8)	0.40 (15)	1.18 (22)	- - - - -
Prairie Falcon				
Per Cent Use	- - - - -	- - - - -	100.0% (30)	- - - - -
Fledglings/Nest	- - - - -	- - - - -	3.41 (27)	- - - - -
Great Horned Owl				
Per Cent Use	7.3% (3)	80.5% (33)	9.8% (4)	2.4% (1)*
Fledglings/Nest	1.33 (3)	1.45 (29)	2.00 (2)	2.00 (1)*

* Nest at a school house in a small town, not actually in cultivated land.

young in or near large tracts of cultivated land. Of the large raptors which nest on the study area, only Swainson's hawks regularly nested near cultivated land.

The habitat preferences of ferruginous hawks were quite different from those of Swainson's hawks. Well over half of all ferruginous hawk nests were in unbroken grasslands, while about one-third were in creek bottoms. A small number of ferruginous hawk nests were on cliffs or in trees near cultivated land. The two congeneric, sympatric buteos used the other's dominant nesting habitat 30 to 35 per cent of the time.

Golden eagles nested most often in the vicinity of well defined cliff lines but other habitats, with the exception of cultivated land, were also used. Great horned owls nested along creek bottoms more consistently than any of the other large raptors. Over 80 per cent nested in creek bottoms, with the other 20 per cent of the population about equally divided between nesting on cliffs and in unbroken grasslands. The great horned owl nest listed as being in cultivated land was actually about 25 feet from the second floor, sixth grade classroom of a schoolhouse in a small town on the study area. Thus, great horned owls were also absent from farmed lands as a nesting species.

The number of young fledged per nest in each habitat shows some interesting and unexpected trends, although some sample sizes are small due to infrequent use of one or more of the four habitats by a particular species (Table 16).

Swainson's hawks, for example, were less successful at fledging young in their dominant habitat (creek bottoms) than in unbroken grasslands or cultivated land. Overall, however, since more Swainson's hawks nested in creek bottoms, more young were fledged in that habitat (i.e. 57.7 per cent of 131 young known to have fledged from 1970-1972.)

The ferruginous hawk was most successful in its dominant nesting habitat (unbroken grasslands) where 1.73 young were fledged per nest, compared to 1.33 young fledged per nest in creek bottoms. Of 105 young known to have fledged from 1970-1972, 68.3 per cent were reared in unbroken grasslands, while only 26.6 per cent of the 105 fledglings were from creek bottoms. Productivity figures for golden eagles and prairie falcons will be discussed in the next section.

Great horned owls fledged an average of 1.45 young per nesting attempt in creek bottoms. Sample sizes for the other habitats are too small to allow meaningful comparisons between habitats.

Differential Use of Available Nest Supports

The actual placement of nests -- whether they were in trees, on erosional remnants or small outcroppings, creek banks, cliffs, the ground, or man-made structures -- also varied from species to species (Table 17). While Swainson's hawks nested in trees 100 per cent of the time, ferruginous hawks showed the most versatility with regard to nest placement. Trees, erosional remnants, creek banks, cliffs, the ground and man-made

Table 17. Supporting structures of raptor nests in the shortgrass prairie -- northeastern Colorado, 1970-1972.

	Tree	Erosional Remnant	Creek Bank	Cliff	Ground	Man-made Structure
Swainson's Hawk						
Per Cent Use	100.0% (150)	- - - - -	- - - - -	- - - - -	- - - - -	- - - - -
Fledglings/Nest	1.00 (130)	- - - - -	- - - - -	- - - - -	- - - - -	- - - - -
Ferruginous Hawk						
Per Cent Use	69.0% (49)	11.3% (8)	5.6% (4)	5.6% (4)	5.6% (4)	2.9% (2)
Fledglings/Nest	1.52 (44)	1.60 (5)	0.00 (1)	3.00 (2)	2.75 (4)	3.00 (1)
Golden Eagle						
Per Cent Use	25.5% (14)	5.4% (3)	16.3% (9)	52.8% (29)	- - - - -	- - - - -
Fledglings/Nest	0.79 (14)	0.67 (3)	0.00 (6)	1.18 (22)	- - - - -	- - - - -
Prairie Falcon						
Per Cent Use	- - - - -	- - - - -	- - - - -	100.0% (30)	- - - - -	- - - - -
Fledglings/Nest	- - - - -	- - - - -	- - - - -	3.41 (27)	- - - - -	- - - - -
Great Horned Owl						
Per Cent Use	85.3% (35)	- - - - -	4.9% (2)	9.8% (4)	- - - - -	- - - - -
Fledglings/Nest	1.35 (31)	- - - - -	3.00 (2)	2.00 (2)	- - - - -	- - - - -

structures were all used by the latter species. Nevertheless, the majority of the ferruginous hawks, 69.0 per cent, nested in trees. This is a departure from the findings of Weston (1969) in Utah where only 11 of 27 nestings, 40.7 per cent, were in trees. Ground nesting was quite uncommon on the Pawnee National Grassland (5.6 per cent) compared with northcentral Utah (51.9 per cent).

Great horned owls nested in trees 85.3 per cent of the time and only occasionally nested on creek banks and cliffs.

Productivity of 130 Swainson's hawk nests (in trees) was 1.00 young per attempt. There was a tendency for ferruginous hawks nesting in trees to fledge fewer young (1.52 per attempt) than those not nesting in trees (2.15 per attempt as calculated by treating the last five columns of the ferruginous hawk productivity data in Table 17 as a single category).

Golden eagles, as might be expected, were more successful when nesting on cliffs. The fledging rate of 1.18 young per nesting attempt on cliffs (and 0.87 in all habitats combined) is considerably less than 1.52 as reported by Boeker and Ray (1971) for golden eagles nesting on the prairies east of the Rocky Mountains and along the eastern front range in New Mexico, Colorado and Wyoming. Thus, there was a large discrepancy between Boeker's and Ray's 5-year average for 213 nestings (1964-1968) in their three-state study area and the three-year average (1970-1972) for 45 nestings in a small part of the same study area as herein reported.

For the most part, this discrepancy results, I believe, from the difference between intensive and extensive study, particularly with regard to project planning and goals, and later, methods of analysis. Both approaches have considerable merit. Due to the time factor involved in the coverage of three states (even by air and subsequent followup on the ground), all of Boeker's and Ray's study area could not be covered early enough in the season to detect most of the early nest failures. As stated above, early nest failure was an important factor which decreased the overall productivity figures herein reported.

Of the 150 nest sites studied by Boeker and Ray, 93 per cent were on cliffs where productivity would be expected to be higher than average for the entire population. There was a bias in Boeker's and Ray's study against eagles nesting in trees (25.5 per cent of the prairie population), because of the difficulty of locating such nests from aircraft. During the study herein reported, the poor success of golden eagles nesting at sites away from cliffs lowered the average productivity considerably. Of particular note on the Pawnee National Grassland was the failure of all golden eagle nests on relatively low creek banks. This habitat was not intensively studied by Boeker and Ray and, thus, a bias against another 16.3 per cent of the prairie population must be taken into account.

The cause of most nest failures on creek banks was that the nests were built where previous runoff had created an irregularity in the bank. The next torrential rain, a common characteristic of early spring weather on the prairies, simply washed the nests off of the cliffs. The low production of golden eagles along creek bottoms was not limited to creek bank nests. Golden eagles nesting in trees along creeks fledged only 0.67 young per nesting attempt, about the same as for the entire population, but not approaching the 1.18 young per nesting attempt on cliffs.

The most striking differences between our productivity figures and those previously reported in the literature for the same general area are for prairie falcons. An average of 3.41 young were fledged from 8 nests in 1971 and 19 nests in 1972 (27 total). This was slightly more than triple what Enderson (1964) reported for 82 nestings in northeastern Colorado and Wyoming from 1960 through 1962, exactly ten years ago. The clutch size of prairie falcons in 1972 was 4.33 eggs per nest and hatchability was nearly 4.00 eggs per nest.

Human Habitation and the Nesting of Large Raptors

The influence of past and present activities of the inhabitants of northeastern Colorado on the current nesting habits of five species of raptors is shown in Table 18. All species considered collectively shows that 104 of 347 nestings (30.0 per cent) were at man-created nest sites. Both Swainson's and ferruginous hawks used man-created nesting situations about 40.0 per cent of the time. Swainson's hawks

Table 18. The influence of past and present land use practices on the nesting of birds of prey in the shortgrass prairie -- northeastern Colorado, 1970-1972. Percentages compare the number of nestings at man-created situations to the number at natural situations.

	Man-Created Nesting Situations	Natural Nesting Situations	Total No. of Nestings
Swainson's Hawk			
Per Cent Use	40.0% (60)	60.0% (90)	150
Fledglings/Nest	1.12 (51)	0.95 (79)	130
Ferruginous Hawk			
Per Cent Use	40.8% (29)	59.2% (42)	71
Fledglings/Nest	1.42 (24)	1.85 (33)	57
Golden Eagle			
Per Cent Use	9.0% (5)	91.0% (50)	55
Fledglings/Nest	1.00 (5)	0.85 (50)	55
Prairie Falcon			
Per Cent Use	- - - - -	100.0% (30)	30
Fledglings/Nest	- - - - -	3.41 (27)	27
Great Horned Owl			
Per Cent Use	24.0% (10)	75.6% (31)	41
Fledglings/Nest	1.20 (10)	1.60 (25)	35

fledged more young per nesting attempt in man-created situations than in natural situations. Ferruginous hawks, on the other-hand, fledged more young per nesting attempt where no evidence of past human habitation was found. Golden eagles nested in man-created situations only 9 per cent of the time and fledged 1.00 young per nesting attempt from such sites, more than average for the entire population. Man has had no hand in creating nest sites for prairie falcons. Over 24 per cent of the great horned owls nested in man-created nest sites over the three-year period. The owls fledged more young from natural nest sites.

Several types of man-created nest sites were used by the birds of prey (Table 19). For all species combined, most (66 per cent) of the non-natural nest sites were at abandoned farmsteads. However, about 38 per cent of the Swainson's hawks, 31 per cent of the ferruginous hawks and 33 per cent of the great horned owls which utilized non-natural nest sites used trees growing where man had attempted to manipulate the natural water supply, i.e. where ditch systems or artificial water impoundments had been constructed.

The influence of the past activities of man on the nesting of the two buteos in unbroken grasslands is particularly noteworthy. The fact that Swainson's hawks fledged more young per nest from the 45 nests in unbroken grasslands than from nests in the other habitats has already been mentioned. Analysis of those 45 nest sites showed that 44 of them, or 98 per cent, were at abandoned farmsteads, abandoned

Table 19. An analysis of the types of man-created situations used by nesting birds of prey in the shortgrass prairie -- northeastern Colorado, 1970-72.

	Abandoned Farmsteads	Abandoned Ditches	Man-made Ponds	Total no. of Nests
Swainson's Hawk				
Per Cent Use	61.7% (37)	21.6% (13)	16.7% (10)	60
Fledglings/Nest	1.14 (29)	1.08 (13)	1.11 (9)	51
Ferruginous Hawk				
Per Cent Use	69.0% (20)	17.2% (5)	13.8% (4)	29
Fledglings/Nest	1.25 (16)	2.20 (5)	1.00 (3)	24
Golden Eagle				
Per Cent Use	100.0% (5)	- - - - -	- - - - - -	5
Fledglings/Nest	1.00 (5)	- - - - -	- - - - - -	5
Great Horned Owl				
Per Cent Use	66.7% (6)	22.2% (2)	11.1% (1)	9*
Fledglings/Nest	1.33 (6)	1.00 (2)	0.00 (1)	9*

* Nest near schoolhouse not included in these data.

ditches or man-made ponds. The only exception was a situation where the historical activities of man were suspected, but not actually found.

Likewise for ferruginous hawks, but to a lesser degree. Twenty-eight of 41, or 68.3 per cent, of the ferruginous hawk nests in unbroken grasslands were in man-created situations. The reason the percentage does not approach 100 in this case is the diversity of the nesting habits of ferruginous hawks.

All 3 of the great horned owl nests in unbroken grasslands were at abandoned farmsteads.

Comparison of Past and Present Populations.

The question which is usually raised at this point concerns whether or not there are more of these raptorial birds in northeastern Colorado now than there were, say, 150 years ago. This is a difficult question, of course, since no quantitative studies of nesting raptors have ever been conducted in the area with the exception of Enderson's (1964) work with prairie falcons and the research herein reported. If historical occupancy of eyrie sites is used as a criterion for population stability, comparisons of Enderson's and our data show that the number of adult prairie falcons has apparently not changed during the past decade. Productivity was substantially higher in the early 1970's than in the early 1960's, but the same number of adults occupied essentially the same eyries. Furthermore, since nesting habitat for prairie falcons has precise limits (Table 16), and since man has not inadvertently improved the available nesting habitat (Table 18), it is likely that about the same number of prairie falcons have occupied the area for many decades.

It can also be said with reasonable certainty that Swainson's hawks were more abundant in the early 1970's than during the late 1800's and early 1900's. Swainson's hawks nested only in trees (Table17). Until man planted trees such as the boxelder (*Acer negundo*), Chinese elm (*Ulmus parvifolia*), Russian olive (*Elaeagnus angustifolia*), honeylocust (*Gleditsia triacanthos*), cottonwoods (*Populus* sp.?), and willows (*Salix* sp.?) away from creek bottoms, Swainson's hawks could not nest in otherwise unbroken grasslands. In addition, Swainson's hawks will nest in or near cultivated land (Table 16). The extremely detrimental effect of cultivation on the nesting of raptors is not as serious for Swainson's hawks.

It is also relevant that the nest sites in creek bottoms and near natural springs where Swainson's hawks must have nested historically are still available. In general, man cannot live immediately adjacent to the creeks because of periodic flooding. Furthermore, the activities of men were rather slight in the gallery forests along creeks in the spring due to strict posting of the area, closed hunting seasons, and intense patrolling of newborn calves by ranchers. This eliminated much casual disturbance of nesting raptors by irresponsible people, and the local farmers and ranchers rarely interfered recognizing the value of predatory birds to their interests.

It was pointed out in the presentation of Table 16 that Swainson's hawks fledged more young (30 per cent more) in unbroken grasslands and cultivated land than in creek bottoms. Likewise, Swainson's hawks fledged 18 per cent more young in man-created nesting situations than in natural nesting situations (Table 18). If these unexpected trends persist, there may be further increases in the population nesting in unbroken grasslands through long-term selection for such an adaption. This can only occur to the extent that man-created nest sites are available, however. The potential for intentional management of Swainson's hawk populations is great should the need ever arise.

The evidence for an increase in the number of ferruginous hawks in northeastern Colorado since the coming of white man is not as clear cut. Ferruginous hawks do not depend solely on trees for nest sites (Table 17) and they rarely nested near extensive cultivation. Of the 71 nestings of this species, only 1 was in a cultivated situation (Table 16). Even though 68.3 per cent of the ferruginous hawks which nested in unbroken grassland nested in man-created situations, it is more difficult than with Swainson's hawks to weigh the relative importance of the negatives, such as cultivation and base line levels of human interference, against the positives of inadvertent improvement of nesting habitat. Ferruginous hawks were less successful when nesting in trees than when nesting in other situations. Similarly, these hawks were less successful at fledging young at abandoned farmsteads, ditches and man-made ponds than at natural nest sites.

Thus, with the ferruginous hawk, possibilities other than population increase exist. There may have been a decrease in the population since man arrived primarily due to destruction of habitat through cultivation. Inasmuch as 69.0 per cent of all ferruginous hawks in the area nested in trees, a common occurrence even at abandoned farmsteads in unbroken grasslands, there may have been a shift from ground and cliff nesting to tree nesting without a decrease or increase in numbers. Further considerations regarding the nesting success of ferruginous hawks in northeastern Colorado will be published elsewhere (Olendorff and Stoddart, in prep.)

Great Horned Owls nested in man-created situations 24.0 per cent of the time (Table 18), yet such nestings appear inconsequential with regard to allowing this species to utilize the shortgrass prairie more uniformly. First, great horned owls fledged fewer young at man-created nest sites than at natural nest sites. Second, if one analyzes a map of all known nest sites of great horned owls, the dependence upon gallery forests along creeks is obvious. Dispersal of nesting pairs away from creek bottoms is not common. Thus, although man has inadvertently created nesting situations for raptors in unbroken grasslands, the great horned owl has not adapted to them as readily as the buteos. It is unlikely that the number of great horned owls in northeastern Colorado is greater now than before white man came to the area.

Since golden eagles use man-created nest sites only 9.0 per cent of the time, man has probably had little positive effect on this species. Indiscriminate shooting of these very large and conspicuous raptors by the general public and destruction of nesting habitat by ranchers and farmers probably hold the number of nesting golden eagles in northeastern Colorado below the number present during the late 1800's. Likewise, electrocution of eagles by distribution lines of electric companies figures heavily as a mortality factor on the Pawnee National Grassland and adjacent areas (Olendorff, 1972a).

PREDATOR-PREY RELATIONSHIPS

Per Cent Composition of Diets

The following analysis of food habits (Table 20) was based on numbers of individual prey items collected at nests by forced regurgitation of food from the crops of young birds, and simply by identification of prey items laying in and under the nests. Data from 1970-72 were analyzed. The following numbers of prey items were included in the calculations: ferruginous hawk--131, Swainson's hawk--105, great horned owl--90, and golden eagle--119 for a total of 445. Fifty of the prey items for great horned owls were taken from Ryder (1972). The data in Table 20 represent the percentage composition of the diets of nestling birds, although the assumption that adults eat what they feed their young is probably valid in general.

Marti (1970) analyzed the diet of great horned owls in northeastern Colorado in detail between 1967 and 1969 by identifying animal remains in waste pellets regurgitated by the owls. Since he did not analyze data from owls nesting in shortgrass prairie separately, and since all data used to construct Table 20 were collected in a similar manner (but not by pellet analysis), we chose not to use Marti's data. In general, however, Table 20 shows a greater use of lagomorphs and a lesser use of mice and voles by great horned owls than reported by Marti. These trends involve biases inherent in the techniques used; large prey are more

Table 20. Prey of four large raptors of the shortgrass prairie in northeastern Colorado. Figures are percentages of the total number of prey items for each species separately and then collectively (last column). Percentages are given to two decimal places because of the large number of categories, not to give significance to the fractional percentages.

Prey Species	Ferruginous Hawk	Swainson's Hawk	Great Horned Owl	Golden Eagle	All 4 Species
Mammals (Total)	(75.56)	(43.83)	(85.57)	(93.28)	(74.84)
Long-tailed Weasel	0.76	-----	-----	-----	0.22
Thirteen-lined Ground Squirrel	41.20	14.30	-----	4.20	16.64
Eastern Fox Squirrel	-----	-----	-----	0.84	0.23
Northern Pocket Gopher	7.64	6.67	31.12	0.84	10.34
Ord's Kangaroo Rat	-----	3.81	7.78	-----	2.47
Deer Mouse	-----	6.67	1.11	-----	1.80
Northern Grasshopper Mouse	-----	-----	2.22	-----	0.45
Voles (Microtus Sp.?)	-----	0.95	4.44	-----	1.12
Jackrabbit (Sp.?)	11.45	0.95	4.44	31.10	12.81
Cottontail (Sp.?)	12.98	8.58	34.46	56.30	27.86
Unidentified Rodents	1.53	1.90	-----	-----	0.90
Birds (Total)	(24.44)	(53.32)	(14.43)	(6.72)	(24.49)
Greed-winged Teal	-----	-----	2.22	0.84	0.67
Bufflehead	-----	-----	2.22	-----	0.45
American Kestrel	0.76	-----	-----	-----	0.23
Ring-necked Pheasant	-----	0.95	1.11	4.20	1.57
Killdeer	1.53	1.90	-----	-----	0.90
Mountail Plover	-----	0.95	-----	-----	0.23
Long-billed Curlew	0.76	-----	-----	-----	0.22
Mourning Dove	-----	-----	3.33	-----	0.67
Great Horned Owl	-----	-----	-----	0.84	0.22
Burrowing Owl	-----	0.95	-----	-----	0.22
Red-headed Woodpecker	-----	-----	1.11	-----	0.22
Horned Lark	8.40	9.51	1.11	-----	4.94
Black-billed Magpie	-----	-----	-----	0.84	0.23
Western Meadowlark	9.17	14.30	2.22	-----	6.52
Lark Bunting	1.53	22.86	1.11	-----	6.07
Unidentified Birds	2.29	1.90	-----	-----	1.12
Amphibians & Reptiles (Total)	(0.00)	(2.85)	(0.00)	(0.00)	(0.68)
Tiger Salamander	-----	0.95	-----	-----	0.23
Unidentified Snakes	-----	1.90	-----	-----	0.45

often found laying in nests than small prey, and remains of large prey do not always find their way into pellets. Nevertheless, in the present analysis, where species comparisons are made, the biases act similarly for all species.

Ferruginous Hawk. This species took more thirteen-lined ground squirrels than any other prey. In addition to the ground squirrel, the following species each accounted for more than 5 per cent of the total number of prey items: northern pocket gopher, jackrabbits (white-tailed and black-tailed combined), cottontails (primarily desert cottontails, *Sylvilagus audubonii*), horned larks and western meadowlarks.

During the breeding season, ferruginous hawks took about 3 times as many mammals as birds. Nearly all birds were taken as recent fledglings, including the long-billed curlew (*Numenius americanus*), a very uncommon breeding species. Birds are probably even less important to this hawk during other seasons, although hibernation of the thirteen-lined ground squirrel may necessitate heavier predation on birds during the winter.

In 1967 and 1968 in the Cedar Valley of Utah Weston (1969) found that ferruginous hawks killed 44 per cent Ord's kangaroo rats (*Dipodomys ordii*) and 30 per cent black-tailed jackrabbits. The only other prey species accounting for more than 5 per cent of the total number of prey items were the whitetail antelope squirrel (*Ammospermophilus leucurus*) and the deer mouse (*Peromyscus maniculatus*). Avian species accounted for only 4.4 per cent of the total. No Ord's kangaroo rats were found as prey in ferruginous hawk nests on the Pawnee. Jackrabbits were taken less frequently in northeastern Colorado than in Utah.

Swainson's Hawks. Birds were far more important as food to Swainson's hawks (over 53 per cent) than to the other raptors for which food habits data were available. The most common prey species was the lark bunting (22.86 per cent), although the western meadowlark and horned lark accounted for 14.30 and 9.51 per cent of the total prey, respectively. Birds were taken primarily as fledglings, but it was not uncommon to find adult avian prey in Swainson's hawk nests.

The thirteen-lined ground squirrel was the most important mammalian prey, although cottontails, deer mice, and northern pocket gophers were all taken more than 5 per cent of the time. Nearly all lagomorphs were subadults, often very young.

Swainson's hawks took a wider variety of prey (16 species in all) compared to the other diurnal raptors. Ferruginous hawks and golden eagles took 11 and 9 species, respectively. The Swainson's hawk was the only species noted to take amphibians and reptiles on the Pawnee, although Weston (1969) reported several reptiles in ferruginous hawk nests in Utah.

Great Horned Owl. These large owls preyed largely upon mammals, primarily because none of the avian prey species were nocturnal. Thus, important prey included cottontails and northern pocket gophers, with fewer numbers of Ord's kangaroo rats, jackrabbits and voles (Microtus ochrogaster and M. pennsylvanicus) being taken. All other prey species were found in great horned owl nests only incidentally. Note that the thirteen-lined ground squirrel, a diurnal mammal, was not found in great horned owl nests. Marti (1970) did not report a single occurrence of this ground squirrel among 2,288 prey items from great horned owl pellets. Simultaneous pellet analyses during the present study would probably have revealed higher percentages of deer mice, grasshopper mice and voles in the great horned owl diet. In spite of the heavy reliance on gophers and cottontails, note that the great horned owl diet was nearly as diverse (15 species) as that of the Swainson's hawk.

Golden Eagle. The largest of the raptors on the Pawnee also relied heavily on mammalian prey, over 87 per cent of which were cottontails and jackrabbits. In addition to rabbits, only thirteen-lined ground squirrels and ring-necked pheasants occurred more than 1 per cent of the time, showing nearly a 96 per cent reliance on 4 prey species. Golden eagles apparently had the least diverse diet of the large raptors for which data were available, although the likelihood of small prey items being missed was always present.

All Species Combined. With regard to numbers, cottontail rabbits were preyed upon most heavily, accounting for about 28 per cent of all prey. Thirteen-lined ground squirrels (16.64 per cent), jackrabbits (12.81 per cent) and northern pocket gophers (10.34 per cent) also accounted for more than 5 per cent of the collective large raptor diet. Important avian prey included the three most common species, namely western meadowlarks (6.52 per cent), lark buntings (6.07 per cent) and horned larks (4.94 per cent). Overall, about three-quarters of the impact of raptors on prey population numbers was on mammals (74.84 per cent). Note the similar mammalian to avian prey ratios for ferruginous hawks and for all species combined.

In general, larger raptors took more mammals and fewer birds as prey (Figure 10). This was the result of at least two complementary factors. First, the mammal population averaged a greater weight per individual than the bird populations, and large raptors selected larger prey. This was substantiated by the data in Table 20. Second, partly as a result of the first point, smaller avian prey species were more vulnerable to predation by small raptors. The latter are, as a rule, more agile than large raptors. This was also supported by the data in Table 20, at least circumstantially, in that the diversity of the diet of the diurnal raptors increased as the size of the raptor decreased.

The relationship shown in Figure 10 held only for the diurnal raptors, including burrowing owls (data from Marti, 1970). The nocturnal owls preyed more heavily on mammals, particularly the nocturnal mammals. It is quite probable that data collected for diurnal raptors in other ecosystems will not fit the trend line shown in Figure 10. Similar

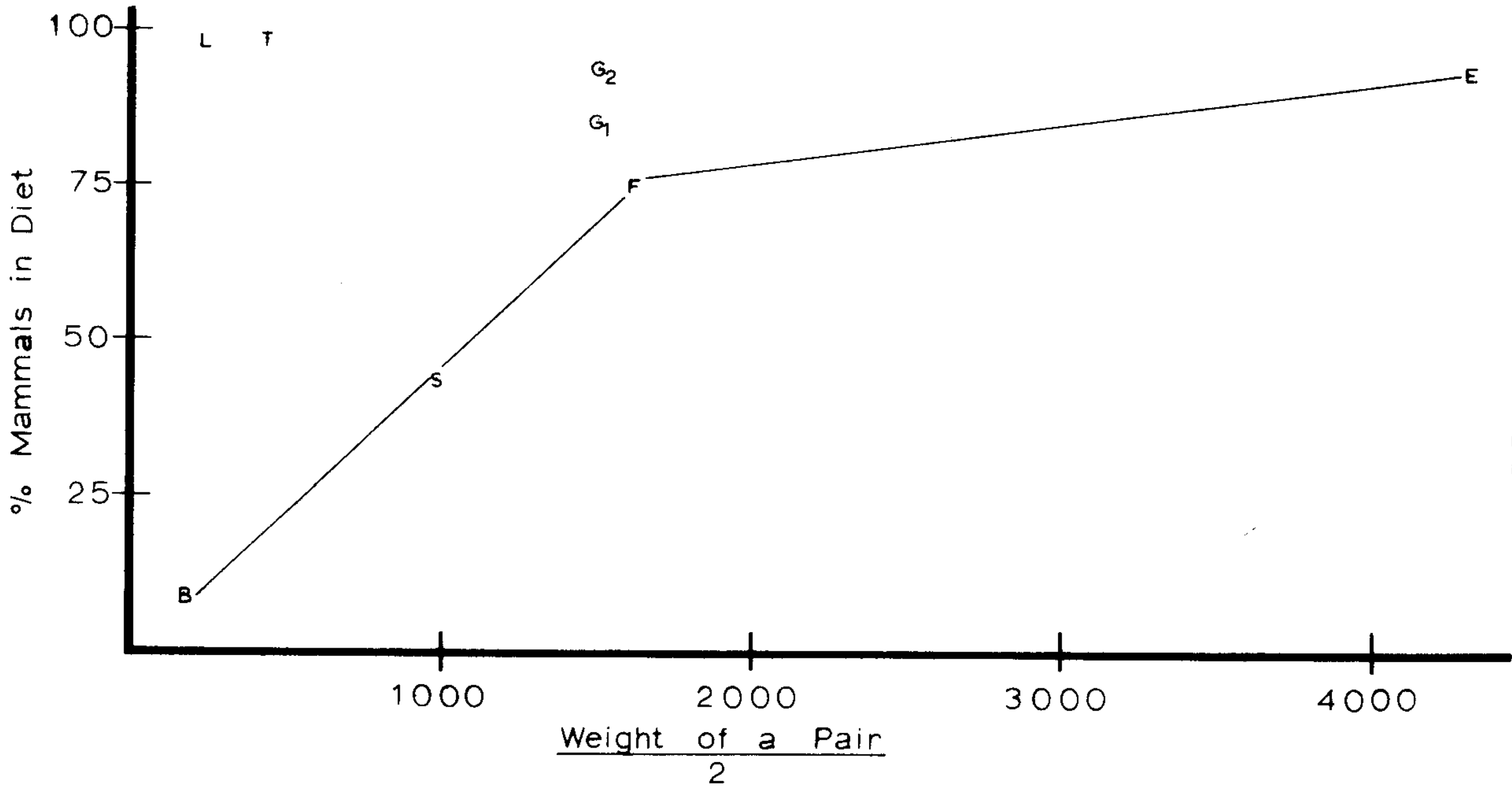

Figure 10. The relationship between body size of raptors and the percentages of mammals in their respective diets in northeastern Colorado. (B = burrowing owl; L = long-eared owl; T = barn owl; and G_2 = great horned owl from Marti, 1970). (S = Swainson's hawk; G_1 = great horned owl; F = ferruginous hawk; and E = golden eagle from Table 20).

plots should be made only with data collected on several sympatric species exposed to the same general prey base.

Comparison of Raptor Biomass with the Biomass of the Prey Base

Thorough analyses of predator-prey relationships on a biomass basis will be made in a subsequent IBP Technical Report. The present discussion will compare raptor biomass (adults only) with non-raptor avian biomass and rodent biomass on the 414-sq mile study area in 1971 and 1972 (Table 21). Biomasses are averages for all grazing treatments for the spring and summer months only.

Non-raptor avian biomass was between 62 (1972) and 95 (1971) times greater than large raptor biomass. Rodent biomass was over 200 times the raptor biomass during both years.

The data presented in Table 21 suggest that the prey base was not a limiting factor on raptor populations in either 1971 or 1972. In very general terms, large raptors remove food from the ecosystem equal to an average of about 8 per cent of their body weight per day during the spring and summer months (Craighead and Craighead, 1956). During the 152 days from 1 April through 30 August 1972, the 125 g/100 ha of adult raptors removed food equal to about 12 times their own biomass. Each young bird produced during the breeding season (57 g/100 ha) removed about 5.0 times the biomass of an adult in food through 45 days of age (Olendorff, 1971). Together, adults and young removed about

Table 21. Comparison of raptor biomass with biomasses of grouped components of the potential prey base. The inputs to the ratios are g/100 ha; the ratios are unitless.

Ratio	1971	1972
$\frac{\text{Non-raptor Avian Biomass}}{\text{Raptor Biomass}}$	$\frac{10143}{107} = 95$	$\frac{7697}{125} = 62$
$\frac{\text{Rodent Biomass}}{\text{Raptor Biomass}}$	$\frac{30000}{107} = 280$	$\frac{28300}{125} = 226$

2,145 g of food per 100 ha or about 6.0 per cent of the combined non-raptor avian and rodent biomasses (2145 ÷ (7697 x 28300) x 100 = 5.96 per cent). Similar calculations for 1971 showed that the large raptors on the 414-sq mile study area took only 3.8 per cent of the non-raptor avian and rodent prey (1526 ÷ (10143 + 30000) x 100 = 3.80 per cent).

It should be pointed out further, in support of the aforementioned suggestion, that cottontail rabbits, jackrabbits and northern pocket gophers were not included in the calculated prey base. These exclusions were necessary, since the population densities of the species listed were unknown for 1971 and 1972. The combined biomass of lagomorphs and gophers would contribute considerably to the prey base because of their large sizes. Using 1970 hare densities (Donoho, 1971) as an example, addition of black-tailed and white-tailed jackrabbits alone could nearly double the prey base. The indirect calculations for food consumption by the raptors are valid regardless of the size of the prey base. Thus, the addition of rabbits and gophers would decrease the per cents of exploitation of the prey base significantly.

FURTHER DISCUSSIONS

Importance of Interspecific Differences in The Nesting Phenologies

At least three species of large raptors (great horned owls, Swainson's hawks and ferruginous hawks) compete for nest sites in northeastern Colorado. The degree of overlap of nesting habitats was shown elsewhere in this report (Table 16). For example, the probability of Swainson's hawks nesting in a tree in a creek bottom was 0.66 (calculated from Tables 16 and 17). The probabilities of great horned owls and ferruginous hawks doing the same were 0.69 and 0.24, respectively. The probabilities of the three species (in the same order) nesting in trees in unbroken grasslands were 0.30, 0.06, and 0.41, respectively. The most overlap of nesting habitat in creek bottoms was between Swainson's hawks and owls, while in unbroken grasslands the significant overlap was between the two buteos.

Great horned owls began nesting about 37 days before ferruginous hawks and 64 days before Swainson's hawks (Fig. 4). In general, ferruginous hawks laid eggs as great horned owls hatched; Swainson's hawks laid eggs as great horned owls fledged. Of all nest sites available, great horned owls had first choice, ferruginous hawks had second choice and Swainson's hawks took those that remained. It is also relevant that great horned owls do not build their own nests. They used either sand-covered ledges on cliffs or creek banks, or nests built by other species such as buteos, eagles, magpies and crows.

Three nest sites existed near the IBP Pawnee Site and the Central Plains Experimental Range. The apparently preferred site was near a windmill with a small group of trees which obtained water from the overflow of the windmill. This site not only had larger trees than the other sites, but it was also isolated (by federal no-trespassing signs) from constant interference by man. The second site consisted of a few trees near a long abandoned farmstead, not far from a windmill and only 50 ft from a well-travelled dirt road. The third site, apparently the least desirable, was about 20 ft from a similar gravel road and consisted of fewer, smaller trees. The three sites were roughly in a north-south line about 1½ miles long, with the "preferred" site on the north end and the "least suitable" site on the south end.

In 1970 great horned owls did not nest at any of the sites. Ferruginous hawks nested at the preferred site, and Swainson's hawks used the middle site. The least desirable site was vacant. In 1971 great horned owls, the earliest nesters, occupied the preferred site. Ferruginous hawks nested at the middle site, while Swainson's hawks, the latest nesters, used the least desirable site. All were successful. In 1972 great horned owls nested at the middle site in the nest used two years earlier by Swainson's hawks. Presumably there was no adequate stick nest at the preferred site, since the young owls virtually destroyed that stick nest in 1971. A pair of ferruginous hawks were observed perched near the preferred site several times in 1972, but no attempt was made to repair the nest. An apparent non-nesting pair of ferruginous hawks was observed in the area throughout the summer of 1972. Swainson's hawks again used the least preferred site and, like the owls, successfully fledged young in 1972.

In another case of this type Swainson's hawks used a preferred site in 1970 when ferruginous hawks did not nest in the area. In 1971 ferruginous hawks nested at the preferred site, and the Swainson's hawks were forced to a tree near a road. Their newly constructed nest was blown out of the tree. The ferruginous hawks fledged three young. In 1972 ferruginous hawks were absent and Swainson's hawks again nested at the preferred site and fledged 3 young.

The suggestion is that there is an advantage to early nesting, at least with regard to nest site choice. It is interesting to note that the overall nest successes of the three species (1970-72) decreased in the temporal order in which they nested. Great horned owls successfully fledged at least one young 74.0 per cent of the time, while ferruginous hawks and Swainson's hawks did so 69.8 and 54.6 per cent of the time, respectively (Table 8). These may or may not be statistically significant differences, but the trend is evident. Factors such as the flimsiness of nests built by Swainson's hawks and the high frequency of destructive winds on the Pawnee add to the disadvantage of being forced to use the least desirable nest sites.

It is clear that late nesting species were at times "forced" to use less desirable nest sites than they would use normally. The best examples involved great horned owls and Swainson's hawks. Young owls often fledged as the adult hawks established territories. Occasionally Swainson's hawks had to evict owls from a small group of trees in order to nest. The constant harrassment by the hawks seemed to have a negligible effect on the owls, but in one such case in 1971 the nesting attempt of the Swainson's hawks failed in the egg stage. At the same nest in 1972 the young owls were shot about one week before fledging. The Swainson's hawks successfully raised young about 30 feet from the owl nest, even though the adult owls remained nearby and one dead owlet dangled over the edge of its nest. In another close nesting of these species the hawks laid only one egg (2.32 eggs was average), and the single young hawk was finally fledged quite late in the season.

Circumstantial evidence of the importance of interspecific competition was provided by the greater nest success of Swainson's hawks in 1972 following relatively poor nest success by ferruginous hawks and great horned owls. Nest success of ferruginous hawks on the 414-sq mile study area decreased from 70.0 per cent in 1971 to 50.0 per cent in 1972. Nest success of great horned owls decreased from 83.3 to 30.8 per cent. During the same years Swainson's hawk nest success increased from 33.3 per cent to 70.6 per cent. Many non-nesting pairs of owls were observed in 1972. Apparently, when the Swainson's hawks arrived, there was less conflict with the other species. In at least 7 instances in 1972, Swainson's hawks utilized unoccupied ferruginous hawk territories or great horned owl territories occupied by non-nesting pairs.

The Effects of Weather

Mean monthly temperatures from June 1970 through September 1972 are plotted in Figure 11. All available precipitation amounts are also shown. In general, 1972 was warmer and drier from February through May than during the same months in 1971. Mean monthly temperatures were higher in 1972 by the following numbers of degrees: February--4.1 C (7.4 F), March--5.7 C (10.3 F), April--1.3 C (2.3 F), and May--2.3 C (4.1 F). January and June temperatures were comparable in the two years. Major rainfall did not occur until 6 June 1972, while rainfall came earlier by several weeks in 1971. Rainfall was far below the CPER 30-year means for March, April and May in 1972. June is normally the wettest month at the Central Plains Experimental Range, but May runs a close second. Rainfall in June 1972 was about triple the 30-year mean.

Abiotic Variables and Year-to-year Intraspecific Differences in Nesting Phenologies. It was shown above that the raptorial species which wintered in temperate zones,

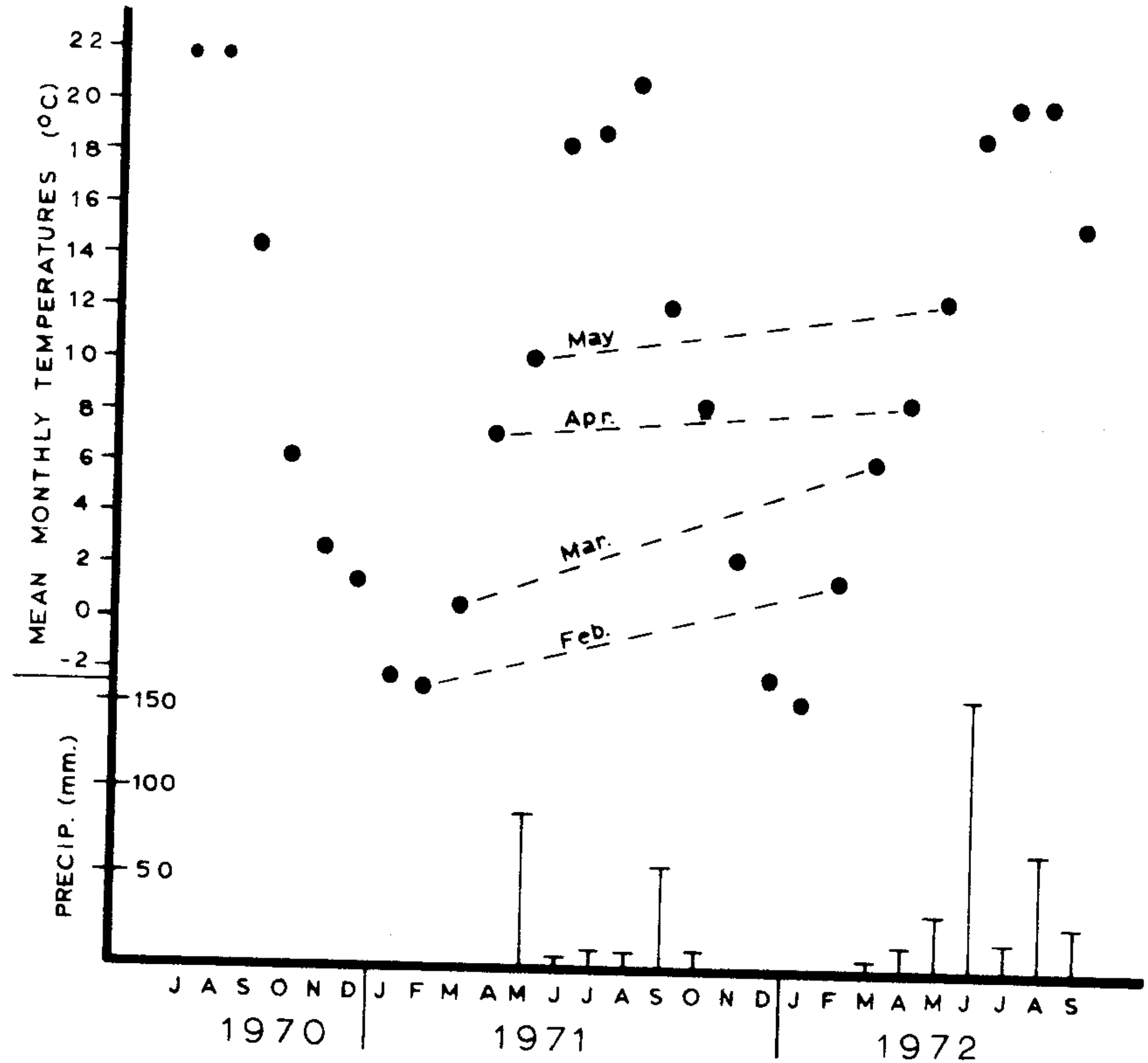

Figure 11. Mean monthly temperatures and available spring and summer precipitation amounts at the Central Plains Experimental Range, Nunn, Colorado, July 1970 - September 1972.

arrived in northeastern Colorado in February, March and early April and then nested, laid eggs one to two weeks earlier in 1972 than in 1971. In addition, most of these species showed greater asynchrony of nesting in 1972 than in 1971. The data illustrated these trends for some species better than others. Earlier nesting in 1972 was shown best for ferruginous hawks (Fig. 6), prairie falcons (Fig. 9) and great horned owls. Asynchrony of nesting was best illustrated by the same species (see General Considerations).

On the other hand, the Swainson's hawks which wintered in the arid regions of South America and arrived to nest in northeastern Colorado from mid-April to early May did not nest earlier or show greater asynchrony of nesting in 1972 relative to 1971.

I am not prepared to attribute these differences in nesting phenologies to any particular abiotic variable. The year-to-year differences in temperature and precipitation suggest cause-and-effect relationships, however. It is possible that higher population levels of thirteen-lined ground squirrels and Ord's kangaroo rats in April 1972 compared to March 1971 (Grant, pers. comm.), led to earlier nesting by several of the raptors. High mammal numbers probably would not lead to asynchrony of nesting. Furthermore, as shown above, it is unlikely that prey population levels limited raptor population levels or altered raptor behavior in 1971 or 1972.

The mammals which were in high numbers in April 1972 were mammals particularly adapted to xeric environments. Warm, dry weather early in 1972 may have lowered winter mortality of mammals in general and surely did hasten the end of hibernation by thirteen-lined ground squirrels. Nevertheless, the data suggest that mammals and raptors responded to abiotic variables, not to population levels and behaviors of each other.

Wind Destruction of Nests and Eggs. The heavy rains of May and June in northeastern Colorado are typically accompanied by gusty or continually strong winds. The fact that Swainson's hawks build relatively loose, precariously placed nests, often in the least desirable nest sites, has been alluded to previously. Such nests and their contents are very vulnerable to wind caused destruction.

In 1970, Swainson's hawks were hit very hard by 5 days of strong and gusty winds between 27 June and 1 July, a time when eggs were in the late stages of incubation or newly hatched. Nearly one-third (6 of 19) of the known nests were definitely destroyed by the wind during those 5 days. The nests were all tipped (not necessarily completely blown out) and 13 eggs and young were found below nests. In one case the whole nest tree, a living cottonwood in a healthy grove, was felled.

Accurate quantification of the extent of wind damage was not possible in 1971 or 1972, but in 1971 there were gusty or strong winds on 24 days in May, June and July.

The failure of 5 out of 37 Swainson's hawk nests (13.5 per cent) was definitely attributed to wind damage that year. In 1972, gusty or strong winds occurred on only 8 days during May, June and July, and only 3 out of 67 nests (4.5 per cent) definitely failed due to the wind. Many nests which failed for unknown causes, particularly those where only eggshells were found on the ground, probably were also destroyed by the wind.

Thus, in addition to the low potential for interspecific competition in 1972, the pausity of damaging winds also apparently contributed to the higher fledging success (Table 5) and higher nest success (Table 8) of Swainson's hawks compared to 1970 and 1971.

The Beneficial Effects of Shading and/or Remoteness of Nest Placement

The ferruginous hawk was the most versatile species on the PNG with regard to nest placement (Table 17). Most nests were in trees, but even tree nest sites varied considerably, particularly with regard to the amount of shading afforded the nest. In IBP Technical Report 151 (Olendorff, 1972b) a lower productivity of ferruginous hawks in unshaded as opposed to shaded nests was noted. Another year's data and analysis of twice as many nestings have allowed more detailed definitions of the relationships involved and have significantly altered the preliminary suggestions.

The 43 nests for which adequate data were available (1970-72) were first divided into three categories: 1) nests in trees which afforded shade during the warmer portion of the day, 2) nests in dead or sparsely leafed trees which gave little or no shade to the nests, and 3) unshaded nests on flat ground, erosional remnants or creek banks (Table 22). If a nest was destroyed by wind or human interference, the fledging success of that nest was not included in the calculations. Such exclusions (3 in all) did not change the conclusions, but did allow better expression of the apparent relationships.

Clutch size in trees which afforded shade to the nests (3.50) was 21.5 per cent greater than in all unshaded situations combined (2.88), and 30.1 per cent greater than in unshaded tree nests (2.69) (Table 22). Similar relationships were evident for maximum brood size and fledging success. The probability of an egg hatching was also greater in shaded nests (0.908), but the probability of fledging if hatched was slightly greater in unshaded nests (0.967 as opposed to 0.922). All this resulted in a higher probability of fledging at egg laying in shaded (0.838) rather than unshaded (0.722) nests.

These findings suggest that direct sunlight in ferruginous hawk nests was detrimental to overall nesting success. It might be expected _a priori_ that the probability of hatching would be greater in shaded nests, since overheating is much more damaging to eggs than periodic cooling. It is also reasonable that sunlight might be an advantage to developing young birds, assuming ferruginous hawks are less prone to heat prostration than other species (e.g., golden eagles).

Table 22. The apparent effect of nest shading on the nesting performance of ferruginous hawks. Sample sizes are in parentheses.

Nesting Situation	Clutch Size	Maximum Brood Size	Fledging Success[2]	Prob. of Hatching		Prob. of Fledging if Hatched		Prob. of Fledging at Egg Laying
Shaded--Trees	3.50(14)[1]	3.18(17)	2.93(14)	0.908	x	0.922	=	0.838
Unshaded--Trees	2.69(13)[1]	2.00(14)	1.86(14)	0.744	x	0.930	=	0.692
Unshaded--Ground	3.08(12)	2.33(12)	2.33(12)	0.756	x	1.000	=	0.756
Unshaded--Combined	2.88(25)	2.15(26)	2.08(26)	0.747	x	0.967	=	0.722

1/ Some clutch sizes unknown.

2/ Nests where wind damage and human interference caused nest failure not included.

Nevertheless, the 21.5 per cent difference in clutch size, which had to be established each year long before the trees had leaves, was not expected. The above relationships may in fact exist, but the reasons given for the differences may be incorrect.

Sample sizes prevented a detailed analysis of the effects of man's current activities on the nesting performance of ferruginous hawks. (The next section involves such an analysis for Swainson's hawks.) Nevertheless, it was known that ferruginous hawks usually nested in more remote, less conspicuous places than Swainson's hawks. Of the 43 ferruginous hawk nestings used in the above analysis, 31 (72.1 per cent) were in remote or otherwise inconspicuous places. The easily accessible nest sites were apparently less desirable, presumably due to the disturbance of the general public. In addition, more unshaded nests (34.6 per cent) than shaded nests (17.6 per cent) were easily accessible.

An analysis of the effect of accessibility of nests on the nesting performance of ferruginous hawks showed that clutch size was about 14.5 per cent greater at remote nests (3.23) than at nests easily accessible to the general public (2.82) (Table 23). The probability of fledging at egg laying in remote nests (0.808) was 24.5 per cent greater than the same probability in easily accessible nests (0.649). Thus, the differences in clutch sizes, probabilities, and other nesting parameters in shaded and unshaded nests may be

Table 23. The apparent effect of nest accessibility on the nesting performance of ferruginous hawks. Sample sizes are in parentheses.

Nesting Situation	Clutch Size	Maximum Brood Size	Fledging Success	Prob. of Hatching		Prob. of Fledging if Hatched		Prob. of Fledging at Egg Laying
Remote	3.23(28)	2.74(31)	2.61(28)	0.848	x	0.954	=	0.808
Accessible	2.82(11)	2.09(12)	1.83(12)	0.741	x	0.876	=	0.649

attributable, instead, to the accessibility (i.e. the disturbance) of the nests. The high incidence of nest desertion by incubating ferruginous hawks and the general secrecy of their habits corroborate the detrimental effect of easy accessibility.

The beneficial effect of shading cannot be totally dismissed, however, since direct human interference is more likely to cause total rather than partial nest failure. Hatching is a period when high temperature or low humidity (exposure) may cause a high incidence of embryonic mortality. Much of the mortality of ferruginous hawk eggs on the PNG involved a failure in late incubation of only 1 or 2 eggs of a 3- or 4-egg clutch. In 1971 when much of the embryonic mortality was noted ferruginous hawks hatched during the first extended warm spell of the summer. Any detrimental effect of a lack of shading may have been maximized by the synchronous nesting of all ferruginous hawks in 1971.

The Effect of Man's Current Activities on the Nesting Performance of Swainson's Hawks

Analysis of the effects of current land use was limited to Swainson's hawks, the species for which sample sizes were largest. It was assumed that the same general findings would follow from analyses involving all tree nesting species. Apparently, Swainson's hawks nesting on the PNG in 1971 and 1972 had a slight advantage over those nesting on private land (Table 24, Part A). Nest success was 57.9 per cent on

Table 24. Details concerning nest and fledging successes of Swainson's hawks on the 1,000-sq mile study area in various situations related to man's current activities. 1971 and 1972 data combined.

Category	No. of Nests (% of Total)	Nest Success	Young Fledged Per Nest
A. Land Use Near Nests			
Private	85(81.7%)	49.5%	1.11
Pawnee Nat. Grassland	19(18.3%)	57.9%	1.16
B. Accessibility of Nests			
Posted or Remote	49(47.1%)	55.2%	1.24
Free Access	55(52.9%)	47.3%	1.00
C. Proximity of Nests to Roads			
Near Road	72(69.2%)	55.6%	1.26
Not Near Road	32(30.8%)	40.6%	0.78
D. Types of Roads Near Nests			
Improved	38(52.8%)	47.4%	1.11
Unimproved	34(47.2%)	68.8%	1.44
E. Accessibility of Nests Near Roads			
Posted	24(33.3%)	66.7%	1.62
Free Access	48(66.7%)	50.0%	1.08

the PNG, compared to 49.5 per cent on private land. The difference in fledging success was very small, however, and only 18.3 per cent of all Swainson's hawks on the 1,000-sq mile area actually nested on federal land.

A beneficial effect of limiting access to Swainson's hawk nests was evident (Table 24, Part B). In most cases access was limited by posting the land with "no trespassing" signs, but in a few cases remoteness provided an adequate buffer. Nest success and fledging success were 52.2 per cent and 1.24 young fledged per nest, respectively, in posted or remote areas, while on land with free access the same parameters were 47.3 per cent and 1.00 young fledged per nest. The number of nests at which access was free was nearly equal to the number with limited access. It is possible that over the years the free access policies of the U. S. Forest Service on the PNG will actually be detrimental to nesting, a fact which was not manifest in 1971 and 1972 (Table 24, Part A) due to the small number of nests actually on the PNG.

Northeastern Colorado is extensively parcelled into sq-mile plots by section line roads. In addition to improved gravel and paved roads, there are many miles of trails used by farmers and ranchers. Some of the latter are private and posted. Since nearly all abandoned farmsteads are near roads and trails, and since many creek bottoms are paralleled by trails, it was not surprising that nearly 70 per cent of all Swainson's hawk's nested near raods (Table 24, Part C). Both nest success and fledging success were considerably greater near roads, an unexpected result. Fledging success, for example, was about 62 per cent greater near roads than away from roads.

It made a difference, however, if the nearby roads were improved (38 nests) or unimproved (34 nests) (Table 24, Part D). Nest success and fledging success were lower near improved roads than near unimproved raods. It was also important, particularly near roads, whether or not the nest was on posted land or land with free access to the public (Table 24, Part E). Only one-third of the nests near roads were on posted land, but these nests produced exactly 50 per cent more young per nest (1.62) compared to nests on land with free access (1.08). This suggests that posting all land with raptor nest sites during the nesting season would be a fruitful management practice by private land owners and the administrators of the PNG.

(The proper citation of the following section of this report is as follows: Olendorff, Richard R., and John W. Stoddart, Jr. 1973. Suggested future research toward effective raptor management. In: The ecology of nesting birds of prey of northeastern Colorado. By Richard R. Olendorff. U.S. IBP Grassland Biome Tech. Rep. No. 211. Pages 163-211.)

SUGGESTED FUTURE RESEARCH TOWARD EFFECTIVE RAPTOR MANAGEMENT

The needs for further raptor research in northeastern Colorado and parts of several other midwestern states fall into several categories: 1) long-term studies of population dynamics, 2) long-term studies of predator-prey relationships (specifically rates of exploitation of prey populations), 3) field testing of both management and emergency conservation measures applicable to birds of prey, and 4) long-term management of existing populations of birds of prey. The following suggestions involving such research (which resulted from the studies herein reported) are the subject of a proposal submitted to the National Science Foundation (NSF Identification Number P3B0566-000) by the Department of Fishery and Wildlife Biology, Colorado State University (Richard R. Olendorff, Principal Investigator; Drs. Gustav A. Swanson and Ronald A. Ryder, Faculty Associates).

The parts of this proposal which have not been included in earlier sections of the present paper are included here in fulfillment of the desires of the Colorado Division of Wildlife for such suggestions. Furthermore, in that raptor management is a much discussed endeavor at the present time, this information is of interest to many biologists working with raptors, as well as with other species of animals which now or in the future may need management. In general, the proposal has been edited only to put it into a more readable form for presentation here. The contribution of John W. Stoddart, Jr., who helped develop several of the suggestions is gratefully acknowledged.

Summary of Suggested Research

This section represents the ideas of several biologists who are concerned about the global declines in populations of birds of prey. If present trends continue and widely applicable conservation and management techniques are not developed in the next decade for falcons, hawks, eagles and owls, many species throughout the world will be regionally extirpated and, perhaps, forced to extinction. No fewer than 20 species and subspecies of diurnal and nocturnal raptors of the world are now considered by the U.S. Bureau of Sport Fisheries and Wildlife to be in danger of extinction. The peregrine falcon, the osprey and the bald eagle have so decreased in numbers throughout most of their ranges that soon even emergency conservation measures may not spare them the perilous status of the California condor and the Florida Everglade kite. It is already late to begin assisting some threatened species of raptorial birds.

Of the nesting birds of prey of the shortgrass prairie and the foothills of the Rocky Mountains in northeastern Colorado some are endangered, some are substantially reduced in numbers, some are locally persecuted, and others are common and in no apparent danger. This wealth of dissimilar species and the problems they encounter provide a perhaps unique opportunity for basic and applied research to develop the necessary management and conservation techniques, as well as attendant knowledge of raptor population dynamics.

To achieve this goal we suggest the following research: 1) a five-year, year-round basic study of raptor and prey population dynamics on a 1000-sq mile control study area and on an equally large experimental study area, and 2) a multifaceted applied study of methods to increase populations of birds of prey on the experimental area. The latter should involve a) construction of artificial nest-sites and other techniques to allow more efficient utilization of the grassland ecosystem by birds of prey, b) general habitat and existing nest-site improvement, c) experiments to avert numerous types of nesting failures, and d) experimental efforts to increase annual productivity, for example by clutch size manipulations during egg-laying and by captive breeding followed by reintroduction of captive-bred young into the wild. Pilot reintroduction experiments of the kind suggested should precede any attempts to re-establish decimated raptor populations or to revitalize remaining, non-viable populations with new breeding stock (a much discussed program at present). In addition, a thoroughly researched set of guidelines should be developed for state, provincial, national, and international agencies and organizations to follow in their attempts to manage and conserve birds of prey as a valued natural resource.

The methods used during the suggested study should include the newest and most effective techniques applicable to basic field research in ornithology. Crude rather than ecological nesting densities should be determined. All population information should be computerized for rapid retrieval and analysis. Radio-telemetry should be used to determine the sizes of home ranges and winter territories of a number of species. Sampling procedures developed by the IBP Grassland Biome Project should be followed in studies of predator-prey relationships. Pesticide analyses should be conducted in a fully equipped laboratory. Time-lapse cameras are available, as is excellent veterinary and avian science consultation, in support of captive breeding efforts involving several different species.

Support for the proposed study, both direct and indirect, would result in considerable interagency cooperation and a mutual understanding of this current ecological problem by biologists, conservationists, wildlife management officials, and the general public. Further cooperation from the private land owners in the study areas assures very desirable liaison between the participants of the study and those agriculturists who would directly benefit from the research.

Objectives of Suggested Research

1) To study raptor and prey population dynamics for five years (or more) on two grassland study areas in northeastern Colorado;
    a) To compare population levels and interactions of avian predators and their prey on a 1000-sq mile control

study area where only population studies would be conducted, with corresponding population dynamics and predator-prey relationships on an experimental 1000-sq mile study area where attempts would be made to increase raptor populations;

b) To determine long-term trends in the crude nesting densities, annual productivity, and migration and wintering population levels of grassland birds of prey;

2) To develop widely applicable management techniques for raptorial birds directed, primarily, toward increasing existing raptor population levels:

a) To provide artificial nest sites and to improve natural nest sites for birds of prey to allow more complete utilization of habitat and prey resources;

b) To avert numerous types of nesting failures such as wind-caused nest destruction and human interference;

3) To develop emergency conservation measures for threatened or endangered species of raptors;

a) To research methods of increasing annual productivity of selected species in the wild by clutch-size manipulations during egg-laying;

b) To assist, on a local basis with local birds, the continent-wide attempt to develop methods of breeding birds of prey in captivity;

c) To provide a reintroduction locale and to reintroduce captive-bred young into the wild by foster parentage and other methods, through cooperation of researchers involved in the study herein suggested with personnel at other local and distant centers of captive propagation activity;

d) To determine if captive-bred raptors and raptors held in captivity for long periods of time can become part of a breeding population; and

4) To develop, in cooperation with other researchers of raptor management and conservation techniques, guidelines for state, national, provincial and international agencies and organizations to follow in reaching decisions concerning avian predators.

Population Dynamics

The theoretical aspects of animal population dynamics have been thoroughly debated since the importance of density-dependent factors was stressed by Nicholson (1933). Publications disputing the importance of density-dependent factors (Andrewartha and Birch, 1954; Andrewartha, 1961) and accepting, but modifying, Nicholson's theories (Lack, 1954; Wynne-Edwards, 1962) have added considerable impetus to what Lack (1966) calls "a three-cornered argument on population theory".

Preliminary population study of the birds of prey of the PNG (Olendorff, 1972b; Olendorff, this report) compared with IBP bird and mammal population studies (references cited elsewhere) lead to the speculation that availability of nest sites, a density-independent factor, may ultimately limit the size of nesting populations of all raptors present in northeastern Colorado during the summer months. Food, at first glance, is not considered to be limiting (Olendorff, this report).

Odum (1971, p. 195) makes the following statement: "In low-diversity, physically stressed ecosystems, or in those subject to irregular or unpredictable perterbations, populations tend to be regulated by physical components such as weather...." The shortgrass prairie is a "low-diversity, physically stressed ecosystem," which is stressed by extremes of temperature, precipitation and wind. Such factors may, in fact, produce situations where food is, at least, a proximate limiting factor.

Long-term research is needed to sort out the factors which limit raptor populations in the study areas and the relative importance of each factor. Such considerations will give direction to management efforts with birds of prey. Studies of raptor population dynamics and predator-prey relationships suggested below would show, for a large group of raptors, whether availability of nest sites and/or weather are limiting and whether density-dependent factors such as reproductive rate, nestling starvation, or intraspecific conflict are also important. The results of the suggested study would lend support to or dispute each of the three divergent theories of population dynamics. Furthermore, an analytical bonus would be provided by the study design, a design which allows comparisons of research conducted on an experimental area with appropriate, supportive research conducted on a "control" study area (see below).

Nesting Densities and Annual Productivities. The feasibility of determining crude nesting densities (pairs per unit total space) and ecological nesting densities (pairs per unit of suitable habitat space) of the large birds of prey in vast areas of shortgrass prairie is already known. Likewise for productivities of the same birds. Previous studies on the PNG included successful attempts to find, in 1971, virtually all of the large raptor nests on a 414-sq mile area (Olendorff, 1972b) and, in 1972, on a 1,000-sq mile area (Olendorff, this report).

Similar basic population studies should be conducted in several steps during the study herein suggested: 1) a mile by mile search for active nests should be made each year on a 1,000-sq mile area (minimum size) in the northwestern corner of Weld County, Colorado, where management and conservation techniques (see below) are to be field tested (see Fig. 12). This area includes the IBP Pawnee Site, the Central Plains Experimental Range, the entire western portion of the PNG, one large and several smaller creek bottoms, and a major line of cliffs. Such search would yield data on the number of pairs and biomasses of adults of each species per unit area at the beginning of the nesting season. 2) During the weeks after hatch, the nests should again be visited to band and color mark the young, to remove addled

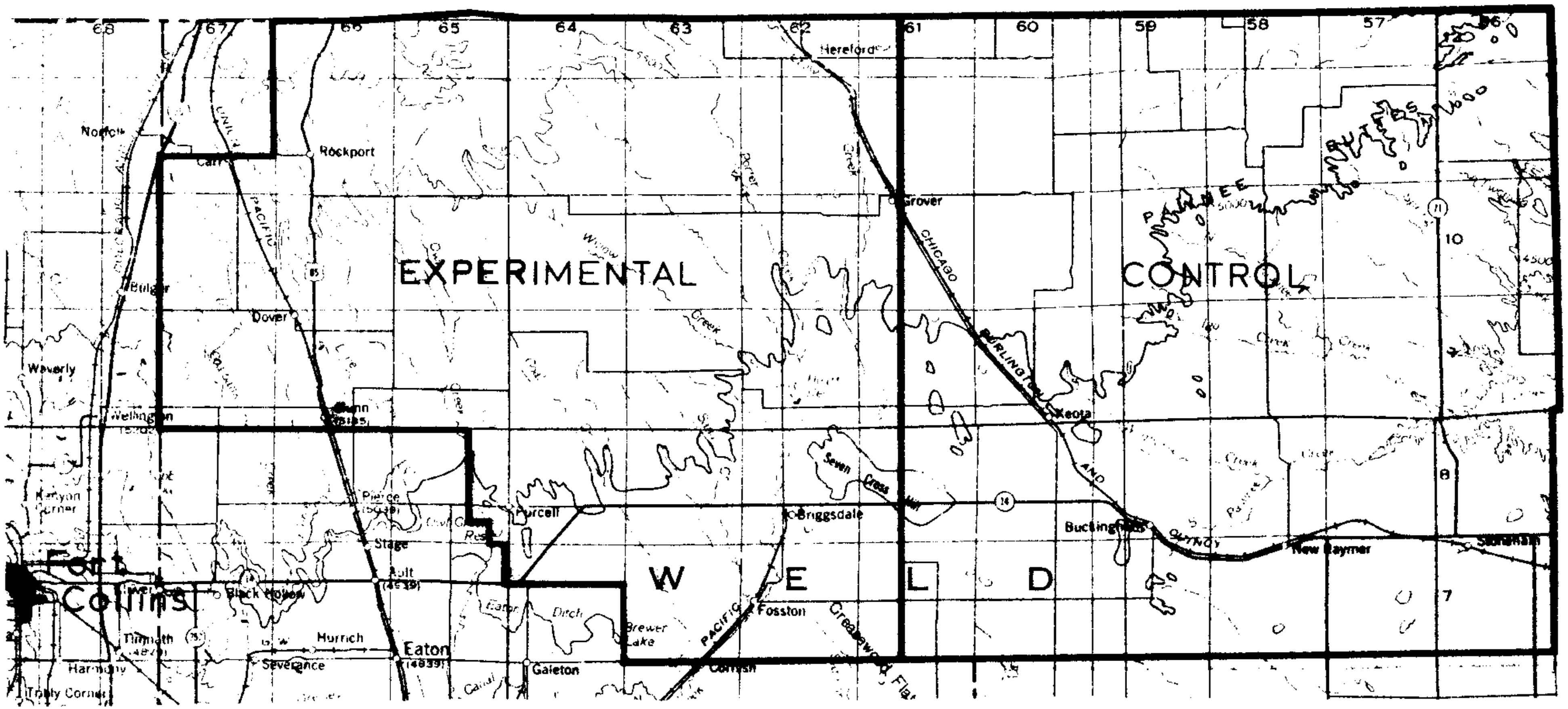

Figure 12. The experimental and control study areas showing their relationship to Fort Collins where the research will be coordinated. (1 in. equals 8 mi.)

eggs for pesticide analyses, to locate "runts" and diseased birds, and to detect predation, wind destruction and other causes of nest failure. 3) The nests should be visited a third time as the birds are fledging to determine nest productivity and to obtain fledging weights for calculations of productivity per pair and biomass production per unit area.

This basic population study should be conducted during every year of the project. It would be an unprecedented study except for the preliminary work of Olendorff (1972b and this report), since crude and ecological nesting densities of a group of raptorial birds would be determined simultaneously on a large area over a period of several years. The results of such study would allow meaningful calculations of predator-prey biomass relationships and would, as mentioned above, enhance the evaluation of the management studies (see below). In fact, the success of the management techniques to be field tested could not be evaluated without knowledge of crude and ecological nesting densities. Therein lies one of the most important conceptual bases of the study herein suggested. Data collected in 1971 and 1972 (Olendorff, 1972b, and this report) would serve as base line population levels.

As a "control", a similar population study should be conducted on a 1000-sq mile area (minimum size) in north-eastern Weld County, Colorado, contiguous with, but not overlapping, the area where the management techniques would be field tested (see Fig. 12). This area includes the eastern portion of the PNG, several medium-sized creek bottoms, and cliffs comparable to those on the experimental area. In fact, the major cliff-nesting species, golden eagles and prairie falcons, occur in nearly equal numbers on the suggested experimental and "control" areas. The "control" population study should also be conducted each year, although base line population levels would have to be established during the first year of the study. Study in the "control" area in 1971 and 1972 was not intensive, although about 80 nest sites were located.

All nesting population information should be computerized to facilitate analysis using the nest site as the point of reference. In 1970, 1971 and 1972 all nest sites were given seven-letter codes indicating species, township, range, section and quarter-section. The intention of doing so was that if a long-term management study was ever done in the area, the seven-letter codes could be converted directly into FØRTRAN variables for use in an information retrieval system and as a tool for analysis of population dynamics. One of the first tasks during the study herein suggested should be to computerize the occupancy records of all known nest sites, including information on clutch size, productivity and timing of the breeding cycle going as far back as 1960 for a number of nests. The CSU computer center could be utilized for this work, including the CDC 6400 and attendant computer facilities.

Population Censusing During the Non-breeding Season. Work on migrating and wintering raptors has lagged in northeastern Colorado due to inadequate funding. The birds of prey of the PNG have not been intensively studied from 1 October through 15 March, yet migrant and winter populations may have an indirect effect on nesting populations through the depletion of prey resources. It is virtually impossible to determine crude densities of migrating and wintering birds of prey on large enough land areas to adequately quantify population levels in all grassland habitats. If one censuses a small area it is not representative of the entire grassland. If one censuses a large area, say 144 sq miles, the census cannot be done quickly enough to avoid resightings, different activity patterns of the birds depending on the time of day, and sudden changes in wind conditions which are characteristic of weather on the shortgrass prairie.

The above mentioned problems reduce the effective censusing methods to the determination of relative ecological densities in different habitats during several consecutive years. Such an approach would allow comparisons between treatments and between years. Censuses should be made every 1 to 3 weeks depending on the season along at least three pre-determined routes from 15 August through 1 May during each year of the study. In addition to the relative densities, such censuses would yield follow-up information on the color-marked birds of the nesting populations which may also winter on the study area.

Raptor Mortality and Pesticides. It is not a simple matter to quantify mortality of wild birds. Mortality is a complex factor of population dynamics. Some of the mortality factors of the birds of prey of the PNG (as well as many other areas) have been determined. Quantification, however, is almost wholly lacking, especially on long-term basis. For example, some data on wind destruction of nests, avian predation on hawk eggs, external parasites, incubation failure, nestling starvation, human interference and electrocution are in hand, yet far more documentation is needed over a number of years in order to evaluate these factors. One must be able to consider the average effects of the mortality factors over a period of several years.

Mortality could be approached in at least three ways during the study herein suggested. First, mortality factors should continue to be defined through field observations. Second, each dead hawk, (embryos, nestlings, juveniles and adults) encountered during the study should be examined and a cause of death determined, if possible. Over the five-year period scores of mortalities would probably be encountered by the researchers. In this way, one could calculate the relative importance of the mortality factors, but not how the factors relate to the resident populations. Finally, band returns of several hundred marked birds would probably be available for analysis. Eventually rough life tables would be calculable for populations of most raptors of the shortgrass prairie, but this would not be feasible for two to three decades in most cases due to the life expectancy of the individuals in the marked populations.

One other need is to determine the effects of pesticides, particularly on those species eliciting the most concern of biologists and conservationists (e.g. prairie falcon, golden eagle, ferruginous hawk, burrowing owl), and species which migrate to countries which still use persistent pesticides extensively. (Swainson's hawks migrate to South America). It must be determined if pesticides are a limiting factor on raptor populations in the study area.

The approach to pesticides during the first two years of the suggested study would be minimal, primarily involving the collection of unhatched eggs for the analysis of eggshell thinning. If thinning was noted, the contents of all unhatched eggs would be analyzed for residue levels. If high organochlorine levels are present, further studies with statistical designs to eliminate biases should be proposed. If no eggshell thinning, embryonic mortality, or high residues are found in the raptors or in their avian prey during these pilot investigations, pesticide studies could be abandoned.

Determinations of Territory Sizes Using Radio Tracking. Radio-location telemetry has proven to be widely applicable to the study of birds of prey in the field (Dunstan, 1970; Dunstan, in press; Southern, 1964; Southern, 1965; Nicholls and Warner, 1972; Cochran, 1972; and many projects now in progress). Radio tracking could be used for three separate projects: 1) determination of territory sizes during the nesting season, 2) determination of sizes of winter hunting territories, and 3) post-fledging followup of reintroduced captive-bred young and young birds which were produced in the wild under natural conditions.

Since emphasis would be placed on determinations of territory sizes of grassland species, the specifications of the transmitters needed could be quite broad. Battery life of two weeks would be adequate. Use of a pulsed signal with a current drain of about 0.4 milliamps should prolong battery life far beyond two weeks. Designs for such transmitters, giving a range of 3 to 4 miles (more than adequate for the study area), are readily available (Mark Fuller, pers. comm.). Dependable transmitters are also available for purchase (AVM Instrument Company, Champagne, Illinois).

Several birds should be tagged during the nesting season each year of the study, including, at least, prairie falcons, golden eagles, ferruginous hawks and Swainson's hawks. Only a few days should be required to determine the home or winter range peripheries of each bird. The mobility provided by section line roads and other trails on the study areas should permit contact with the birds almost on demand.

Determinations of territory sizes for both nesting and wintering birds, when correlated with population information, should allow more accurate evaluation of the potential of the area for management. Considerations of actual and potential densities (both crude and ecological) should be possible. Radio tracking would also yield information concerning the post-fledging period of young birds. This is a little studied portion of the raptor life history, during which considerable mortality is suspected to occur.

Banding and Color Marking. Historical occupancy of nests and survival of specific adults at nests are important indicators of the longevity of birds. Such information is necessary if management is to be undertaken from the most knowledgeable position possible, particularly since detailed life tables are very difficult to construct for wild populations. To study the survival of young and adults, as many birds as possible should be color marked on the study area. This work must be coordinated with the banding program of the U. S. Bureau of Sport Fisheries and Wildlife. The color-marking scheme should be advertised in regional and national ornithological journals. Useful information should feed back from federal band returns, observations and recaptures on the study area, and from amateur and professional ornithologists throughout the ranges of the birds. Color marking should also yield data on the success of captive-bred birds reintroduced into the wild (see below).

The value of color marking is questionable, since color marks often fade or deteriorate in other ways resulting in loss of the tags. However, success with nesting populations has been obtained with colored "jesses" on marsh hawks (Hamerstrom, 1969, and pers. comm.), on several grassland species (Olendorff, unpubl.), and with patagial wing markers on golden eagles (Kochert, 1971) and ferruginous hawks (Powers and Howard, pers. comm.). A new technique developed in Europe (Picozzi, 1971) looks particularly promising for long-term nesting population studies. It is a type of patagial wing tag which has been successful with hen harriers (marsh hawks). A color-marking technique should be chosen before the first breeding season of the suggested study.

In any event, federal bands should also be placed on all captured birds, including nestlings. About 300 nestling raptors have already been banded in northeastern Colorado in recent years, and returns of Swainson's hawks from as far away as central Argentina have been received (Ryder, unpubl.). Knowledge gained about migration patterns, territory, dispersal and on turnover within the populations to be studied, as can be determined from banding and color-marking studies, is worth the extra time and effort to mark the birds.

Predator-Prey Relationships

The raptor management studies outlined in the next section are based on the assumption that the availability of nest sites, <u>not food</u>, is the principal limiting factor of raptor populations in northeastern Colorado. This assumption is made on the basis of preliminary analyses using raptor population data collected in 1971 (Olendorff, 1972b) and prey population information provided by several IBP investigators (e.g. Grant, 1972; Strong and Ryder, 1971; Van Horn, 1972). The assumption is supported by the dramatic adaptation of the two dominant buteos in the area to nesting in man-created situations following the exodus of farmers and homesteaders 40 to 50 years ago. In grassland which is unbroken except for isolated erosional remnants, abandoned farmsteads and abandoned ditches, 98 per cent of all Swainson's hawks and 68 per cent of the ferruginous hawks nest in man-created situations (Olendorff, this report). These artificial nest sites became the centers of occupied territories in spite of 40 years of varying prey population levels and weather conditions.

Simultaneous monitoring of both predator and prey populations has rarely been attempted in the past, although where this has been done, particularly on a long-term basis, significant results have been obtained (Hagen, 1969; Korschgen and Stuart, 1972). On a short-term basis, the research team at Rochester, Alberta, has been able to describe rates of exploitation of certain prey species by red-tailed hawks and great horned owls (literature cited elsewhere). Similar concurrent avian predator and prey population studies are an important part of the project herein suggested.

Furthermore, the study design, centered around experimental and "control" study areas, should yield data permitting at least partial resolution of the question of whether clutch size of raptors is adapted to brood size, as optimized by parental feeding ability. Lack (1966, p. 309) makes the statement that "the large prey on which large raptors depend are in general much sparser than the small prey on which small raptors depend, and that their respective clutch sizes have been adapted to the availability of food for their young." Amadon (1964) supports this view.

Censusing Prey Populations. Considerable background information on bird and mammal populations of the shortgrass prairie is available through IBP, although that information deals primarily with unbroken grassland. During the suggested study, prey population levels should be determined for the three remaining grassland habitats, namely cliff lines, creek bottoms and cultivated land. The techniques to be used should be similar to those used by IBP mammalogists and ornithologists (Swift and French, 1972) where practical. Small mammals, for example, are live trapped on a 12 x 12 grid of pairs of traps for five consecutive days at least three times per year. All mammals are marked and released. This is followed by five days of trapping, marking and re-leasing on assessment lines. IBP investigators determine densities of avian populations using the strip-census method of Emlen (1971).

The primary goal of the prey censusing studies would be to gain an adequate understanding of animal populations in all habitats on the shortgrass prairie which are foraged by birds of prey, and to use that population information during the evaluation of the raptor management techniques and emergency conservation measures described below. In this instance IBP studies and studies herein suggested would be very complementary, although not overlapping. As noted above, the predator and prey population data would be useful to population theorists.

Direct Predator-Prey Interactions. The prey caught by birds of prey should be analyzed and correlated with prey population levels to determine if the raptors use the different prey species in proportion to the abundance of the latter. Data should be collected during routine visits to nests by recording the prey items brought to the nests. Additional food consumption data could be obtained through observations of kills and birds eating carrion,and analyses of pellets of indigestible material regurgitated by the raptors.

The Potential for Management of Prey Species. We do not suggest management of prey species at this time except for a pilot prairie dog control experiment using perch poles erected in prairie dog towns (see below). It is important to note, however, that several IBP investigations have shown higher populations of some major prey species in areas of light or no grazing pressure by large herbivores (cattle and antelope). It is evident upon visiting fenced windmills, for example, on the PNG, that these discontinuities of habitat provide wildlife breeding areas. If food is found to be a limiting factor of raptor populations on the PNG, the potential exists for development of a scatter pattern of exclosures, as has been done for prairie chickens (Hamerstrom, Mattson, and Hamerstrom, 1957), to provide nesting and breeding habitat for small birds and mammals.

Management Techniques for Raptorial Birds

There are many reasons why raptor populations are not managed effectively in the United States. First, public sentiment shifted very slowly to the cause of raptor protection because of the lack, until recently, of international treaties which included birds of prey. General ecological awareness (also of recent development) has played no small part in the shift of public sentiment and the enactment of the necessary legislation. The concept of birds being barometers of environmental contamination has also given the general public recent impetus and reason to protect raptors.

The second reason raptor populations are not adequately managed today is the overwhelming emphasis, both historically and currently, on the management of game species. The research dollar has been spent, for the most part, on species which have recreational potential or negative effects on agriculture. This is changing, however, with the development of management programs in most states for non-game species.

Birds of prey are sure to receive a fair portion of the funding for these programs.

Finally, and perhaps most important, management of raptors is difficult, if not impossible, today, because most previous raptor research was not conducted with management aims in mind. The distinction which needs to be made is between raptor research aimed at managing populations of game animals (which has received some attention in the past) and raptor research directed toward or, at least, useful in managing raptor populations (which has been neglected in the past).

The studies listed above under the headings "Population Dynamics" and "Predator-prey Relationships" are essentially basic studies seeking an understanding of raptorial birds and their prey base in the shortgrass prairie in greater depth than has heretofore been possible. Intensive raptor studies conducted on the PNG in 1971 and 1972 and the on-going population studies herein suggested would provide a firm basis for experimentation with raptor management techniques.

In general, the management techniques suggested for development on the 1000-sq mile experimental area include 1) increasing raptor populations by providing artificial and natural nest sites to allow more complete and/or more uniform utilization of the various grassland habitats, and 2) averting nesting failures of many types by nest site improvement. Other techniques (which also may prove to be useful management measures in healthy populations) are considered in the next section on emergency conservation measures.

The only large scale raptor management program now being conducted in North America is being sponsored by the Canadian Wildlife Service. Under the direction of Richard Fyfe much pioneering research is being done. The types of study which are herein considered general management of populations (as opposed to the emergency conservation measures discussed in the next section), and which Fyfe and his co-workers have pioneered, include 1) switching young birds to the nests of the same and different species to test certain possibilities of foster parentage (see below), 2) blasting or digging artificial holes in cliffs for prairie falcons, and 3) erecting artificial nest platforms for ferruginous hawks (Fyfe, pers. comm.). The extent to which such research has been carried out in Canada will be mentioned below.

Several points should be made concerning the overlap in research strategies (or lack of same) between the study herein suggested and that of the Canadian Wildlife Service. First, there is need for international, cooperative research in this field, since the problems involved are international in scope. Migratory birds know no political boundaries. Second, such cooperative research would allow comparisons between two widely separated areas, one (Pawnee) a shortgrass prairie and the other a combination of short-, mixed- and tallgrass prairies. Third, the Canadian research team is not determining crude nesting densities of the entire group of large raptors in an area. Biases exist, with some exceptions regarding individual species and small areas, in favor of birds nesting along riverbeds and birds nesting in areas known to support high nesting populations. Furthermore, Fyfe and his co-workers are not, for the most part, doing intensive, simultaneous studies of prey populations as are herein suggested. The Canadian Wildlife Service is progressing on a broad pioneering front in the field of raptor management.

In short, the study herein suggested, in addition to developing certain raptor management techniques, should generate more theory regarding raptor population dynamics and predator-prey relationships than will Fyfe's studies. This is an advantage for future study in the United States, but it is neither a shortcoming nor a criticism of the Canadian studies. The difference is in approach. In Canada emphasis is being placed on the applied aspects of raptor management. Here basic research complements applied research in a manner which would not only develop management concepts, but would also yield data to support, refute and, perhaps, develop significant population theories.

Outside of the two studies discussed above, only ospreys and American kestrels have received noteworthy management efforts in North America. Osprey research by Paul Spitzer of Cornell University and several cooperating ornithologists throughout the eastern United States has begun to show promising success with clutch-size manipulations. The studies of Sergej Postupalsky in the north-central United States (Postupalsky, 1968, and pers. comm.) have demonstrated the effectiveness of artificial nest platforms for ospreys. A high percentage of the man-made nest structures erected in Michigan by Postupalsky and his co-workers are now used by ospreys. A management plan primarily involving habitat improvement for ospreys in the Deschutes National Forest in Oregon has also been developed (Roberts, 1970).

American kestrel population management has also been tried. Hamerstrom and Hart (in prep.) increased kestrel populations on the Buena Vista and Leola Marshes in central Wisconsin from 3 to 12 pairs between 1968 and 1971 by erecting artificial nest boxes. Heintzelman (1970) also discusses kestrel nest boxes.

One major hypothesis of the study herein suggested is that the availability of adequate nest sites is the major limiting factor of raptor populations in the area to be studied. We anticipate that raptor populations would, on the average, permanently increase after new nest sites were provided up to a point when intraspecific competition for adequate territories became limiting. This should occur despite fluctuating prey populations, adverse weather conditions, varying annual mortalities, and other factors not directly related to nest sites. The management techniques described below, correlated with population studies described above, should test this important point.

Since raptor management can only be approached at the species level (although some of the techniques would be applicable to more than one species), the suggested studies are listed below species by species.

Ferruginous Hawk. There is apparently far more otherwise suitable habitat on the PNG for ferruginous hawks to nest than is being used due to a shortage of adequate nest sites to attract the hawks. In general, nesting ferruginous hawks are found along creek bottoms, in relatively inaccessible areas, and in small tracts of the PNG with trees or rock outcroppings. It is uncommon for this species to nest near extensive cultivation, near well travelled roads, or in rolling hills of pure grassland where no trees occur. Indeed, the greater portion of the PNG and adjacent area is unbroken grassland, or near roads and cultivated lands.

Of all the ferruginous hawks nesting in northeastern Colorado, about 40 per cent nest in situations created by man, mainly those created by homesteaders and farmers who left the area in the 1920's and 1930's (Olendorff, this report). Over 68 per cent of the nests in essentially unbroken grasslands are in man-created situations. These nest sites are deteriorating as the trees planted at the abandoned homesteads reach maturity and die or simply die from the lack of water. Death of trees is hastened by cattle which seek the shade of the trees or use them as rubbing posts. In doing so they destroy the grass around the trees and the wind blows the earth away. This exposes the trees' roots and, coupled with abrasion of the bark, kills them. Many former ferruginous hawk nest trees have disappeared and at least one-third of those remaining will be felled by cows and/or wind within a decade.

The deterioration of nest trees has developed to the point that wind-caused nest destruction, even during the nesting season, is becoming a serious check on productivity. Two important points need to be made. First, the nesting of the hawks in man-created situations indicates a potential for management of the species. Secondly, all of the above listed nest-site problems can be lessened or eliminated in a number of ways: 1) by erecting artificial nest structures as has been done for ospreys in Michigan (Postupalsky, pers. comm.), 2) by fencing single trees and small groves of trees where the hawks nest, and 3) by planting new trees in small, fenced enclosures near semi-permanent water.

When one looks at a map of the ferruginous hawk nests on the PNG and adjacent areas, it is readily obvious that certain portions, often in blocks of over 100 sq miles, do not support nesting ferruginous hawks at all. If these voids are analyzed further, they can be attributed primarily to cultivation or, in unbroken grassland areas, to a lack of adequate nest sites. Cultivation destroys an area as far as the nesting of ferruginous hawks is concerned, yet the potential for nesting remains in unbroken grasslands. Apparently only a discontinuity of habitat suitable for raptors to nest need be provided.

During the first several months of the suggested study new nest sites should be developed for ferruginous hawks on the experimental area by placing artificial nest structures in typical nesting habitat for this species. An example of one structure to be tried is shown in Figure 13. Others might simply be platforms on the top of poles. Each nest structure should be fenced, where appropriate, and two or three trees should be planted inside the fences. As the trees mature many years later, the artificial structures could be removed leaving just the trees as a nest site. Since ferruginous hawks have nested on man made structures such as windmills, house chimneys and telephone poles in the past, the structures should be adopted quite readily. Pioneering work by Fyfe and his co-workers (Fyfe, pers. comm.) with 4 artificial nest structures for ferruginous hawks produced 100 per cent occupancy the summer after they were erected. It is not known whether this produced an increase in the number of nesting pairs or if the pairs nesting at the artificial sites were drawn from other nearby sites. The study herein suggested would yield important information about actual increases in the ferruginous hawk population of an area after erection of artificial nest structures, since both historical and on-going population studies will have established base population levels.

Ferruginous hawks also have problems with temperature-humidity relationships during incubation. These are critical factors, particularly at hatching. Hatchability in unshaded

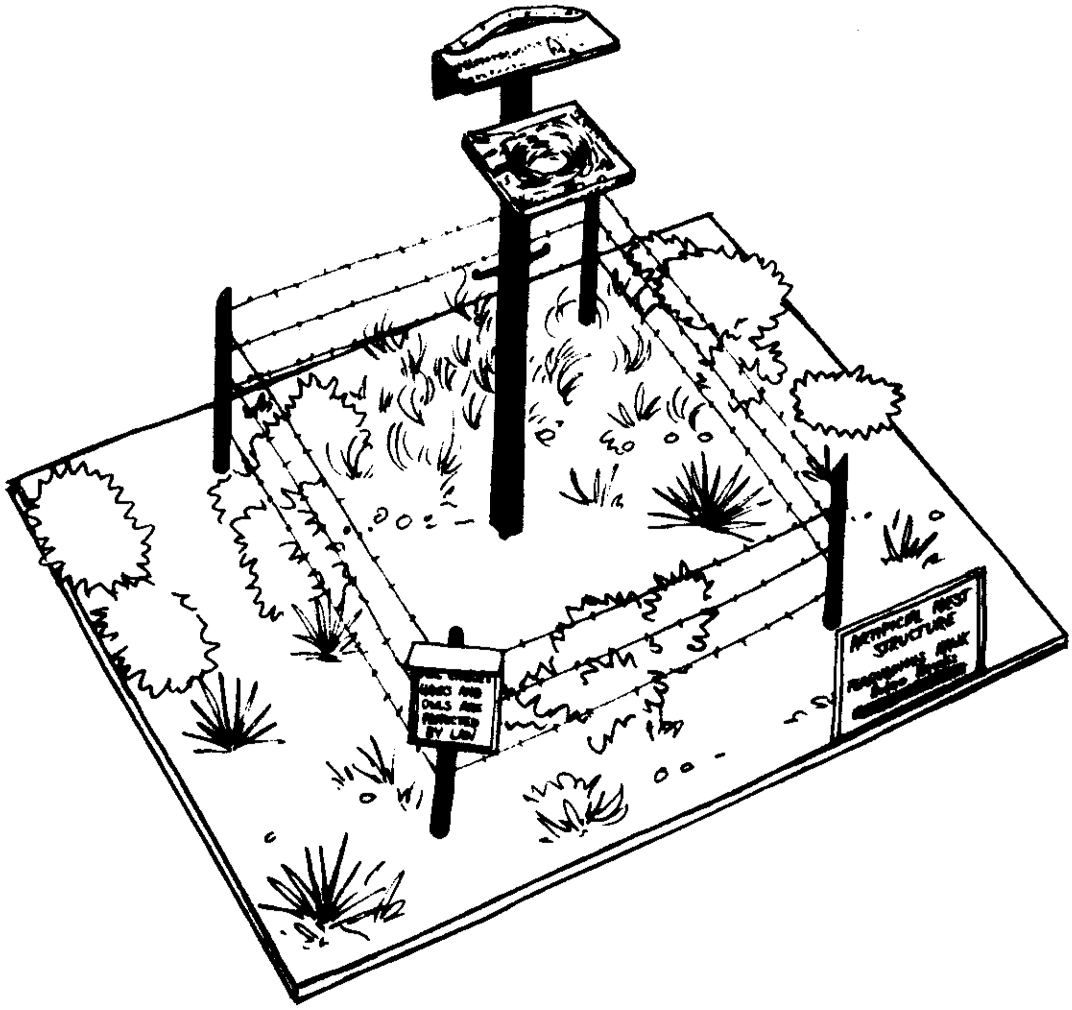

Figure 13. Proposed artificial nest structure for ferruginous hawks. Overall height will be about 16 feet. The fence is to prevent cattle from killing newly planted trees (not shown).

nests is about 10 per cent less than in shaded nests. It is believed (Olendorff, 1972b) that a lower humidity level in unshaded nesting situations is one factor in this diminution of hatchability. This could possible be improved by shading devices built over the artificial and natural nesting situations.

Another very serious idiosyncrasy of ferruginous hawks is an extremely high rate of nest abandonment during the early egg period if they are molested. Productivity would be increased by limiting or prohibiting human access, where possible, to the vicinity (within 300 yards) of the nests during the incubation period.

An intriguing experiment involving ferruginous hawks would be to test the hypothesis that locally uncommon or rare species could be increased in an area by switching the young of the rare species into nests of other more abundant, closely related species. The most attractive possibility of this kind is reintroducing peregrine falcons to the Rocky Mountains to revitalize their decimated population by placing captive-hatched peregrines in prairie falcon nests (see below). This is not as yet practical, but the principle could be tested with wild ferruginous and Swainson's hawks.

By placing two ferruginous hawk eggs or young in each of several Swainson's hawk nests for three or four years in succession, it is possible that the foster ferruginous hawks would return to the same area, perhaps the same nest, to breed. Fyfe (pers. comm.) has evidence that young peregrine falcons do, in fact, return to their birthplace, if only briefly. This procedure might be used to create new ferruginous hawk nesting territories, since ferruginous hawks nest several weeks before Swainson's hawks. There is, however, just enough temporal overlap in the nesting of the two species to allow the switching of young birds. Again, this approach assumes that the young will return near to their place of birth to breed, a point which could be proven or disproven by the extensive banding and color-marking campaigns involved in the population dynamics studies mentioned above.

It may be possible to increase productivity (immediately) and the population level (within a few years) of ferruginous hawks in the area significantly by using all of the above methods. This would be an important accomplishment with a species now considered rare and close to endangered by some authorities.

One specific instance where the ferruginous hawk could be used to man's benefit is as a natural control agent for black-tailed prairie dogs. When President Richard Nixon issued an executive order in February 1972 prohibiting the use of poisons on federal lands, he eliminated all effective methods of prairie dog control. Unless special exception is made, or the order is rescinded, prairie dog populations will probably increase considerably during the next several years on the PNG. It is possible, however, that artificial nest structures and hunting poles erected in prairie dog towns will attract ferruginous hawks and other raptors, thereby increasing the vulnerability of prairie dogs to predation and increasing the prey base of the raptors. Artificial perches should also be erected during the nest structure experiments discussed above.

Prairie Falcon. 1)Providing new nest sites. Prairie falcons always nest on cliffs. If holes or ledges of adequate size are not present on a cliff, the falcons will not nest or will go somewhere else to nest. Many cliffs lack adequate ledges. There are four major lines of cliffs in northeastern Colorado, three of which are inhabited by moderate to high populations of prairie falcons. The fourth, which is outside the experimental and "control" areas, supports a very low number of nesting prairie falcons due, apparently, to the absence of nest sites. As noted by John W. Stoddart, Jr., (pers. comm.), geological forces and erosion have produced overhangs but not adequate ledges or holes along nearly the entire length of these cliffs. Nevertheless, the terrain and habitat surrounding these low-yield cliffs are comparable to the other three cliff lines. All factors seem to indicate a potential for a high nesting density of falcons, yet they do not occur in expected numbers.

Providing nest sites on these cliffs and thereby increasing the population of prairie falcons over several years would be a significant management program. This has been shown feasible by Fyfe (unpubl.), and could be accomplished with a minimum of effort in an experiment involving the 8 to 10 miles of cliffs near the intensive study areas which do not have adequate nest sites for more than two or three pairs of prairie falcons. Certain stretches of the well occupied cliff lines also do not support nesting prairie falcons.

Preferably in late fall, ledges and holes should be created in the low-yield cliffs. Based on past experience with prairie falcons and study of the cliff faces, the best sites should be selected and developed. At some sites only a shovel and a small pick would be needed to dig a hole in chalky earth under a volcanic cap. Other sites may require more elaborate techniques, e.g. blasting with dynamite, but most cliff faces offer a number of possibilities. In extreme situations small barrels could be attached to the cliffs by driving steel supporting rods into the rock or chalky earth. Use of the barrels as nest holes by large falcons would be an important innovation.

The nest sites should be developed an average of one-half mile apart. Subsequent follow-up over a five-year period would be needed to evaluate the results. It is intended that this area become an important part of an experiment to determine if captive-bred prairie falcons and, perhaps, those flown in falconry for two years can become part of a breeding population (see below).

Extension of the nest site construction to the other major cliff lines and many small and/or isolated cliffs not supporting prairie falcons at the present time should also be attempted. Renovation of sites threatened and destroyed by erosion, and enlargement of ledges and holes of inadequate size for large broods could be accomplished by the same techniques. Making marginal nest sites into adequate nesting situations and concurrently building populations on major cliff lines in the manner outlined herein should also prove to be fruitful. Increases could be to levels 3 to 5 times current nesting densities of this falcon in certain areas.

2) Circumventing infertility and nesting mortality. From 17 prairie falcon nests for which adequate data are available for 1972, 3.18 young fledged per nest. If 7 infertile eggs had been viable and 7 young birds infested with blood-sucking mites had been reared, productivity would have been 4.00 young per nest, an increase of 26 per cent.

Infertility probably cannot be prevented directly, but fertile eggs taken during "recycling" and indeterminate laying experiments (explained below) could be used to replace infertile eggs. Blood-sucking mites seem to occur in great numbers only in nests which rarely or never receive direct sunlight. As a consequence the young birds become infested. Ledge alterations to widen the nest openings, or destruction of the proven unsatisfactory sites and reconstruction of adequate ledges nearby, should reduce or eliminate the mite problem. If not, treatment of sick birds in the nests with pyrethrum is feasible.

These simple experiments and preventive measures, while requiring only a minimum of funds and time, may produce immediate results. There is every reason to believe that the birds are capable of withstanding any disturbance connected with the management efforts. The significance of successful results far outweigh the risk of failure. If successful, the techniques could be used to assure a high level of productivity on a larger area in future years, or to justify taking excess eggs to hatch and rear artificially for various research projects involving captive birds. A direct benefit of this experiment would be to supply birds for the new eyrie sites discussed above. In fact, such productivity increases (and others mentioned in the next section) may be mandatory to supply those birds.

Golden Eagle. One of the more serious problems of golden eagles is the existence of terrain apparently satisfactory in every regard except the lack of nest sites. A number of pairs are observed each year building nests in which no eggs are laid or else the eggs are promptly destroyed by predators. In some cases nests are destroyed by continuing erosion after heavy spring rains. Some nests in holes on cliffs have become so filled with sticks brought by the eagles that they are no longer habitable. About one-third of the known golden eagle nest sites in Weld County, Colorado, could be considered inadequate for one reason or another. Correction of these inadequacies would help the golden eagle considerably. This could be accomplished in most cases by artificial nest structures and ledge alterations. Also, golden eagles may respond to artificial nest structures erected for ferruginous hawks and, as a result, increase their population in that way as well. This is predictable since golden eagles often nest on windmill towers. A pair nested on a 36-foot high gunnery tower in Rush Valley, Utah, in 1967 and 1968 (Camenzind, 1969).

Golden eagles are also prone to desertion during the early egg period. Limiting or prohibiting access to eagle nests during certain periods of the year is in order. Electrocution by high tension lines is also a problem of eagles on the PNG. Cooperation by the participants of the suggested study with local Rural Electrification Associations and the Colorado State Division of Wildlife would continue to develop effective means of decreasing this mortality factor. Poisoning and shooting of eagles (illegal means of predator control) are not serious problems on the suggested study area. There is little question that the PNG could support more eagles. The techniques developed would be even more valuable in areas where the species is rare.

Burrowing Owl. Biologists, farmers and ranchers believe that burrowing owl populations have decreased concurrently with control efforts in prairie dog towns. The commensal relationship involved is not absolute -- burrowing owls do use the holes of badgers, for example -- yet the owls are often seen in prairie dog towns. Existing prairie dog towns should be preserved on a size-limited basis and not destroyed completely. Restoration of old prairie dog towns and control of their size should also be attempted. Such control may include erecting hunting poles for birds of prey in the towns and poisoning of prairie dogs which establish burrows outside a fenced area set aside for the town. These techniques should be tried wherever possible during the course of the study herein suggested.

Sparrow Hawk (American Kestrel). Hundreds of square miles of the PNG and adjacent areas lack nesting sparrow hawks, apparently due to the absence of nest sites. Installation of nest boxes on poles, windmill towers, old houses, cliffs and in trees, should increase the sparrow hawk population tremendously. It is believed that a thorough nest-box campaign involving at least 100 nest-boxes (at first), and run by a local bird club, could increase sparrow hawk populations ten fold or more with only beneficial effects on the grasslands.

Swainson's Hawk. The failure rate of Swainson's hawk nests ranges between 47 and 59 per cent during most years. The most significant cause of nest failure is wind destruction of nests, eggs and young hawks. One could probably double the productivity of Swainson's hawks on the experimental area simply by placing 50 wire-basket nest structures in known nesting trees. Since Swainson's hawks nest primarily in trees -- a few nests on power poles and wildmill towers have been reported -- they are limited to creek bottoms or scattered trees. It is quite possible that artificial nest structures built for ferruginous hawks may also attract Swainson's hawks, yet the only direct management needed for this relatively abundant species is something to avert wind destruction of nests and monitoring for pesticides.

One additional experiment involving Swainson's hawks, primarily, would be to put about 40 artificial nest structures in cultivated fields where farmers have destroyed all trees. Some tracts of plowed land on the study area are over 100 sq miles in extent. The Swainson's hawk, which eats mostly insects and small rodents, feeds almost entirely on species that farmers consider pests. Furthermore, these hawks often nest near cultivated land, unlike all of the other large raptors of the PNG. Allowing the hawks to exploit the relatively untapped prey resources of winter wheat fields by providing nest sites for them would be beneficial to the hawks and may help the crops. Applied research of this type should be readily accepted and encouraged by the farmers.

Great Horned Owl. This owl needs little or no management, although it is dependent upon nests of magpies, crows and hawks for most of its nest sites. Great horned owls do not build their own nests. Some of the artificial nest structures would certainly be preempted by great horned owls, thereby giving them the opportunity to increase their numbers. One management program involving great horned owls would be to put permanent wire basket nests in known great horned owl territories to encourage year-to-year territory stablization. This may produce a greater tenacity for specific nest sites by the other large raptors, thereby reducing interspecific competition between great horned owls and hawks. This may be particularly beneficial to red-tailed hawks which are uncommon on the suggested study area.

Emergency Conservation Measures for Raptorial Birds

The management programs suggested above can be considered a type of conservation or "wise use" of a valued natural resource. There is need, however, for the development of emergency conservation techniques applicable to raptorial birds. Populations of some species and subspecies are already below the biological threshold where even well planned, purposeful research might bring about extinction. It is possible, however, to develop conservation techniques for endangered species using closely related species which are currently more abundant. Such techniques could then be applied to endangered species locally or, where necessary, in distant parts of the world.

Knowledge concerning several types of emergency raptor conservation techniques is now in high demand by state, provincial and national wildlife management agencies. Of particularly urgent need are methods of propagating birds of prey in captivity such as those being researched by the Cornell Laboratory of Ornithology, the Patuxent Wildlife Research Center, the Canadian Wildlife Service, and many private individuals.

Information received at the Raptor Research Foundation meetings in Sioux Falls, South Dakota, November, 1971, summarized the progress made in captive breeding of raptors. About 56 privately operated efforts, usually involving one or two pairs of falcons or hawks, have been started in the last decade, including two large projects sponsored by Cornell University (T. Cade) and the Canadian Wildlife Service (R. Fyfe). Both of the latter involve several species of birds of prey. Most of the projects have appeared since 1968 and have produced as of July, 1972, 20 prairie falcons, about 18 peregrine falcons, 4 African lanner falcons, well over 200 sparrow hawks, 4 ferruginous hawks, 5 red-tailed hawks, 3 goshawks, at least 7 Harris' hawks, and 4 golden eagles, thus demonstrating the feasibility of captive breeding. Very few attempts to reintroduce captive-bred birds of prey into the wild have been made, however.

Thus, methods of reintroduction need to be developed. Not even a location for reintroduction research has been chosen in the United States. Such a location is herein suggested as are several prospective methods of reintroduction. Few people now working with captive propagation have addressed themselves to this problem with sufficient accomplishment. Nor have they approached (due to a lack of opportunity) the problem of whether or not captive-bred birds or birds held in captivity for long periods of time will breed successfully in the wild.

There is a critical need for a project to culminate (when the time comes), through cooperative reintroduction programs, several captive propagation studies now in progress. We must know how to reintroduce captive-bred birds or, at least, how to artificially increase productivity of wild pairs, if we are to save certain raptors from extinction. Research with a high priority on reintroductions and other emergency conservation techniques is herein suggested.

The purpose of the suggested research is 1) to assist, on a local basis, the continent-wide research effort to perfect methods of propagating birds of prey in captivity, 2) to reintroduce captive-bred raptors into the wild through foster parentage and controlled release, 3) to evaluate "recycling", and removal of eggs to stimulate indeterminate laying (see below), as feasible methods of increasing productivity of wild populations, 4) to develop methods of artificially feeding wild pairs of birds in an effort to partially control their diet (and intake of toxic chemicals), and 5) to determine if captive-bred, reintroduced birds and birds held in captivity for long periods of time can become part of a wild breeding population. Details of the research techniques and strategies will be found below.

In general, with the exception of the small, <u>local</u> captive breeding project, we suggest specific research problems which would culminate or at least offer solutions for other captive propagation projects, large and small, by providing a reintroduction locale. Thus, no matter where prairie falcons, anatum peregrine falcons, golden eagles, American kestrels and a number of other species are bred, through cooperative agreements, they could be reintroduced into the wild in northern Colorado. Few, if any, of the captive propagation projects in the United States have come to grips with this phase of "saving raptors from extinction."

Some of the techniques to be researched during the study herein suggested have been pioneered or suggested by others, particularly Tom Cade, Research Director of the Cornell Laboratory of Ornithology, and Richard Fyfe, Wildlife Biologist with the Canadian Wildlife Service. Both Fyfe and Cade are involved with the development of techniques for captive propagation of birds of prey. Fyfe (pers. comm.) has also pioneered other emergency conservation techniques. For example, Fyfe and his co-workers have placed fertile prairie falcon eggs laid in captivity (but not young birds) under wild prairie falcons. Young from the eggs laid in captivity fledged from their foster home. The Canadian group has released captive-bred young prairie falcons into the wild by allowing the young birds freedom around the breeding loft near Fort Saskatchewan, Alberta. The parent prairie falcons fed the young through the wire of the enclosure during the controlled release. Many confiscated red-tailed and Swainson's hawks illegally taken as nestlings have also been returned to the wild. Fyfe and his co-workers have recycled (see below) at least 10 pairs of prairie falcons and one pair of anatum peregrine falcons in the wild with moderate success. They have experimented with indeterminate laying with captive, but not wild, falcons.

It is an understatement to say that much research remains to be done with regard to developing emergency conservation techniques for birds of prey.

Captive Propagation and Reintroduction. It is suggested that researchers bring together, mainly from stocks now in captivity, about 25 pairs of adult raptors, and place them in facilities adequate for captive propagation. Only species native to Colorado should be bred, and the captive-bred young should be reintroduced only in Colorado. Such local attempts go far toward eliminating variables such as photoperiod, temperature, humidity and other factors for which compensations must be made at locations distant from the points of origin of the parent birds.

Although some of the captive-bred birds should be retained as additional breeding stock, the main thrust of this part of the suggested research should be to produce young prairie falcons, peregrine falcons, and golden eagles in captivity for reintroduction experiments. We have included the peregrine falcon in these experiments because of the critical status of North American populations (Hickey, 1969). The *anatum* peregrines of the Rocky Mountains, although not completely extirpated, are apparently in the throes of a near total population collapse.

Nevertheless, an attempt to re-vitalize the remaining Rocky Mountain population with captive-bred birds may prove fruitful if carried out in the next five years or less. A regional effort to save this subspecies is very necessary and is in no way a duplication of any other captive breeding program because of its beginning-to-end, local approach. The PNG ends only 25 miles from Fort Collins, the foothills of the Rocky Mountains, and past nest sites of peregrine falcons. Prairie falcons now occupy many of the old peregrine nest sites. This close relative of the peregrine should serve well as a vehicle for reintroduction of new peregrine breeding stock into the Rocky Mountains through foster parentage.

Four different approaches to reintroduction could be taken. Some of these are long-standing ideas of a number of people, but none have been researched on a large scale. Pioneering efforts have already been mentioned. First, captive-bred young could be placed in nests of the same species when still a few days of age. Although reintroduction of captive-bred birds by foster parentage has never been tried to my knowledge, no problems are anticipated, since wild birds, particularly young ospreys, have been successfully switched from nest to nest in recent years (Spitzer, unpubl.). The same has been done with golden eagles and ferruginous hawks (Craig, Olendorff and Stoddart, unpubl.). The captive-bred birds should be followed by radio tracking to determine their fate during the immediate post-fledging period, a critical and unstudied portion of a raptor's life history.

Second, captive-bred young of one species could be placed in nests of different species. This has been done successfully with wild birds by Fyfe, who put prairie falcons into ferruginous hawk nests. Meyburg (1970) used Black Kites (Milvus migrans) to rear young Lesser Spotted Eagles (Aquila pomarina). Combinations include peregrine falcons placed in prairie falcon and red-tailed hawk nests in the Rocky Mountains, prairie falcons placed in ferruginous hawk nests, and golden eagles placed in ferruginous hawk nests on the PNG. Any attempt to re-establish the decimated peregrine falcon populations in the United States must be preceded by tests such as these. Again, the foster young should be followed by radio tracking after fledging.

Third, hand-reared, captive-bred young could be allowed to "fledge" from a small shelter in which they are fed during the late growth period. After the birds "fledge", the shelter would become a feeding station until the birds are independent. Their progress during this controlled release period should be followed by radio tracking. This method is a modification of a falconry technique called "hacking" during which young birds are allowed freedom to build muscles and develop hunting skills. During the study herein suggested, the young would remain free instead of being trapped back into captivity.

Finally, Cade (1971) suggested that falconry could be utilized as a method of carrying birds of prey through the critical subadult period during which the majority perish.

Through cooperation between the participants of the suggested study, the Cornell Laboratory of Ornithology, several state wildlife agencies, and a number of competent falconers, Dr. Cade's plan could be implemented using prairie, instead of peregrine, falcons. Success with prairie falcons would lend further justification to similar programs with peregrines. State wildlife authorities must be willing to issue permits to falconers for the removal of about 20 young prairie falcons from the wild during the nesting season. The falconers, by previous agreement, would be required to relinquish the birds to personnel from Cornell and participants of the suggested study for controlled release into the wild during subsequent springs. The release technique would be similar to that described in the preceding paragraph. The banded and color-marked birds would become part of a study to determine if such birds can become part of a breeding population (see below).

Experimentally Increasing Productivity of Wild Populations. That falcons will "recycle" and lay a second clutch of eggs when the first clutch is removed has been known since the days when egg collecting was an active hobby (Olendorff, 1971a). Only recently, however, has the potential for indeterminate laying been demonstrated in captive falcons (Porter and Wiemeyer, 1972; Enderson, unpubl.). The latter is a phenomenon whereby birds will continue to lay if the eggs are removed as they are laid, except for one which is left in the nest. Indeterminate laying is untested in wild falcons, yet it may be the most useful management tool of recent discovery, particularly if the indeterminate layer is a rare or endangered species. The research outlined below is designed to test "recycling" (a much used technique in current propagation projects) and indeterminate laying in wild prairie falcons and to increase productivity of a wild population. Similar experiments have been attempted in recent years with ospreys by Paul Spitzer (unpubl.) of the Cornell Laboratory of Ornithology, and a pilot project has been suggested for peregrine falcons (Lejeune, 1972). Richard Fyfe (unpubl.) has accomplished recycling in wild prairie and peregrine falcons.

Experiment I. As soon as five eggs are laid in certain eyries, all eggs should be removed and placed in several other eyries (up to 6 eggs per eyrie). If theory prevails, fourteen days later the recycled birds should begin a second clutch in the same eyrie or one nearby. If successful, the productivity of that pair would nearly be doubled depending on the size of the second clutch, and the productivity of the foster parents would be increased 20 to 50 per cent.

Experiment II. Eyries should be located in which no more than 2 eggs have been deposited. One egg should be removed from each eyrie and stored in an incubator as shauld each subsequent egg until a total of ten eggs are produced by each pair. Five eggs should then be replaced into the eyrie (for a total of 6). The remaining four eggs from each eyrie should be placed in other eyries. Again productivity of the pair would be doubled or nearly so and the productivity of the foster parents would be increased significantly.

Dietary Supplementation of Wild Pairs. This small experiment is designed to test the feasibility of feeding pairs of wild raptors a controlled diet or supplying an overabundance of food to pairs which have been given extra young to rear (up to 7 or 8 total). Diet control might be a useful technique for pesticide studies where limiting or augmenting the pesticide intake is necessary. Rearing more than the normal number of young might be used in management and conservation efforts, as well as in field documentation of the theoretical aspects of clutch size-brood size relationships with regard to parental feeding ability.

A small number of wild pairs of prairie falcons should be provided a very large excess of food by releasing game birds near their nests or by maintaining a pigeon loft within their hunting territory. Similar experiments should be conducted with ferruginous hawks and Swainson's hawks using laboratory mice.

Return of Captive Birds to Wild Breeding Populations. Rather than propose specific research strategies in this case, several possibilities, to be pursued as opportunities arise, are suggested below. All of the possibilities take advantage of the area (mentioned in the previous section) where a line of cliffs is not used extensively by prairie falcons because of the lack of adequate nest ledges and holes. The majority of reintroductions of prairie falcons would be conducted there, rather than in areas where reintroduced prairie falcons would be forced to compete with resident pairs. In this way, after creation of new nest sites in the low-yield cliffs, if there is any chance at all of reintroduced birds remaining in or returning to the place of reintroduction to breed, there would be ample places to nest and a low level of intraspecific competition to attract the birds. The bonus is that long-term followup of the reintroduced birds may be possible in order to determine if the birds enter the new breeding population.

Thus, when prairie falcons become available for reintroduction, several strategies should be used depending on the source of the birds. 1) With captive-bred young, controlled release could be carried out at 4 to 5 weeks of age or at 10, 22 or 34 months of age depending on the point to be made. Using the latter time schedule the birds would be released during the month of March when approximately 1, 2 or 3 years of age, and when reproductive urges might prevent or limit dispersive movements. 2) As suggested by Cade (1971), birds taken by falconers and released when 2 or 3 years old may have a better chance of reaching breeding age than birds fledged naturally. It is important, however, to know if these birds can, in fact, become part of a breeding population. This requires followup, the kind of followup which may be made possible by taking advantage of the area now relatively uninhabited by prairie falcons.

SUMMARY

Birds of prey, as barometers of environmental contamination, important components of balanced ecosystems, and aesthetically pleasing but historically persecuted animals, have received much recent attention following a twenty-year period of rapid accelleration in the rate of population declines of many European and North American species. Nevertheless, there remains a pausity of adequate information concerning long-term raptor population dynamics, energy utilization and function at the ecosystem level. A multifaceted and penetrating approach must be made if quantitative data concerning raptor populations, ecological impact, management and conservation are to be synthesized to fill the urgent need of wildlife managers and ecosystem analysts in their efforts to slow the deterioration of important agricultural and wildlife habitats.

The Pawnee National Grassland and adjacent, privately-owned land in northeastern Colorado provide nesting habitat and food for one of the densest populations of raptorial birds in North America. Nesting populations of many birds of prey are sufficiently high to allow most types of basic and applied raptor research. Virtually no ecosystem in North America other than grasslands allows study of a large enough land area to evaluate adequately the use of that ecosystem by birds of prey. In addition, the private land owners of northeastern Colorado are amenable to biological research.

The major nesting raptors of the area include ferruginous, Swainson's and red-tailed hawks, prairie falcons, American kestrels, golden eagles, great horned owls and burrowing owls. The earliest eggs of the five major species were laid on or near the following dates: great horned owl--28 February, golden eagle--11 March, ferruginous hawk--6 April, prairie falcon--12 April, and Swainson's hawk--3 May. With the exception of prairie falcons (which were extremely successful on the study area), nest successes of the species decreased in the temporal order in which they nested. The advantage of early nesting apparently involved the earliest nesters choosing the most suitable territories and nest sites. The data further suggest that nest building was more important to the earlier-nesting, resident ferruginous hawk, than to the later-arriving, later-nesting, migratory Swainson's hawk. Courtship flights of the latter species (for which the time to nest was limited by the migratory life history) were spectacular and more often observed, but Swainson's hawks typically built very unsubstantial nests. Ferruginous hawks, on the other hand, spent considerable time and energy choosing nest sites and building large, sturdy nests, but were never observed in courtship flight.

Fledging dates for the five major species were as follows: great horned owl--8 May to 18 June, golden eagle--30 June to 22 July, ferruginous hawk--26 June to 28 July, prairie falcon--13 June to 10 July, and Swainson's hawk--13 July to 21 August.

Overall productivity parameters from 1970-72 were calculated (Table 5). With the exception of ferruginous hawks, the probability of hatching (comparing between species) decreased in the same order as clutch size, brood size and fledging success (Table 7). In other words, the more eggs laid by a species, the higher the probability of hatching. Swainson's hawks experienced the lowest (0.513) and prairie falcons the highest (0.774) probability of a freshly laid egg culminating in a fledged young. With the exception of prairie falcons, the overall probability of fledging at egg laying was lower the later in the season egg laying commenced. Prairie falcons had the highest nest success (fledged at least one young per attempt) of the large birds of prey on the PNG between 1970 and 1972 (88.8 per cent) (Table 8). If nest success of ferruginous hawks and great horned owls was less than 70 per cent, Swainson's hawk nest success was greater than 50 per cent. The converse was also true.

On a 414-sq mile unbroken grassland study area in 1971, 42 pairs of large birds of prey used 42.5 per cent of the potential nest sites. In 1972, 50.5 pairs used 51.8 per cent of the nest sites. Swainson's hawk breeding density and productivity were higher in 1972 than in 1971 (Tables 10 and 11). I believe this was in response to at least three factors: 1) There was a lower breeding density of ferruginous hawks in 1972 than in 1971, and their nest success and productivity of young were also lower in 1972; 2) Although there were about the same number of adult great horned owls present in each of the two years, nest success and productivity of young were very low in 1972; 3) There were fewer days on which potentially nest-destructive winds blew in 1972. Swainson's hawks apparently filled a void where interspecific competition for nest sites was at a low level and were further aided by good weather conditions.

The biomass figures, both for adults and young on the 414-sq mile study area, were dominated by Swainson's hawks both in 1971 and 1972 (Table 12). For all large raptors combined, biomass was about 20 per cent greater in 1972 than in 1971. Biomass averaged 166.9 g/km^2 for the two years, including an average of 116.0 g/km^2 for adults and a biomass production of young of 50.9 g/km^2. The biomass of the young produced was less than half (43.9 per cent) of the biomass of the adults present.

In 1972 on a 1,000-sq mile study area representing all locally available nesting habitats, the large raptors were represented by the following percentages of the total number of adults present: Swainson's hawks--42.8, ferruginous hawks--16.4, great horned owls--19.3, golden eagles--7.6, prairie falcons--8.8 and red-tailed hawk--5.1. All species combined, there were 15.85 pairs of large raptors for every 100 sq miles, or 1 pair for every 6.3 sq miles. Only about half (53.3 per cent) of all adult pairs produced at least one young (Table 13). All species collectively produced 201 young in 1972 on the 1,000-sq mile area or 20.1 per 100 sq miles (Table 14). This was 36.5 per cent greater than on the 414-sq mile area during the same breeding season; most of the difference was attributable to the high production of prairie falcons on the 1,000-sq mile area.

For all species and age classes combined, the biomass of large raptors on the 1,000-sq mile area was 252.8 g/km^2 at the end of the 1972 breeding season, or 39.0 per cent greater than on the 414-sq mile area (Table 15). The biomasses of the individual species were increased by the following percentages: Swainson's hawk--47.4, ferruginous hawk--74.6, great horned owl--24.3, golden eagle--20.1, and prairie falcon-- 142.2. Ferruginous hawks excepted, the magnitudes of these percentages increase as the size of the raptor decreases.

Each of the four nesting habitats was used differently by each of the five species of large raptors (Table 16). The two congeneric, sympatric buteos used the other's dominant nesting habitat 30 to 35 per cent of the time. Swainson's hawks were less successful at fledging young in their dominant nesting habitat (creek bottoms) than in unbroken grassland or cultivated land. The ferruginous hawk had a higher fledging success in its dominant nesting habitat (unbroken grassland). The different species of large raptors also used the available nest supports to different degrees, the ferruginous hawk being the most versatile species with regard to actual nest placement (Table 17).

Man has been an important factor in the distribution of nesting birds of prey in northeastern Colorado. Considering all species collectively, 104 of 347 nestings (30.0 per cent) were at man-created nest sites (Table 18). Both Swainson's and ferruginous hawks nested at abandoned farmsteads and in volunteer cottonwoods near abandoned ditches and man-made ponds about 40.0 per cent of the time (in all habitats combined). In unbroken grassland only, 44 of 45 Swainson's hawk nests (98.8 per cent) and 28 of 41 ferruginous hawk nests (68.3 per cent) were at man-created nest sites. Man's past activities probably allowed an increase in the total Swainson's hawk population during the decades following the exodus of homesteaders in the early 1900's. It is uncertain if there are more ferruginous hawks today than historically. The adverse effect of cultivation on the nesting of these hawks, and the unknown effects of the everyday use of much of the land for recreation complicate the relevant speculations.

During the breeding season, the collective diet of Swainson's and ferruginous hawks, great horned owls and golden eagles included about 3 times as many mammals as birds (Table 20). The two or three most common prey species (on the basis of the total number of prey items identified) of each of the large raptors were as follows: Swainson's hawk--lark bunting, western meadowlark and thirteen-lined ground squirrel; ferruginous hawk--thirteen-lined ground squirrel, cottontails (sp.?) and jackrabbits (sp.?); great horned owl--cottontails (sp.?) and northern pocket gopher; and golden eagle--cottontails (sp.?) and jackrabbits (sp.?).

Swainson's hawks took a wider variety of prey compared to the other diurnal raptors. The great horned owl diet was as diverse as that of the Swainson's hawk. The golden eagle preyed on only 4 species 96 per cent of the time. Cottontail rabbits (sp.?) were preyed upon most heavily, accounting for about 28 per cent of all prey of the four raptors for which food habits information was available. In general, larger diurnal raptors took more mammals and fewer birds as prey than smaller diurnal raptors (Figure 10).

Non-raptor avian biomass was between 62 (1972) and 95 (1971) times greater than the large raptor biomass. Rodent biomass was over 200 times the raptor biomass during both years (Table 21). Calculations showed that raptors took prey equal to about 6.0 per cent of the bird and rodent biomass in 1972 and only 3.8 per cent in 1971 (between 1 April and 30 August each year). Cottontail rabbits, jack-rabbits and northern pocket gophers were not included in the prey base due to inadequate data. The addition of rabbits and gophers would decrease the per cents of exploitation of the prey base significantly. All this supports the suggestion that the prey base was not a limiting factor on raptor populations in either 1971 or 1972.

Mean monthly temperatures were higher and precipitation amounts were lower in 1972 than in 1971 from February through May. It was shown that these differences in abiotic variables occurred simultaneously with differences in nesting phenologies of the more sedentary raptorial species, but not the late-arriving, migratory Swainson's hawk. The early-nesting species laid eggs earlier in 1972 than in 1971, but also showed considerable asynchrony of nesting by the population of each species as a whole in 1972.

Clutch size of ferruginous hawks in trees which afforded shade to the nests was 21.5 per cent greater than in all unshaded nesting situations combined, and 30.1 per cent greater than in unshaded tree nests (Table 22). Similar relationships were evident for maximum brood size and fledging success. The probability of an egg hatching was also greater in shaded nests, but the probability of fledging if hatched was slightly greater in unshaded nests. All this resulted, apparently, in a higher probability of fledging at egg laying in shaded rather than unshaded nests. These findings suggest that direct sunlight in ferruginous hawk nests was detrimental to overall nesting success.

Considerable doubt that sunlight was the only factor was cast by an analysis of the remoteness of ferruginous hawk nests. Shaded nests tended to be more remote than unshaded nests. Accordingly, ferruginous hawks were more successful at remote nesting sites.

An analysis of the effects of man's current activities on the nesting performance of Swainson's hawks showed advantages to the following: 1) nesting on the PNG rather than on private land, 2) nesting on posted land or in otherwise remote places rather than where access to the nest was relatively free, and 3) nesting on posted land <u>near</u> unimproved roads.

The needs for further raptor research in northeastern Colorado fall into several categories: 1) long-term studies of population dynamics, 2) long-term studies of predator-prey relationships (specifically rates of exploitation of prey populations), 3) field testing of both management and emergency conservation measures applicable to birds of prey, and 4) long-term management of existing populations. Detailed suggestions for such research conclude the present report.

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