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THE LARGE BIRDS OF PREY OF THE PAWNEE NATIONAL GRASSLAND: NESTING HABITS AND PRODUCTIVITY, 1969-1971

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ABSTRACT

The potential of the Pawnee National Grassland and adjacent areas for long-term raptor research and management is great. This paper considers fundamental data on nesting and productivity of the large birds of prey in that area during 1970 and 1971. The study was an effort to document the status and timing of the raptors' reproductive cycles, their absolute population densities, nesting habits, biomasses, and interactions with man.

Lengthy discussions of biomass, intra- and interspecific nesting competition, and the relationship between man and the grassland raptors are included, as are tables of standard productivity data such as clutch sizes, brood sizes, pairs per unit area, young produced per unit area, abandonment rates, young per successful nest, and young produced per pair. Differential utilization of grassland habitats is considered in detail.

Determination of absolute nesting densities of Swainson's Hawks, Ferruginous Hawks, Great Horned Owls, and Golden Eagles showed that 42 pairs of large birds of prey nested in a 414-sq mile area in 1971, about 10 pairs per 100 sq miles. These birds produced 11.1 young per 100 sq miles. (Figures are also given in the metric system in the text.) The adults and young on the 414-sq mile study area represented a biomass of 151.5 g/km^2. Considering estimated populations in a 2,266-sq mile portion of Weld County, Colorado, a collective biomass of 230.2 g/km^2 was calculated for the large birds of prey.

With regard to nesting habits, it was quantitatively demonstrated that man has played an important role--often a positive role--in the utilization

of grasslands by birds of prey. Over one-quarter of all nestings by birds of prey are in situations created directly or indirectly by man. Differential utilization of grassland habitats was analyzed using the following habitat categories: bluff lines, cultivated land, creek bottoms, and pure grasslands. Swainson's Hawks and Great Horned Owls most often nested in creek bottoms, while Ferruginous Hawks nested in pure grasslands more commonly. All Prairie Falcons and most Golden Eagles nested along bluff lines. Only the Swainson's Hawk consistently nested near cultivated land with widely scattered trees.

INTRODUCTION

The Pawnee National Grassland and the adjacent, privately-owned lands provide suitable nesting habitat and food for one of the densest populations of raptorial birds in North America. The number of species and the number of individuals in the area change seasonally. Some are common all year; others occur in large numbers only in a particular season and are absent during other parts of the year, while a few species are observed only rarely. Within any given year, of North America's 30 species of falconiforms 15 or 16 use this portion of northeastern Colorado; six or seven of this continent's 15 owls are part of the same avifauna.

The occurrence of 23 species of raptors in a study area presents an excellent opportunity to study them as a collection of predators and to study their intra- and interspecific relationships, absolute and relative nesting densities, differential utilization of grassland habitats, seasonal and annual cycles, predator-prey relationships, growth of nestlings, migration, and all aspects of their behavior. Such study is facilitated by the relatively unlimited visibility and ease of movement of the observer on grasslands. The presence of the International Biological Program, Grassland Biome project, Pawnee Site allows highly integrative and thorough analyses of data.

The uniqueness of the Pawnee National Grassland as a study area is increased by the rather stable land-use practices of the 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 nonirrigable land of northeastern Colorado was suitable for only two forms of agriculture, namely cattle ranching and dryland grain production. Barring the development of spectacular irrigation projects and unnatural decimation of the birds of prey of this region, their habitat and thus their nesting populations should remain relatively unchanged for the next several decades. The latter is an attribute of the area which will allow research to solve some basic problems of raptor biology, but as this study will show, the populations will still need a management influence.

Through a long-term population study of the raptors and the prey of this area, great insight could be gained into the fundamental concepts of raptor population management, including construction of pertinent life tables, increasing populations by erecting artificial nest structures to supplement the available trees, controlled acquisition of birds for scientific and recreational purposes, and monitoring population levels.

This study is an attempt to promote such long-term study for the purpose of developing America's first major raptor management area. This particular paper deals with basic population data and details of the nesting habits of the Swainson's Hawk, Ferruginous Hawk, Great Horned Owl, Golden Eagle, and Prairie Falcon. Future papers will deal with migration, growth of nestlings, food habits, and finally, a synthesis report on the role of avian predators in the dynamics of the grassland ecosystem.

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 on the Pawnee National Grassland;
2. to determine the absolute population densities of the larger birds of prey nesting on a 414-sq mile area;
3. to determine the relative population densities of the larger birds of prey nesting in four different grassland habitats (creek bottoms, bluffs, planted agricultural land, and pure grassland) on a 2,266-sq mile area;
4. to discuss the biomass of birds of prey in grasslands;
5. to discuss some of the factors, such as man's activities, which influence population densities and nesting habits of birds of prey; and
6. to discuss the potential of the Pawnee National Grassland as a raptor management area.

Personnel

The raptorial birds of northeastern Colorado have been studied by several ornithologists and students in the last 10 years (see Ryder, 1969, 1972). Through the coordination of the International Biological Program, 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. Following the initiative of Gerald Craig and myself, funding from the Frank M. Chapman Fund of the American Museum of Natural History and the International Biological Program (through Dr. Ryder) has made it possible to carry out more intensive study of these top carnivores.

This report includes analyses of new studies conducted between May 1, 1969, and October 15, 1971. During the summer 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, 1971). During the summer of 1970 Gerald Craig and I, with some assistance by John W. Stoddart, Jr., of Denver, 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 the most intense effort to date. From March 15 through October 10 my full-time work involved all aspects of the biology of the birds of prey of the Pawnee National Grassland 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. 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 are gratefully acknowledged.

GENERAL CONSIDERATIONS

The birds of prey which occur on the Pawnee National Grassland and the relative status of each are listed in Table 1. Those which

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
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
Long-eared Owl (*Asio otus*)	Rare W
Short-eared Owl (*Asio flammeus*)	Uncommon FWSpSu
Snowy Owl (*Nyctea scandia*)	Rare FWSpSu
	Very Rare W

* Major raptors on the Pawnee National Grassland.

California (Brown and Amadon, 1968). The wintering range of the Swainson's Hawk is quite different. A few winter in Florida or elsewhere, but most migrate to Argentina. The Swainson's Hawk is by far the most migratory of the large birds of prey of the Pawnee National Grassland.

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 Lark (*Eremophila alpestris*), and Western Meadowlarks (*Sturnella neglecta*) are important avian prey.

Swainson's Hawks arrive on the breeding grounds in northeastern Colorado in mid-April (Fig. 1) and apparently move straight to their nesting territories. The first observation of this species in 1971 was on April 13 by Ronald A. Ryder. A pair of birds was sitting in a lone tree with a nest from which young were fledged successfully in both 1970 and 1971. The pair was observed almost daily from April 13 on. Very few Swainson's Hawks were observed away from territories all spring. Most Swainson's Hawk territories were filled by May 1, 1971. A courtship flight was observed on April 24, but it did not result in copulation.

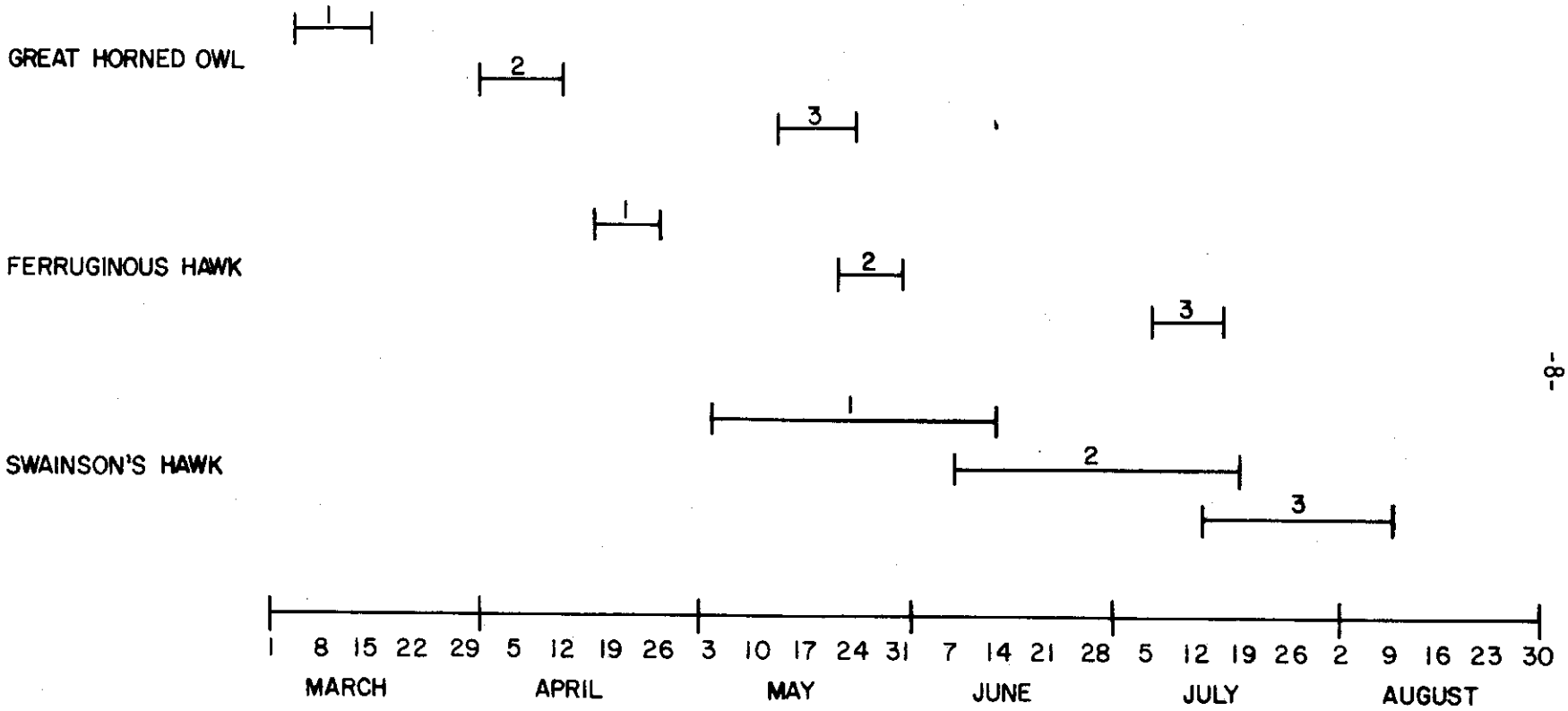

Fig. 1. The timing of the breeding season of Great Horned Owls, Ferruginous Hawks, and Swainson's Hawks on the Pawnee National Grassland in 1971. Egg-laying period, 1; Hatching period, 2; Fledging period, 3.

Copulation of Swainson's Hawks was observed on May 15, May 26, and June 11. Twice it occurred on fence posts and once in a tree. The observation of June 11 involved a very late arriving pair or a renesting attempt because most birds were on eggs by that time. Some already had young.

By extrapolating back from fledgingor 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 May 3. Egg-laying continued throughout the month of May, with 11 of 13 closely observed clutches being laid between May 10 and May 29. The peak laying date was May 14 (Fig. 1).

The eggs of Swainson's Hawks are variously colored, ranging from almost immaculate off-white to extensively 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 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 × 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 2).

Hatching occurred primarily between June 14 and July 3 in 1971. The earliest hatching was about June 7, while one late clutch known to be a renesting hatched on July 18. If these birds had been raised, they would not have fledged until August 25. They did not survive. Most Swainson's Hawks fledged between July 22 and August 1. The earliest brood fledged July 12 and the latest August 10. Brood size in successful nests was exactly the same as clutch size in all nests (Tables 2 and 3). In other

Table 2. Clutch sizes of large birds of prey on the Pawnee National Grassland (1970 and 1971 combined).[a/]

Species	No. of Eggs					Average
	1	2	3	4	5	
Swainson's Hawk	5	16	19	2	0	2.43
Ferruginous Hawk	1	5	8	5	0	2.89
Great Horned Owl	0	6	2	0	0	2.25
Golden Eagle	8	14	0	0	0	1.64
Prairie Falcon	0	2	0	4	5	4.09

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

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

Species	No. of Young					Average
	1	2	3	4	5	
Swainson's Hawk	3	10	12	1	0	2.42
Ferruginous Hawk	6	4	6	2	0	2.22
Great Horned Owl	0	15	1	0	0	2.06
Golden Eagle	6	13	0	0	0	1.68
Prairie Falcon	1	2	1	5	3	3.58

[a/] Brood size equals the maximum number of young observed in a nest, whether all were reared or not.

words, if some Swainson's Hawk eggs of a clutch hatch, all of them usually hatch. This was not the case, as will be shown below, with Ferruginous Hawks. The timing of egg-laying, hatching, and fledging is shown in Fig. 1. The period from egg-laying through fledging lasts 70 days in a single nest and 99 days 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 beginning their spectacular migration in earnest. In 1971 large flocks congregated southeast of Briggsdale, Colorado, in a region where such flocks are seen almost yearly. The peak occurred from September 24 through 28. Over 200 Swainson's Hawks were observed on September 28, 1971, in about a 10-sq mile area. All had departed by October 4. Swainson's Hawks are totally absent from northeastern Colorado from early October through mid-April. One Swainson's Hawk banded on the Pawnee in 1970 was recovered in Argentina during the following winter.

Ferruginous Hawk

The Ferruginous Hawk is the largest buteo in North America, but as a species it has the smallest summer range and it is the least studied of the large nesting raptors of the Pawnee National Grassland. It is resident year round in the semiarid regions of the western United States which exclude much of the Rocky Mountains and all of a wide strip along

the Pacific Coast. The northern limit of its breeding range includes the southern portions of the Canadian prairie provinces. To the south the Ferruginous Hawk does not reach Mexico during the nesting season, but it occurs along the southern tier of states from Arizona to northwestern Texas. During the winter Ferruginous Hawks move only slightly to the southwest into Baja, California, south to northern Mexico, and southeast as far as east Texas (Brown and Amadon, 1968).

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 Pawnee National Grassland in 1971 was 1,296 g.

The Ferruginous Hawk is a yearlong resident of the Pawnee but at much lower population levels than Swainson's Hawks in the summer or Rough-legged Buzzards in the winter. On a drive across the Pawnee one can expect to see two to five Ferruginous Hawks per 100 miles almost any time of the year but rarely more than that.

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 Pawnee National Grassland 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.

Being a resident species it is difficult to determine the date when Ferruginous Hawks move to their nesting territories. The first day in

the field in 1971 was March 17, and a Ferruginous Hawk was observed near a nest used in 1970. Another pair was observed sitting in a 1970 nest tree on March 21, 1971, and this and other pairs were seen at nests from that time on. Pending further study, the earliest nesting activity on the Pawnee will be stated as March 10. Weston (1969) observed nesting activity of Ferruginous Hawks in the Cedar Valley of Utah as early as February 25, 1968, and March 6, 1967.

Ferruginous 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. In three instances pairs of Ferruginous Hawks were seen repairing nests 2 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.

Copulation by Ferruginous Hawks was observed on March 10, 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 Fig. 1. Egg-laying began in mid-April of 1971, April 16 being the earliest laying date as determined by using an incubation period of 35 days and extrapolating back from hatching. 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. 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 Hawks, a resident species, was more precisely timed than that of the Swainson's Hawk, a migratory species.

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 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 × 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, 1971). Clutch size varies from one to four eggs with clutches of three most common (Table 2).

Hatching began about May 21, 1971, and continued through June 11. The young birds fledged between July 6 and July 17 after an average of 46 days (range 42 to 48 days) in the nest. Brood size was considerably less in successful nests than was the average clutch size calculated from all nests (Tables 2 and 3). This indicates either a level of infertility or a failure of incubation. That the latter is the case will be discussed below. The mid-points (not necessarily peaks) of egg-laying, hatching, and fledging in 1971 were March 21, May 27, and July 11, respectively. For a single pair of Ferruginous Hawks, egg-laying through fledging their young lasts about 81 days. Egg-laying through fledging lasts 92 days for the entire population; at least that was the case on the Pawnee in 1971.

Young Ferruginous Hawks apparently move away from the actual nest site sooner after fledging than do Swainson's Hawks. One Ferruginous Hawk

banded on the Pawnee in the summer of 1970 was recovered in northern Mexico the following winter.

Great Horned Owl

This species is the dominant large strigiform of the Pawnee National Grassland, and it contributes significantly to the raptor biomass of the area. The food habits of this species and the other three more common owls of northeastern Colorado were studied by Marti (1970) both in the grasslands and in the foothills of the Rocky Mountains. The range of the Great Horned Owl includes all of North America south of the Brooks Range and the Arctic Circle and all of Central and South America. Great Horned Owls weigh nearly as much as Ferruginous Hawks. Craighead and Craighead (1956) list the average of 895 males as 1,304 g and of 772 females as 1,706 g (There is some question as to whether these weights are for different individuals or for multiple weighings of a smaller number of owls.),

Many potential Great Horned Owl territories can be located in late December as has been indicated by comparisons of the Pawnee Site Christmas bird counts and subsequent nesting records. Many studies have indicated that Great Horned Owls migrate little, if at all, so that it is irrelevant to determine the earliest arrival of the species. The date of the onset of courtship would be pertinent, but it was not determined during this study.

Using an incubation period of 28 days and extrapolating back from hatching, the egg-laying period was calculated as March 4 through March 15 (Fig. 1). As with the Ferruginous Hawk, the egg-laying period (and the hatching and fledging periods) was more precisely timed than with the Swainson's Hawk. Incubation often occurred with snow on the ground and when the temperature was below freezing.

Great Horned Owl eggs are immaculate white. The size of nine eggs 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 × 56.3 mm. One set was of average diameter (45.4 and 46.0 mm) but very short (52.4 and 50.6 mm). Clutch size (2.25) and brood size in successful nests (2.06) were quite similar (Tables 2 and 3).

Hatching of nine clutches occurred April 1 through April 12, and the birds fledged between May 13 and May 24 after an average period of 42 days in the nest (Fig. 1). This was 9 weeks earlier than Swainson's Hawks and 7½ weeks earlier than Ferruginous Hawks. The length of the breeding season from egg-laying through fledging of a single brood was 70 days. On a population basis, owls have eggs or young in the nest for 81 days on the Pawnee National Grassland.

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 months after they fledged.

Golden Eagle

This is the largest of the birds of prey which nest on the Pawnee National Grassland. The species is a year-round resident which, apparently, does not undergo an extensive migration from the area. No aspect of the biology of the Golden Eagle was thoroughly studied in 1971, but its natural history as it relates to the Pawnee can be outlined. Some additional information concerning the Golden Eagle in northeastern Colorado is included in a paper by Boeker and Ray (1971), but those investigators omitted much detail because of the large scope of their study.

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 seven male Golden Eagles is listed as 3,924 g and that of four females as 4,692 g by Brown and Amadon (1968). The weights of all of the larger birds of prey, particularly the Golden Eagle, need further documentation. Pending further study of food habits the prey of nesting Golden Eagles on the Pawnee will be stated as cottontails and jackrabbits. In 1971, during roughly 40 visits to eagle nests, nearly all prey items were rabbits. The exceptions were one thirteen-lined squirrel and one Black-billed Magpie (*Pica pica*). Long-tailed weasels (*Mustela frenata*) have been found in Pawnee eagle nests in previous years.

Previous study indicated a movement of Golden Eagles in northeastern Colorado during the first week of March, 1970 (Craig, 1970). Whether this was a movement of more migratory birds toward Canada or Alaska or whether they were Colorado birds moving to their nest sites is unknown. All Golden Eagles had eggs before this study was initiated on March 17, 1971. The only precise information concerning timing of the breeding cycle collected in 1971 includes hatching of one clutch of eggs on May 4 and May 5 (egg-laying approximately March 23 using an incubation period of 43 days) and fledging of three broods, one on June 16 and two on June 17. These data indicate an egg-laying through fledging period of more than 85 days, but the nests involved were not the same for the determination of hatching and fledging dates. That period may well be in excess of 100 days.

The eggs of Golden Eagles range from completely cream-colored to extensively splotched with brown. The average size of three eggs was 57.8 × 76.6 mm. The average weight of two eggs about half incubated was 122.8 g. Clutch size and brood size in successful nests were nearly identical (Tables 2 and 3).

Prairie Falcon

This species was not studied intensively in 1971 although considerable eyrie location and banding were carried out. One can get an excellent synopsis of the life history of the Prairie Falcon by consulting the work of Enderson (1964). Brood size in successful nests (Table 3) was slightly less than clutch size (Table 2). Most Prairie Falcons in the area fledged between June 18 and 25, 1971.

NESTING DENSITIES

Methods

During the nesting period of 1971 population densities of the larger birds of prey were determined on a 414-sq mile (1,073 km^2) grassland study area. Small raptors were excluded from this survey. It was not practical to include them because of the time required to seek out all nests of the smaller American Kestrels and Burrowing Owls.

Geographically, this area essentially corresponds to the western portion of the Pawnee National Grassland and includes exactly 11½ townships (Fig. 2). Just off of the area on the west and south are large tracts of winter wheatland. On the east is a large creek bottom filled with a nearly continuous band of cottonwood trees, and on the north is a line of bluffs

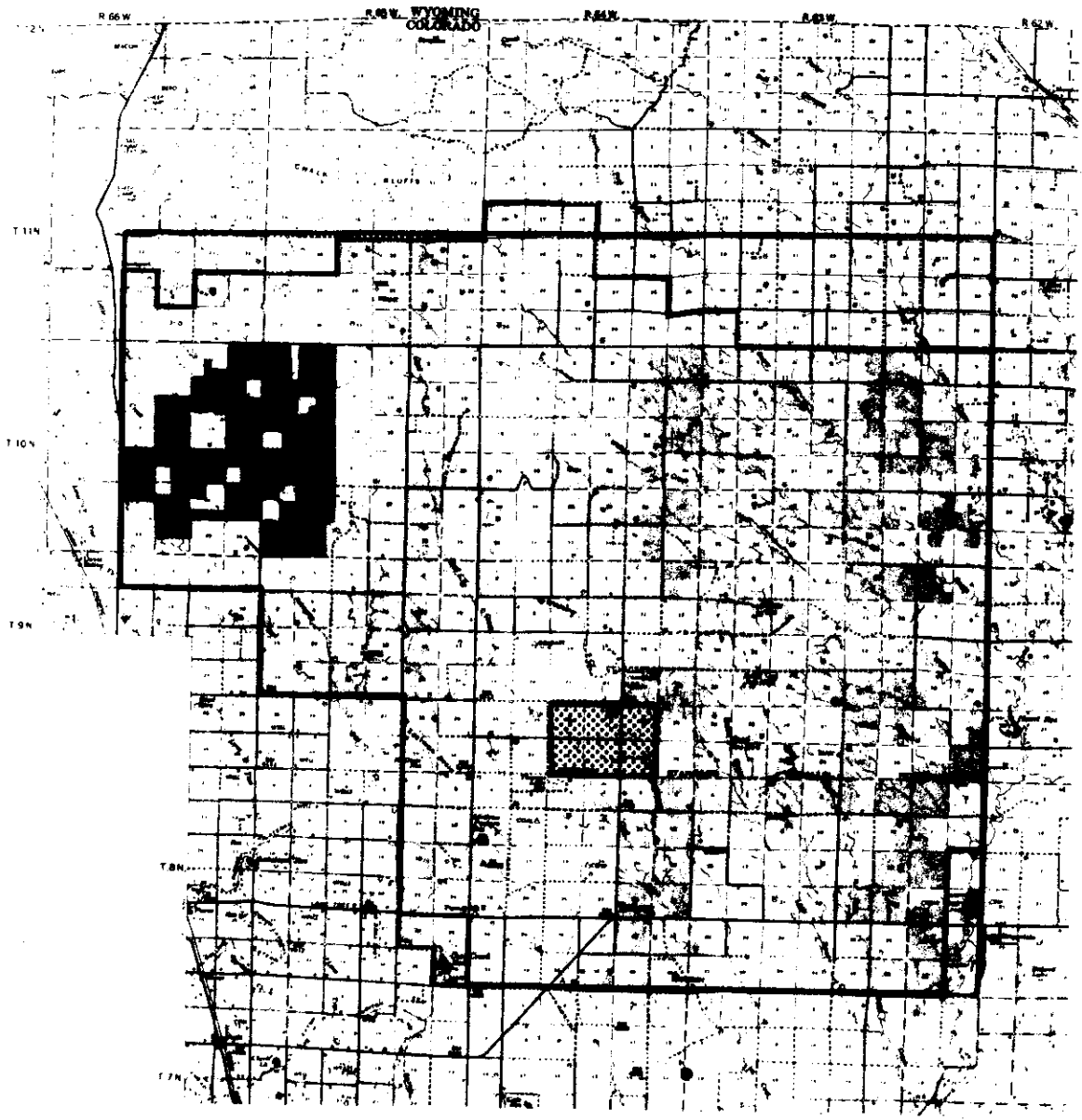

Fig. 2. The 414 sq-mile study area.

and grazing land. Bluffs, large creeks, and large tracts of cultivated land do not occur inside the 414-sq mile study area.

The IBP Pawnee Site and the Central Plains Experimental Range are near the northwest corner of the area. As defined, the entire 414 sq miles is nearly identical in topography, fauna, and flora to the Pawnee Site (Jameson and Bement, 1969). This similarity and not the number and/or distribution of birds there was the justification for the boundaries as established.

Nests were located in this area by searching each township mile by mile using a pickup truck or trail bike or by walking. It is felt that nearly all nests of Ferruginous Hawks, Swainson's Hawks, and Great Horned Owls were found with the possible exception of one or two pairs of ground-nesting Ferruginous Hawks. No Golden Eagles, Red-tailed Hawks, or Prairie Falcons nested on the 414-sq mile area in 1971, although two pairs of Golden Eagles were present.

As the area was searched, each section was classified as being grazing land or cultivated land, and all trees and other potential nest sites were noted (Table 4). Only about 27 sq miles (6.5%) were cultivated, and the largest continous 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. About another eight 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. On the whole 387 sq miles (93.5%)

Table 4. 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

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 around occupied dwellings. Thus, about 97% of the land was usable by raptors without much interference from man.

Results

Nesting population and productivity data for the 414-sq mile grassland study area are summarized in Tables 5 and 6. 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 nest failure rates and the modal brood sizes for those species concerned. Nest failure is defined to include all failure regardless of the cause. Abandonment rate is used interchangeably with failure rate in the tables.

A total of 42 pairs of large birds of prey were observed on the area during the summer of 1971, of which 37 pairs were known to have nested. Thus, 42.5% of the 87 sections with potential nest sites were occupied. Swainson's Hawks were most abundant and produced the most young per unit area in spite of a nest failure rate of 66.7%. No non-nesting population of adult Swainson's Hawks was noted although this would have been difficult to detect because of the species abundance.

Ten pairs of Ferruginous Hawks were present, but only seven of them nested. The other three pairs were frequently observed near nests, but eggs were not produced. No nest failure by Ferruginous Hawks occurred on this study area, although it did occur on the 2,266-sq mile study area The low rate of failure resulted in a production of young Ferruginous Hawks only slightly less than that of young Swainson's Hawks.

Table 5. Nesting population data of raptorial birds on a 414-sq mile (1,073 km^2) grassland study area.

Species	Number of Pairs	Pairs per 100 Sq Miles	Pairs per km^2	Nests Found	Nests Abandoned
Swainson's Hawk	24	5.8	0.022	24	16 (66.7%)
Ferruginous Hawk	10	2.4	0.009	7	0 (0.0%)
Great Horned Owl	6	1.4	0.006	6	1 (16.7%)
Golden Eagle	2	0.5	0.002	0	--
All species	42	10.1	0.039	37	17 (45.9%)

Table 6. Productivity data of raptorial birds on a 414-sq mile (1,073 km^2) grassland study area.

Species	Young per Successful Nest	Young per Known Nest	Young Produced per 100 sq miles	Young Produced per km^2
Swainson's Hawk	2.43	0.83	4.8	0.019
Ferruginous Hawk	2.29	2.29	3.9	0.015
Great Horned Owl	2.00	1.67	2.4	0.009
Golden Eagle	--	--	--	--
All species	2.30	1.2	11.1	0.043

The Great Horned Owl commonly nests on the Pawnee National Grassland, about one pair per two townships (72 sq miles). All successful nests in 1971 produced two young, and the one nest which failed had two eggs. About half as many Great Horned Owls as Swainson's Hawks were produced per unit area in 1971. Two pairs of adult Golden Eagles were frequently observed on the area, but neither pair nested in 1971.

RELATIVE NESTING DENSITIES

Methods

During the nesting periods of 1970 and 1971, a total of 165 nests of large birds of prey were found on a 2,266-sq mile (5,870 km^2) study area comprising the northern portion of Weld County, Colorado. The data cannot be analyzed in terms of raptors per unit area because the area was not systematically and completely searched for nests. The data are useful, however, for analyzing the nest site preferences of the large birds of prey, i.e., their differential utilization of grassland habitats.

For the purposes of this study the grassland ecosystem was divided into four habitats. These are: (i) grassland, like most of the area around the Pawnee Site, (ii) bluff lines which transect the grassland from east to west in one case and north to south in another, (iii) major creek bottoms like Crow Creek, Pawnee Creek, and their tributaries, and (iv) large tracts of cultivated land like those southeast of Briggsdale and west of Nunn and Pierce. Each of these nesting habitats was relatively more or less important to each species of raptor.

For analytical purposes an active nest was defined as one in which an adult was observed actively incubating or in which eggs were deposited. Every known nesting on the 2,266-sq mile area was considered in the

analyses made below, regardless of the outcome of the nesting. A nesting situation used in both 1970 and 1971 was counted only once.

The placement of a particular nest into one of the four grassland habitats 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.

Results

The productivity of the large birds of prey of northern Weld County, Colorado, in 1970 and 1971 is summarized in Table 7. No Red-tailed Hawk nests were found in the area in 1971, although one nesting and one non-nesting pair were observed in 1970. A total of 15 Ferruginous Hawk nests

Table 7. Productivity of the large birds of prey of northern Weld County, Colorado, in 1970 and 1971.

Species	Nests		Nests Abandoned		Young per Successful Nest		Young per Nest	
	1970	1971	1970	1971	1970	1971	1970	1971
Ferruginous Hawk	10	15	6 (60%)	4 (27%)	2.00	2.45	0.80	1.80
Swainson's Hawk	28	38	19 (68%)	23 (61%)	2.00	2.40	0.64	0.95
Golden Eagle	11	20	1 (09%)	7 (35%)	1.70	1.61	1.55	1.05
Prairie Falcon	7[a]	8	3 (43%)[a]	0 (00%)	4.25[a]	4.00	2.43[a]	4.00
Great Horned Owl	8	14	1 (13%)	3 (21%)	1.86	2.00	1.63	1.57

[a] Data of L. R. Grater. Abandonment caused by disappearance of eggs and large nestlings from nests.

were located in 1971 of which four (27%) failed. A failure rate of 60% was noted in 1970. Ferruginous Hawk nests were not climbed during the egg period in 1971, but were in 1970. This, in addition to less wind-caused nest destruction in 1971, led to the lower failure rate in 1971. The number of young produced per successful Ferruginous Hawk nest was higher in 1971 than in 1970. Thus, the increase in the number of young produced per nest (successful and unsuccessful) was the result of higher productivity per successful nest and a decrease in the rate of failure.

Productivity of Swainson's Hawks was also up in 1971 relative to 1970, also as the result of a lower rate of failure and a higher fledging rate in successful nests. Data for young produced per successful nest show parallel increases in 1971 over 1970 levels for Swainson's and Ferruginous Hawks. The lower fledging rate per occupied nest of Swainson's Hawks (0.95) follows from the high failure rate of Swainson's Hawks (more than twice as high as for Ferruginous Hawks).

Golden Eagle production was down slightly in 1971 as the result of a higher rate of nest failure. This decreased production was probably an artifact of data acquisition. Since the observers were in the field early in the 1971 nesting season, several instances of creek-bank nests being destroyed early in the season by heavy rains and continued erosion were noted. Similar early failures would not have been detected in 1970. The suggestion is that there are more non-nesting pairs of Golden Eagles during the summer months than originally expected. This corroborates the data presented above for the 414-sq mile study area where two non-nesting adult pairs were observed. No renesting of Golden Eagles occurred subsequent to destruction of the original clutch of eggs.

This study did not include data for Prairie Falcons in 1970. Data from Grater (1970) were used for 1970-1971 comparisons. No Prairie Falcons or eggs disappeared from the study area in 1971. The productivity was at a high level.

Great Horned Owls reproduced at about the same rates in 1970 and 1971. A slightly higher incidence of nest failure was compensated for by a higher production in successful nests in 1971. Fourteen pairs fledged 1.57 young per nest in 1971.

Data concerning partitioning of the grassland ecosystem by nesting birds of prey are summarized in Table 8. Swainson's Hawks were found predominately along creek bottoms (60% of the time) and cultivated land (14.1%). None were found nesting on bluffs.

Ferruginous Hawks nested more in pure grassland areas (64.5%), but used creek bottoms nearly one-third of the time (29.0%). The two buteos each used the other's dominant habitat about the same percentage of the time (29.0 vs. 25.3%). Ferruginous Hawks also nested on bluffs but not in cultivated land.

The Great Horned Owl was the most consistent nester in creek bottoms (84% of the time), but owls also nested occasionally in pure grassland areas (4.0%) and in bluffs (8.0%). The Great Horned Owls listed as nesting in cultivated land raised two young 30 ft from the window of the second floor, sixth grade classroom of the Grover schoolhouse.

Exactly 36.0% of the nesting Golden Eagles used trees and banks along creeks. This was a much higher percentage than expected, although most (56.0%) did nest in more typical cliff nests. The two nests in pure

Table 8. Partitioning of the grassland ecosystem by nesting birds of prey. The number of nests found in each habitat is followed by the percentage (in parentheses) of the total number of nests in that habitat for each species.

Species	Bluff Lines	Cultivated Land	Creek Bottoms	Pure Grassland	Totals
Swainson's Hawk	0 (0.0)	10 (14.1)	43 (60.6)	18 (25.3)	71 (100.0)
Ferruginous Hawk	2 (6.5)	0 (0.0)	9 (29.0)	20 (64.5)	31 (100.0)
Great Horned Owl	2 (8.0)	1 (4.0)[a/]	21 (84.0)	1 (4.0)	25 (100.0)
Golden Eagle	14 (56.0)	0 (0.0)	9 (36.0)	2 (8.0)	25 (100.0)
Prairie Falcon	13 (100.0)	0 (0.0)	0 (0.0)	0 (0.0)	13 (100.0)
TOTALS	31 (18.8)	11 (6.7)	82 (49.7)	41 (24.8)	165 (100.0)

a/ This nest was in downtown Grover.

grassland were in a tree by a windmill and on a 13-ft high erosional remnant. Prairie Falcons nested on bluffs and nowhere else.

Considering all large raptors collectively, half (49.7%) nested along creek bottoms, and one-quarter (24.8%) nested in pure grassland areas. Bluffs were used 18.8% of the time. Cultivated land was used least often by nesting birds of prey, but as other data will show, crop land is an important food source during the migration period.

The actual placement of nests by all of the large birds of prey collectively was in trees three-quarters (75.2%) of the time (Table 9). Bluff ledges and potholes in cliffs were used 18.8% of the time, while creek banks, erosional remnants, the ground, and man-made structures were used to lesser extents.

Ferruginous Hawks were the most versatile nesters. This species used all of the observed nesting situations, but nested in trees much more often than not (77.4% of the time). Golden Eagles nested on bluffs most often (56.0%), but trees (28.0%) and creek banks (12.0%) were also important. Great Horned Owls used trees extensively (88.0% of the time), but also nested in potholes on cliffs and creek banks.

Swainson's Hawks and Prairie Falcons were the least versatile nesters. In 1970 and 1971 Swainson's Hawks, as expected, were 100% dependent on the presence of trees for spatial distribution during the nesting season, although some ranchers spoke of Swainson's Hawks nesting on telephone and power poles in years past. The dependence on trees has the effect of limiting Swainson's Hawks to creek bottoms and places where man's activities have favored tree growth in grasslands. The distribution of Prairie Falcons during the breeding season was limited to cliffs. The grassland ecosystem

Table 9. Nest site selection by the large birds of prey on the Pawnee National Grassland and adjacent areas. Percentages are given in parentheses.

Species	Trees	Bluffs	Creek Banks	Erosional Remnants	Ground	Man-made Structures
Ferruginous Hawk	24 (77.4)	2 (6.5)	1 (3.2)	2 (6.5)	1 (3.2)	1 (3.2)
Swainson's Hawk	71 (100.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Great Horned Owl	22 (88.0)	2 (8.0)	1 (4.0)	0 (0.0)	0 (0.0)	0 (0.0)
Golden Eagle	7 (28.0)	14 (56.0)	3 (12.0)	1 (4.0)	0 (0.0)	0 (0.0)
Prairie Falcon	0 (0.0)	13 (100.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
TOTALS	124 (75.2)	31 (18.8)	5 (3.0)	3 (1.8)	1 (0.6)	1 (0.6)

is not uniformly transected by bluff lines and, as a result, is not uniformly exploited by Prairie Falcons during the summer. This was also indicated by the absence of nesting Prairie Falcons and the rarity of summer sightings of Prairie Falcons on the 414-sq mile study area.

Man had been a factor in the distribution of nesting birds of prey on the 2,266-sq mile study area. The homesteaders of the early 1900's brought trees with them and planted them near their houses. The trees at the now abandoned homesteads are used by birds of prey as nest sites. The early settlers (as well as the present landowners) made use of windmills, and the overflow provided water for trees. Elaborate but unsuccessful attempts at irrigation were made, and some cottonwood trees got started along the old ditches. Currently, ranchers collect runoff in waterholes made by damming the usually dry stream beds. Some trees can be found at these water holes. The extent to which man and his trees has played a role in the distribution of Ferruginous and Swainson's Hawks on the Pawnee National Grassland is remarkable.

Twenty of the 31 Ferruginous Hawk nest sites (64.5%) were in pure grassland habitat (Table 8). Of these 20 nests, 16 (80.0%) were in trees near windmills, abandoned farmsteads, old ditches, and man-made waterholes or on the abandoned buildings themselves. Swainson's Hawks nested in pure grassland habitat and near cultivated land 39.4% of the time (28 of 71 nest sites) (Table 8). Of these 28 nests, 20 (71.4%) were in trees growing as the result of man's activities.

In all, 51.6% of the Ferruginous Hawks, 33.8% of the Swainson's Hawks, 12.0% of the Great Horned Owls, 4.0% of the Golden Eagles, but none of the Prairie Falcons nested in situations man had created directly or indirectly

(Table 10). For all species collectively, 26.7%, more than one-quarter, nested in such situations. The implications of these considerations will be discussed more fully below.

DISCUSSIONS

Biomass Considerations

In the section on nesting density only the number of raptors per unit area and not their biomass was considered. The following is a calculation of the biomass of the adults before the onset of egg-laying and then the biomass of the adults and young after fledging. For the 414-sq mile study area each species is treated separately, and then all are considered collectively. This is followed by an estimation of the raptor biomass on the 2,266-sq mile study area. Calculations are made in detail below for the biomass on the 414-sq mile study area. The calculations involving the 2,266-sq mile study area are identical. Metric figures are given even though the names of the study areas mention square miles.

The biomass of adult raptors remains stable (for all practical purposes) throughout the breeding season. Considering adult Great Horned Owls first, six pairs were present on the 414-sq mile study area, representing a biomass of 3,010 g/pair or 18,060 g. This calculates to 16.8 g/km^2 of area (Table 11).

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 reduces to 11.5 g/km^2. The combined biomass of Great Horned Owls, adults and young, was about 28.3 g/km^2 after all birds had fledged, i.e., after late May and before appreciable mortality or emigration occurred.

Table 10. The use of nesting situations directly or indirectly created by man by the large birds of prey on the Pawnee National Grassland.

Species	Total Nestings	In Man-made Situations	Percent
Swainson's Hawk	71	24	33.8
Ferruginous Hawk	31	16	51.6
Great Horned Owl	25	3	12.0
Golden Eagle	25	1	4.0
Prairie Falcon	13	0	0.0
All species	165	44	26.7

Table 11. Biomass of adult and young birds of prey on the 414-sq mile study area at the end of the breeding season in 1971 based on absolute nesting densities. Values are in grams per square kilometer followed by percentages (in parentheses) of the total (of each column) for all species combined.

Species	Adults	Young After Fledging	Adults and Young
Great Horned Owl	16.8 (15.7)	11.5 (25.9)	28.3 (18.7)
Ferruginous Hawk	30.0 (28.0)	18.1 (40.7)	48.1 (31.8)
Swainson's Hawk	44.2 (41.3)	14.8 (33.4)	59.0 (38.9)
Golden Eagle	16.1 (15.0)	0.0 (0.0)	16.1 (10.6)
All species	107.1 (100.0)	44.4 (100.0)	151.5 (100.0)

Ten pairs of Ferruginous Hawks were present on the area in 1971. At 3,220 g/pair this amounted to 32,000 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 amounted to 18.1 g/km^2. The total biomass of Ferruginous Hawks on 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 biomass of 47,448 g or 44.2 g/km^2. These birds fledged 20 young at an average of 796 g each. This represented a biomass 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. Biomass of the two pairs was approximately 17,252 g or 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.

Consideration of these data (Table 11) show many things heretofore unquantified. The data on grams per square kilometer are the first to be calculated for raptors based on absolute nesting densities in a grassland, or probably any other, ecosystem. One important finding was that the biomass of the young (44.4g/km^2) was less than half (41.4%) of the biomass of the adults present (107.1 g/km^2). Even if the non-nesting Golden Eagles were eliminated from the calculations, the young to adult biomass percentage would have been only 48.8 (calculated from Table 11). If the two pairs of non-nesting Golden Eagles had produced the usual number of young (1.05 young/nest from Table 7), the percentage would still be very

near 50. Thus, on the Pawnee National Grassland the birds of prey increased their biomass by about half in 1971. Simply stated, each gram of large raptor increased to about 1.5 during the breeding season.

Looking at each species separately, Great Horned Owls increased their biomass by 68.4% (16.8 to 28.3 g from Table 11). Ferruginous Hawks increased their biomass by 60.3% (30.0 to 48.1 g). Swainson's Hawks increased their biomass by only 33.5% (44.2 to 59.0 g). Golden Eagles did not increase their biomass at all. The percentage increase of biomass was held below 50% by a high failure rate of Swainson's Hawk nests and the non-nesting of the Golden Eagles. None of the species (considered individually) even came close to doubling its biomass.

This is another way of looking at the productivity rates (Table 6), provided differences in adult weight and fledging weight for each species are taken into account. The different perspective given by biomass considerations is important to the understanding of the dynamics of an ecosystem. Also emphasized is the point that one must look collectively at all species with similar food habits and not just one or a few "indicator" species. It is unlikely that a single species of bird will respond to or use the ecosystem in the same manner as all species collectively. This probably holds true even if all of the species earn their living in roughly the same way--all as seed eaters, as insect eaters (or both), or as carnivores.

In order to get a closer picture of what happened in 1971 with regard to the large birds of prey in the grassland ecosystem (considered as a composite of the four habitats described above) we must estimate the total populations at the end of the breeding season on the 2,266-sq mile study area. Although one can deal with absolute numbers for 1971 on the 414-sq mile study area and one can rank the species in the order of their importance

(using the percentages in Table 11), these considerations are of limited use because the species composition in that area was biased against Prairie Falcons and Golden Eagles, i.e., the dominant cliff nesters, and to a lesser extent against Swainson's Hawks and Great Horned Owls, i.e., the creek bottom nesters. The 14-sq mile study area is biased in favor of Ferruginous Hawks, the dominant pure grassland nester.

Population estimates for the 2,266-sq mile study area were made after consideration of the densities of large birds of prey on the 414-sq mile study area. In round figures these estimates are 150 pairs of Swainson's Hawks, 40 pairs of Ferruginous Hawks, 45 pairs of Great Horned Owls, 32 pairs of Golden Eagles, and 25 pairs of Prairie Falcons. Anyone who has spent only a small amount of time in the area will consider these estimates to be high. Knowing, however, how much ground was not systematically and thoroughly searched in 1971 and knowing the topography of the area and the nesting habits of the birds, I feel the above estimates are realistic, if not conservative, for the conditions prevailing in that year. Understand, the estimates are of the number of pairs, both nesting and non-nesting.

Based on these estimates raptor biomass was calculated for the 2,266-sq mile study area (Table 12). As expected, the results were quite different from those for the 414-sq mile study area, but the figures, heretofore uncalculable, represent useful estimates of the level of usage of the grassland ecosystem by the large birds of prey. It should be stated that although the productivity data used in these analyses is quite accurate and the weight estimates of adults and young are the best available, the biomass calculations are only as accurate as the population estimates listed above. The latter involves objective decisions by the researcher. It should also be kept in mind that the following conclusions are drawn from

Table 12. Biomass of adult and young birds of prey on the 2,266-sq mile study area at the end of the breeding season in 1971 based on estimates of the total populations. Values are in grams per square kilometer followed by percentages (in parentheses) of the total (of each column) for all species combined.

Species	Adults	Young	Total
Great Horned Owl	23.1 (15.5)	14.9 (18.3)	38.0 (16.5)
Ferruginous Hawk	22.0 (14.8)	15.9 (19.5)	37.9 (16.5)
Swainson's Hawk	50.6 (34.0)	19.3 (23.7)	69.9 (30.4)
Golden Eagle	47.0 (31.6)	19.8 (24.3)	66.8 (29.0)
Prairie Falcon	6.0 (4.1)	11.6 (14.2)	17.6 (7.6)
All species	148.7 (100.0)	81.5 (100.0)	230.2 (100.0)

data involving only 1 year in a very small land area (relative to the size of any of the species entire breeding range or relative to the size of eastern Colorado, for example). Realizing these limitations, however, the figures in Table 12 are considered to be better estimates of the true values for the entire grassland ecosystem than those given in Table 11 for the 414-sq mile study area.

The percentage increases in biomass of the different species listed in Table 12 are as follows: Great Horned Owl, 64.5%; Ferruginous Hawk, 72.2%; Swainson's Hawk, 38.2%; Golden Eagle, 42.1%; and Prairie Falcon, 193.3%. The high efficiency of reproduction of the Prairie Falcon is readily noted. The tripling of the Prairie Falcon's biomass (6.0 to 17.6 g/km^2) was the result of the large clutch size and brood size.

The efficiencies of the other species were grouped in pairs. Swainson's Hawks and Golden Eagles increased their biomass by roughly 40%, while Great Horned Owls and Ferruginous Hawks increased their biomass about 70%. The biomass of all species combined increased 54.8%, compared with 41.4% on the 414-sq mile study area. This difference resulted primarily from the lack of nesting Golden Eagles and Prairie Falcons on the 414-sq mile study area in 1971.

Looking at the individual species the pairing with regard to biomass increases (see above) can also be seen in Table 12 for both age classes, as well as the combined totals for adults and young. This is evidenced in the percentage that each age class contributes to the combined totals for all species. The Prairie Falcon was again in a group by itself, the adults and young together representing only 7.6% of the combined biomass for all species.

The phenomenon of pairs of species having similar biomasses was probably coincidence, but it does produce an interesting ranking of the species for further considerations of the conditions existing in 1971. If the maximum biomass of a species is arbitrarily set at 4, the ratings would be as follows: Swainson's Hawk, 4; Golden Eagle, 4; Great Horned Owl, 2; Ferruginous Hawk, 2; and Prairie Falcon, 1. (Note that these are ratios of the percentages in the third column of Table 12.) This does not imply that this is the order of their trophic impact on the grassland ecosystem, yet it is a good estimate. One cannot state the relative impacts of the species with certainty from these data because of the fact that the food consumption of an eagle weighing 4 kg is not the same in proportion to body size as the food consumption of four 1 kg Swainson's Hawks. This difference and other biomass considerations will be explored more thoroughly in a future paper on the food habits of the birds of prey of the Pawnee National Grassland.

Intra- and Interspecific Nesting Considerations

The average spacing distances between raptor nests have evolved in response to three major factors: (i) the average distance between suitable nest sites, (ii) the intra- and interspecific tolerances of the different species, and, in some cases, (iii) food abundance. The relative importance of these factors varies from habitat to habitat even within comparatively simple ecosystems such as the grassland ecosystem. For example, the distance between suitable nest sites is unimportant throughout most of a band of trees along a creek bottom because nest sites are innumerable. Many bluff lines have far more ledges and potholes than are used by the cliff nesting species. In these habitats intra- and interspecific tolerances (which may vary depending on population levels) play a dominant role in the spatial distribution of nesting pairs in the ecosystem.

In pure grassland and agricultural land the distance between suitable nest sites is necessarily a dominant consideration. The number of nest sites is severely limited in such habitat, particularly with regard to trees in which 75.2% of all large birds of prey nest on the Pawnee National Grassland. Cursory analyses indicate that food abundance does not play an important role in the spatial distribution of nesting birds of prey on the Pawnee. This topic will be discussed more thoroughly in a future report on food habits.

One other factor which has an effect on the limits of cohabitation of an area by large birds of prey is the timing of the breeding season which, as shown above, varies from species to species. In the annual race to nest sites in creek bottoms and pure grassland, for example, Great Horned Owls win, followed in order by Golden Eagles, Ferruginous Hawks, and finally, Swainson's Hawks.

Very close nestings of two different species of raptors are often less productive than if they were further apart. Although it is impossible definitely to attribute low productivity in a particular nest to interspecific conflict, many observations are suggestive of a cause-and-effect relationship. The best examples involve Great Horned Owls and Swainson's Hawks. The latter arrive in the spring to set up territories after Great Horned Owls have young in the nest. In some cases owls are fledging as the Swainson's Hawks move in. Occasionally the hawks must attempt to evict the owls from a small group of trees in order to nest. The constant harrassment by the hawks seems to have a negligible effect on the owls, but in one such incidence the nesting attempt of the Swainson's Hawks failed in the egg stage. In another case the hawks laid only one egg (2.43 eggs was average), and the single young hawk was finally fledged quite late in the season.

Another example of close nesting possibly leading to decreased productivity involved a pair of Ferruginous Hawks and a pair of Prairie Falcons nesting about 70 ft apart on opposite sides of a finger-like projection of a cliff line. The Prairie Falcons had two eggs, only one of which hatched. Likewise for the Ferruginous Hawks; two eggs were laid and one hatched. Both clutches were considerably smaller than average. If one stood at the end of the finger-like projection, the Prairie Falcons defended their eyrie predominately from the right (southwest) where their eyrie was located. The Ferruginous Hawks defended primarily from the left (southeast). An imaginary line from the end of the finger was seldom, if ever, crossed. It is likely that this line was established by conflict of some kind and led to the low productivity by the birds. About 3/8 of a mile from these nests was one of Golden Eagles. The eagles usually left their eyrie toward the north thereby avoiding harrassment by the other birds. The eagles reared a normal brood of two eaglets.

An interesting case of suspected conflict between pairs of Great Horned Owls, Ferruginous Hawks, and Swainson's Hawks occurred in an area where only three suitable nesting territories existed. 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 from constant interference by man. The second site was near a long abandoned farmstead not far from a windmill. It was about 50 ft from a well-travelled road. The third site was about 20 ft from a similar gravel road, but it had fewer and 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. 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 success ratio of the three species involved (all nests found in 1971 being taken into account) decrease according to the temporal order in which they nest. Great Horned Owls are successful 79% of the time, while Ferruginous Hawks are 73% successful at rearing at least one young. This may not be statistically significant, but the trend is evident. Swainson's Hawks rear at least one young in only 39% of the nests they occupy. Factors such as the flimsiness of the 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.

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.

An apparent example of competitive exclusion of Ferruginous Hawks by Golden Eagles (and/or Prairie Falcons) occurred in a large basin surrounded on three sides by bluff lines. The basin is 4 to 5 miles across. The 20- to 60-ft cliffs are nest sites for three to four pairs of Golden Eagles and three to six pairs of Prairie Falcons each year.

Although trees, outcroppings, and bluffs suitable for nesting by Ferruginous Hawks existed in and around the basin, none of these hawks nested there. They nested only outside the periphery, particularly to the northeast and southwest.

The general absence of nesting Red-tailed Hawks on the Pawnee National Grassland and adjacent areas is peculiar. This species seems to be excluded from the area by a lack of dense stands of cottonwood and other deciduous trees along creek bottoms. The only pairs observed during the breeding season were in 1970 along Crow Creek. The only successful nest was not far from the confluence of Crow Creek and the South Platte River. The South Platte is paralleled by a wide, dense band of cottonwood trees which probably attract most Red-tailed Hawks away from the bluffs and lesser forest lines along creeks on the Pawnee. This needs verification, however.

The use of the same nest structure by two species of raptors in different years is another type of interspecific relationship. A nest used by Golden Eagles 1 year was occupied by Ferruginous Hawks in a subsequent year. Other combinations include Ferruginous Hawks and then Great Horned Owls, Ferruginous Hawks and then Swainson's Hawks, Golden Eagles or Ferruginous Hawks followed by Prairie Falcons several years later, and Prairie Falcons followed by Great Horned Owls. Nesting territories (specifically small, isolated groups of trees) have been used by Ferruginous Hawks and then owls (two instances), Swainson's Hawks and then Ferruginous Hawks, and Great Horned Owls followed by Swainson's Hawks in the same year. In the latter instance the Swainson's Hawks were unsuccessful.

It is more common, however, for the same species if not the same individuals to occupy a particular nesting territory in consecutive years. Of 47 nesting territories (not necessarily identical nest structures) occupied both in 1970 and 1971, 39 (83%) were occupied by the same species in both years.

Man and the Grassland Raptors

The unquestionable effect of man on the spatial distribution of the large birds of prey which nest on the Pawnee National Grassland is one of the more interesting findings of this study. That half of all Ferruginous Hawks and a third of all Swainson's Hawks nest in situations created by man is worthy of further discussion.

Farmsteads were the most important of the man-created nesting situations for both of the prairie buteos (Table 13). Of the 16 such situations used by Ferruginous Hawks, 12 (75%) were near abandoned farmhouses. Five of these had active windmills. The other 25% were in trees along abandoned ditches. Of the 24 man-created nesting situations used by Swainson's Hawks, 18 (75%) were at abandoned farmsteads. Three of these had active windmills. Trees near abandoned ditches and man-made ponds accounted for the other 25% of the nests.

All but one of the 40 buteo nests in man-created situations were in trees. The exception was a Ferruginous Hawk nest atop the stone chimney of an abandoned farmhouse. All of the trees used near farmsteads were apparently planted by the homesteaders since often they were not indigenous trees or they were planted in wind breaks or immediately adjacent to the buildings. Those along abandoned ditches and at man-made ponds were mostly volunteer cottonwoods.

Table 13. Detailed analysis of the nesting of prairie buteos in man-created situations. The figures are numbers of nesting situations followed by the percentage (in parentheses) of the total for each species.

Man-created Situation	Ferruginous	Swainson's
Farmstead	7 (43.8)	15 (62.5)
Farmstead and windmill	5 (31.2)	3 (12.5)
Abandoned ditch	4 (25.0)	4 (16.6)
Man-made pond	0 (0.0)	2 (8.4)

Thus, 75% of the effect of man on the spatial distribution of nesting buteos on the Pawnee National Grassland (aside from permanent habitat destruction and background levels of interference by man) was the effect of his early habitation of the area. The other 25% resulted from his attempts to irrigate and to collect water for his cattle. Some of the trees near abandoned farmsteads are now kept alive by active windmills. With few exceptions the man-created nest sites of Swainson's Hawks are not threatened. The future of such nest sites used by Ferruginous Hawks is not as optimistic.

Of the 15 tree nests of Ferruginous Hawks in man-created situations, four were in dead trees. Six others were in trees which appeared stunted by the lack of water. Portions of the latter were already dead, sometimes the major portion. It will only be a matter of time (perhaps just a few years) before all but five of the 15 trees now used by Ferruginous Hawks are dead and blown down by high winds pushing against the bulky stick nests which Ferruginous Hawks build. One blew down in 1971 and destroyed a clutch of four eggs. Considering all known Ferruginous Hawks nests, 10 of 31 (32.3%) probably will disappear within a decade.

This sort of nest destruction has already occurred in certain portions of the prairie provinces of Canada (Stuart Houston, personal communication). There, trees at abandoned farmsteads are the principal nesting sites of Ferruginous Hawks. The disappearance of these trees is several years ahead of the situation on the Pawnee National Grassland. The unhappy result in Canada has been a severe decline in the Ferruginous Hawk population, in spite of the fact that the species is a versatile nester.

Another aspect of the man-created situations is the advantage of tree nests over the other types of nest sites, especially for Ferruginous Hawks. As mentioned, this species is a very versatile nester even to the extent of nesting on the ground. Nests on the ground are subjected to great temperature extremes as are nests which receive direct sunlight during the greater portion of the day. Productivity in eight successful Ferruginous Hawk nests (1969-1971) in trees which afforded considerable shade was 3.00 young/nest, while productivity in seven unshaded nests in trees on erosional remnants and on the ground was only 1.71 young/nest. The degree of shading does affect the productivity of Ferruginous Hawks (statistical parameters to be calculated later).

The cause of this lower productivity in non-shaded nests does not appear to be a smaller clutch size or, for the most part, death of young after hatching due to starvation, predation, or disease. In 1971 four addled Ferruginous Hawk eggs were found in three nests which also had young. All were from unshaded nests, and and all had embryos near hatching age. This substantiates the finding that brood size of Ferruginous Hawks was less than clutch size (Tables 2 and 3). It is suspected that there is a pattern of parental behavior at hatching (or some other factor) which allows unhatched eggs to be overheated by direct sunlight if they are not shaded in some way. Parental behavior is questioned since some eggs hatch. If brooding continued the same as before some of the eggs hatched, all eggs would probably hatch. Variation from year to year is probable since if hatching occurred on cloudy or otherwise cool days, this effect would be minimized. In 1971 the Ferruginous Hawks hatched during the first extended warm spell of the summer, with temperatures between 70 and 75°F

each day. The effect of the sunny, warm weather was maximized by the very synchronous hatching of all young Ferruginous Hawks in the population (see Fig. 1).

Planting trees in pure grassland areas also allows a more uniform spatial distribution of the large birds of prey while nesting, thus minimizing intra- and interspecific conflict and spreading the effect of predation more evenly. The Ferruginous Hawk will nest on the ground but rarely on the extremely flat ground like most of the pure grassland areas on the Pawnee National Grassland. In Weston's (1969) Utah study area, 52% of the Ferruginous Hawks nested on the ground, but usually on the relatively steep sides of the foothills surrounding the valley floor. In the absence of such terrain on the Pawnee, Ferruginous Hawks are virtually limited in their nesting to bluff lines, erosional remnants, and creek bottoms except where trees were planted by the early homesteaders.

With regard to Swainson's Hawks, the effect of planting trees in pure grassland areas was even greater. These hawks nested only in trees (Table 9). Thus, in the absence of trees growing in grasslands and agricultural land as the result of man's activities, the Swainson's Hawk would be restricted to creek bottoms. Today, Swainson's Hawks and probably Ferruginous Hawks utilize the Pawnee National Grassland more uniformly than before man arrived.

The question of whether the populations of these species are greater now than in previous centuries is open for debate. Many other factors necessarily enter such considerations. It can be said, however, that some of man's activities have positive effects on these raptor populations. So far raptor management on the Pawnee has been inadvertent;

the potential for purposeful and direct management indicated by these data should be exploited.

The Pawnee National Grassland as a Raptor Management Area

The concept of raptor management is new. Historically the interest has been either for total protection or for indiscriminate destruction of all falconiforms and strigiforms. The facts remain, however, that (i) all of these birds are in need of considerable pure and applied research on all aspects of their biology; (ii) most are wholly beneficial to the farmer and rancher; (iii) all are aesthetically pleasing to a growing number of people who appreciate birds and wildlife in general; and (iv) some of these birds have a recreational potential in captivity as birds for the practice of the sport of falconry. The scientist, naturalist, falconer, rancher, and farmer all have a stake in the preservation of birds of prey, yet no state game or conservation department manages a single raptor population from a position of adequate knowledge of population levels or of all types of mortality.

The Pawnee National Grassland could become America's first large-scale raptor management area through the cooperation of the Colorado Game, Fish, and Parks Division, the American Museum of Natural History, the International Biological Program, Colorado State University, the United States Forest Service, and the Bureau of Sport Fisheries and Wildlife. The reasoning behind this statement and several suggested research programs aimed at solving some basic problems of raptor management follow.

All of the agencies and institutions listed above are already directly or indirectly involved with the birds of prey of the Pawnee

National Grassland. The Colorado Game, Fish, and Parks Division has and will continue to have the responsibility of establishing the levels of use and study of these birds which are in the best interests of the birds and the people interested in them. Allowing birds to be taken from the wild for research, by zoos, and for falconry will be more easily justified to protectionists, and the perpetuation of the populations themselves will be more effectively guaranteed if a full program of raptor studies is conducted. The findings will be widely applied since such study will be a pioneering effort in raptor management.

The American Museum of Natural History has thus far invested more money than any other funding source for the collection of considerable base-line data on the birds of prey of the area. The full potential of that investment will not be realized if further funding is not made available. Having gotten the project off the ground, the American Museum is looking to other interested parties to carry the project further.

Much of the study to date involves population and productivity data in terms of individuals and biomasses as well as estimations of energy flows involving the birds of prey (to be covered in a planned paper). As an important component of the top carnivore trophic level the birds of prey must necessarily be of interest to the International Biological Program. Funding from this source would certainly yield data with which to improve predator models and general models of the dynamics of the grassland ecosystem--models at which IBP personnel are working intensively.

Colorado State University could also benefit if a long-term study was conducted. In the past, several undergraduate and graduate students have studied the raptors of the Pawnee National Grassland. These Birds still represent many potential thesis and dissertation problems, however. The supportive role of CSU will be helpful as it has been in the past.

The United States Forest Service as the agency which controls the Pawnee National Grassland would receive direct benefit from further research on land within their holdings. Improving and using the resources on such land is an accepted part of the regulatory framework of the U.S. Forest Service. To assist in regulating the use of raptors as a resource is certainly not outside that framework.

The Bureau of Sport Fisheries and Wildlife is involved directly and indirectly in large-scale, long-term study of raptors. The Golden Eagle research conducted primarily by personnel of the Bureau's Southwest Regional Office and Denver Wildlife Research Laboratory includes about 70% of the eagle eyries on the Pawnee. More importantly the Bureau's responsibilities to all raptors will increase after certain international treaties are reopened, amended, or ratified. Such legal actions are pending at this time. The proposed study would allow the Bureau to take a closer look at a collection of raptorial species and not just the federally protected eagles. Funding from the Bureau could significantly enhance the fulfillment of their developing responsibilities and would continue their long association with raptor study which began with A. K. Fisher before the turn of the century.

Thus, many people, agencies, and institutions stand to benefit. But more than that the birds of prey will benefit. As was shown by this

paper, man has had some positive effects on the birds of prey of the Pawnee at least in allowing them to utilize the grasslands more uniformly. The extent to which birds of prey use situations man has created (Table 10) provides unique opportunities for study.

The best attribute of the potential research is the grassland itself. It is large enough to set up two experimental treatments or a treatment and a control. It includes extensive federal landholdings, and the majority of private land owners are amenable to biological research. You are referred to the introduction of this paper for further discussion of the Pawnee National Grassland as a study area.

It should be pointed out, also, that the research which could be conducted there goes far beyond the usual natural history studies. The potential even surpasses quantification of population densities, productivity, and energy flow. Several additional avenues of research with an emphasis on management studies are suggested below.

1. Life table studies. One critical aspect of any raptor management program must be the development of life tables for the species involved. It will be very useful, if not mandatory, to know the life expectancy of nestling birds of prey, of raptors on their first fall and first spring migrations, and of raptors 1, 2, 3, or more years old. Without such information attempts at management will not be totally sound.

As might be expected, this kind of information is not easily obtained. It is nearly impossible to do fruitful research on life tables on a short-term basis. It requires knowing all individuals which appear in the population from year to year. Band returns, sightings of color-marked birds, and population and productivity data from a

closely studied population collected over an extended period of time form the bases for designing meaningful life tables. One must be able to deal with average nesting success. The degree of excellence represented in the results will be directly related to the number of man-hours spent in the field attempting to learn about every individual raptor present.

2. Population manipulation. Two fruitful possibilities immediately come to mind with regard to experimenting with populations. First, by constructing artificial nest structures, attempts could be made to increase existing population levels. Second, by limiting productivity to various subnormal levels, experiments could be conducted on the level of unnatural take possible with no effect on the nesting population.

The latter is vital to management efforts, and it can be explored only through long-term study. The research plan would be to control productivity at a certain number of young per nesting attempt, such as 1.5 for Ferruginous Hawks, 0.7 for Swainson's Hawks, 0.8 for Golden Eagles, 2.0 for Prairie Falcons, and 1.0 for Great Horned Owls. These levels are slightly below those established in 1971 during this study (see Table 7). In a given year this might involve bringing in young from outside the study area to bring the level up or removing birds to nests outside the study area for laboratory research, for falconry, or to zoos. The results of the follow-up would certainly need to be analyzed statistically by computer, the plans for which are already being developed.

The potential for increasing populations of birds of prey on the Pawnee National Grassland by supplying artificial nest structures has been suggested by several people. The results of the study done in

1971 points up this potential by quantitatively showing the extent to which certain birds of prey use situations man has created. Unobtrusive (to man) but practical (to hawks) nest structures could be designed and placed over extensive areas where birds of prey do not nest. Twenty-five to 50 such structures could be effectively placed immediately on the basis of 1970 and 1971 studies in the area. Such structures might be used by Ferruginous Hawks, Swainson's Hawks, Great Horned Owls, and possibly Golden Eagles. Whitewashing certain ledges and potholes on cliffs might attract more pairs of Prairie Falcons to nest. The American Kestrel nesting population could perhaps be increased 10-fold by putting up nest boxes. Currently, American Kestrel nest sites are very uncommon in grassland areas, and those areas which have suitable nest sites are usually occupied by large raptors.

As long-term study develops, other experiments will certainly be conceived. The studies briefly outlined above could easily involve 5 years of extensive study and 5 more years of follow-up. It would be fruitful to work with wintering populations as well. There is no question of the potential of the area or of the feasibility of answering some very penetrating questions.

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