J Raptor Res. 29(3):158–165

PRODUCTIVITY, FOOD HABITS, AND BEHAVIOR OF SWAINSON'S HAWKS BREEDING IN SOUTHEAST COLORADO

DAVID E. ANDERSEN[1]
U.S. Fish and Wildlife Service, Colorado Fish and Wildlife Assistance Office, 730 Simms Street, No. 290, Golden, CO 80401 U.S.A. and Department of Wildlife Ecology, University of Wisconsin, Madison, WI 53706 U.S.A.

ABSTRACT.—From 1984 through 1988, I studied Swainson's hawk (*Buteo swainsoni*) ecology during the breeding season on the Piñon Canyon Maneuver Site (PCMS) in southeast Colorado. The number of nesting attempts located and monitored annually ranged from four in 1984, to 22 in 1987. Nests used by Swainson's hawks were located predominantly in one-seed juniper (*Juniperus monosperma*) or cottonwood (*Populus* spp.) trees. Traditional nesting success estimates averaged 0.64 and ranged from 0.42 in 1985 to 1.00 in 1984. Mayfield estimates of nesting success ranged from 0.27 (1988) to 1.00 (1984). Based on prey remains collected at nest sites, food deliveries to nestlings consisted primarily of small birds (50%) and mammals (45%), and diet breadth over the 5-yr study period was high. Minimum-convex-polygon home-range size of radio-marked adults during the late-nestling and post-fledging period averaged 21.2 km^2 in 1985 and 27.3 km^2 in 1986, with males exhibiting larger home ranges than females (P = 0.15) across years. Compared with other breeding Swainson's hawk populations, breeding area reoccupancy among years on the PCMS was moderately high, home ranges during the late-nestling and post-fledging periods were large, and ground-nesting birds were important in the breeding-season diet.

KEY WORDS: Buteo swainsoni; *Colorado*; *food habits*; *home range*; *reproduction*; *Swainson's hawk.*

Productividad, hábitos alimentarios y conducta de nidificación de *Buteo swainsoni* en el sureste de Colorado

RESUMEN.—Desde 1984 a 1988, estudié la ecología de *Buteo swainsoni* durante la estación reproductiva en el Piñon Canyon Maneuver Site (PCMS), al sureste de Colorado. El número de nidificaciones localizadas y monitoreadas anualmente van desde cuatro en 1984 a 22 en 1987. Los nidos de *B. swainsoni* se localizaron predominatemente en árboles de las especies *Juniperus monosperma* y *Populus* sp. El éxito tradicional del nido fue estimado en un promedio de 0.64 y con un rango de 0.42 (1984) a 1.00 en 1984. Basado en los restos de presa colectados en los sitios de nidificación, el alimento entregado a los polluelos consistió primariamente en pequeñas aves (50%) y mamíferos (45%); la amplitud de la dieta en un período de cinco años de estudio fue alto. Durante los períodos polluelo-tardío y post-volantón (juvenil), el tamaño del rango de hogar (polígono convexo mínimo) de adultos radio-marcados fue en promedio de 21.2 km^2 en 1985 y 27.3 km^2 en 1986; los machos exhibieron mayores rangos de hogar que las hembras (P = 0.15) a través de los años. Camparando la reocupación del área de nidificación entre años en el PCMS, con otras poblaciones reproductivas de *B. swainsoni,* fue moderadamente alta; el rango de hogar durante los períodos polludelo-tardío y post-volantón fue extenso y las aves que nidificaron en el suelo fueron importantes elementos de la dieta en la estación reproductiva.

[Traducción de Ivan Lazo]

Swainson's hawks (*Buteo swainsoni*) breed primarily in grassland and other open habitats (Johnsgard 1990, Andersen 1991). Several studies of Swainson's hawk breeding season ecology have been conducted in grassland habitats (Olendorff 1972, Dunkle 1977, Gilmer and Stewart 1984). However, those studies were conducted in areas that contained a significant proportion of habitat that had been converted to crop production (e.g., irrigated meadows [Dunkle 1977], cultivated lands [Olendorff 1972], and pasture and hay fields [Gilmer and Stewart 1984]). Few studies have been conducted in largely unaltered habitats (Schmutz et al. 1980, Bednarz and Hoffman 1988), and none has been conducted in shortgrass prairie habitat lacking significant human disturbances that include crop production.

Recently, concern has been expressed regarding

[1] Current address: Minnesota Cooperative Fish and Wildlife Research Unit, U.S. National Biological Service, Department of Fisheries and Wildlife, University of Minnesota, St. Paul, MN 55108 U.S.A.

the population status of Swainson's hawks in several portions of their breeding range (Littlefield et al. 1984, Woffinden 1986, Janes 1987, Risebrough et al. 1989, Estep and Tersa 1992). The causes of population declines are not clear (Risebrough et al. 1989), although disagreement exists regarding the influence of crop production in grassland ecosystems on Swainson's hawks (Bechard 1983, Gilmer and Stewart 1984, Schmutz 1984, 1987, 1989, Schmutz and Hungle 1989, Bechard et al. 1990). To place current population levels in historical perspective and to understand the potential impact of conversion of grasslands to agricultural cultivation on breeding Swainson's hawks, information from breeding populations in relatively unaltered habitats may be useful. Herein, I describe the nesting ecology of Swainson's hawks in shortgrass prairie habitats in southeast Colorado, where the predominant land use since the late 1880s has been livestock grazing.

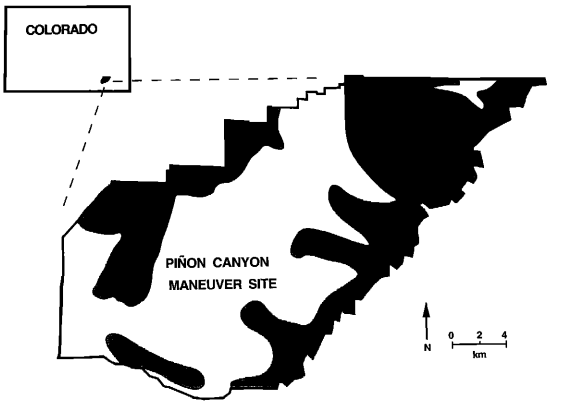

Figure 1. Location of the Piñon Canyon Maneuver Site in southeastern Colorado. Shaded areas represent the approximate extent of pinyon-juniper woodland habitats. Unshaded areas represent shortgrass prairie habitats.

STUDY AREA AND METHODS

The study was conducted on the 1040-km² Piñon Canyon Maneuver Site (PCMS) in southeast Colorado (Fig. 1) from 1984 through 1988. Elevation on the PCMS, located adjacent to the northwest rim of the Purgatoire River Canyon in Las Animas County, ranged from 1310–1740 m (U.S. Department of the Army 1980). Topography consisted of broad, moderately sloping uplands bordered by the Purgatoire River Canyon on the southeast, limestone hills on the west, and a basalt hogback on the south. Average annual precipitation on the semi-arid PCMS was 32 cm, but it fluctuated widely from year to year and among sections of the study area (U.S. Department of the Army 1980). Mean monthly temperature ranged from −1° C in January to 23° C in July.

Vegetation on the PCMS was dominated by shortgrass prairie and pinyon (*Pinus edulis*)-juniper (*Juniperus monosperma*) woodland (Costello 1954, Kendeigh 1961). Dominant perennial grass species included blue grama (*Bouteloua gracilis*), sideoats grama (*B. curtipendula*), western wheatgrass (*Agropyron smithii*), galleta (*Hilaria jamesii*), and needle-and-thread (*Stipa comata*). Dominant trees and shrubs included pinyon pine, juniper, cholla (*Opuntia imbricata*), yucca (*Yucca glauca*), fourwing saltbush (*Atriplex canescens*), broom snakeweed (*Gutierrezia sarothrae*), Bigelow sagebrush (*Artemisia bigelovii*), mountain mahogany (*Cercocarpus montanus*), winterfat (*Ceratoides* spp.), and rabbitbrush (*Chrysothamnus* sp.). For a more complete description of vegetation on the PCMS see Shaw and Diersing (1990). Predominant land use on the PCMS since settlement by people of European descent in the 1880s (Friedman 1985, Knight et al. 1989) has been livestock grazing.

I located Swainson's hawk nests by searching potential nesting habitat (e.g., isolated cottonwood [*Populus* spp.] trees and the ecotone between grassland and pinyon-juniper woodland) on foot or horseback, from a vehicle or all-terrain cycle, and from a helicopter. Locations of old stick nests and observations of Swainson's hawks during the breeding season were plotted on 1:24 000 U.S. Geological Survey topographic maps. Old nests and the immediate vicinity around where adults were sighted were searched for evidence of breeding attempts. Each year I searched the immediate vicinity of all Swainson's hawk nests that had been located in previous years. Nesting attempts and potential nest sites were also identified during productivity surveys conducted from helicopters during June and July for nesting red-tailed (*B. jamaicensis*) and ferruginous hawks (*B. regalis*).

Swainson's hawk territories on the PCMS were defined based on the presence of nesting attempts. Individual nests that were used for nesting in >1 yr were included in the same territory. In addition, different nests between and among years were included in the same territory when the distance between nest sites was smaller than the average minimum distance between nesting attempts among territories from 1984 through 1988 (N = 6 territories), or when individuals equipped with radiotransmitters nested at different nests between years (N = 3).

Accessible nests were climbed to at least once during the nestling period, except in 1987 and 1988, when only a portion of nests were visited. At each visit, nestlings were weighed and the age of nestlings (days since hatching) was estimated based on fourth primary measurements (Petersen and Thompson 1977, D.E. Andersen unpubl. data) Hatching dates were estimated from nestling age, based on a 34-d incubation period (Bednarz and Hoffman 1988).

Terminology and definitions related to reproduction follow those of Steenhof (1987). A breeding territory was identified when young were raised or eggs were laid, or an adult was observed in incubating posture on a nest. Nesting success rates were calculated using both the Mayfield and traditional methods (Mayfield 1961, 1975, Johnson 1979, Steenhof and Kochert 1982)—I used a 34-d incubation period and a 45-d nestling period (Bednarz and Hoffman 1988) in calculating Mayfield nesting success

Table 1. Number of breeding pairs, nesting success, and productivity of Swainson's hawks on the Piñon Canyon Maneuver Site, Colorado, 1984–88.

Year	Number of Pairs		Nesting Success[a]		Young Fledged/ Breeding Pair	Young Fledged/ Successful Breeding Attempt
	Breeding	Successful	Traditional	Mayfield		
1984	4	4	1.00 (4)[b]	1.00 (3)	1.75 (4)	1.75 (4)
1985	12	5	0.42 (12)	0.33 (11)	0.75 (12)	1.80 (5)
1986	15	8	0.53 (15)	0.31 (14)	0.93 (15)	1.75 (8)
1987	22	12	0.60 (20)	—	1.00 (18)	1.64 (11)
1988	7	4	0.67 (6)	0.27 (5)	0.83 (6)	1.25 (4)
Total	60	33				
Mean			0.64	0.48	1.05	1.64

[a] Terminology for nesting success is after Steenhof and Kochert (1982) and Steenhof (1987).
[b] Number of nests from which estimate was derived.

estimates. A nesting attempt was classified as successful when young were ≥50% of average fledging age when the status of the nest was last known (based on feather development and behavior) or were observed free-flying in the vicinity of the nest.

At each nest visit, prey remains were removed from the nest for identification and measurement. Prey remains were identified using guides to local fauna (Armstrong 1972, Burt and Grossenheider 1976, Hammerson 1982, National Geographic Society 1983) or by comparison to reference material collected on the PCMS. Diet breadth was calculated using Levins' (1968) formula based on frequencies across years of individual prey species in the diet, following the suggestion of Greene and Jaksić (1983). Pocket gophers (*Thomomys, Geomys*) were combined into a single group without identification to species. Birds not identified to species were excluded from diet-breadth analyses.

In 1985 and 1986, adult Swainson's hawks that were members of breeding pairs were captured using a variation of the technique described by Bloom et al. (1992). Captured birds were fitted with battery-powered, solar-assisted radiotransmitters attached as a backpack (Andersen 1994). Radio-equipped Swainson's hawks were sexed based on observation of relative size and behavior subsequent to capture.

During the period from capture through migration from the study area (approximately mid-September), Swainson's hawks equipped with transmitters were located and followed for 3–4-hr tracking periods, with locations recorded at 0.5 hr intervals (Andersen and Rongstad 1989). Individual birds were tracked in either the morning or the afternoon at approximately 7–10-d intervals systematically through the study period (Andersen and Rongstad 1989). Fixes were obtained by a single observer during a tracking period and were either based on visual observation or triangulation from telemetry signals. Fixes based only on telemetry signals were obtained by a single observer receiving signals from more than two locations in sequence and plotting signal direction on 1:24 000 topographic maps. Universal transverse mercator grid coordinates were recorded from 1:24 000 topographic maps of the study area to the nearest 100 m for each radio fix, and the behavior (perched or flying) of the bird and whether the fix was based on visual observation or telemetry signal were noted Minimum convex polygon (MCP) home ranges were calculated for the late-nestling and post-fledging period using the computer program SEAS (J.R. Cary, University of Wisconsin, Madison). All sequential locations were included in MCP analyses (Andersen and Rongstad 1989)

Descriptive statistics, pairwise statistical tests, and analysis of variance (ANOVA) procedures follow those outlined in Snedecor and Cochran (1980). Chi-square tests for independence are after Gibbons (1985).

Results

Reproduction. The number of breeding territories on the PCMS ranged from four in 1984 to 22 in 1987 (Table 1). Traditional nesting success averaged 0.64 (coefficient of variation [c.v.] = 0.34), and the average age of young in the nest at the last time when the nest status was known ranged from 65–80% of fledging age. Mayfield estimates of nesting success averaged 0.48 (c.v. = 0.73). Young fledged per successful breeding attempt averaged 1.64 and exhibited little variation (c.v. = 0.14) among years. Estimated hatching dates were concentrated in mid- to late June, and extended into July in 1984, 1986, and 1988. No differences in hatching dates were evident among years (1-way ANOVA, $F_{3,19} = 0.51$, $P = 0.680$).

A total of 34 territories and 60 nests were identified on the PCMS from 1984 through 1988. Swainson's hawk nests were primarily located in junipers (76% of 60 nests) and cottonwoods (15%), with four of the remaining nests in elms (*Ulmus* sp.) planted

Table 2. Number and frequency of occurrence of prey remains collected at 20 Swainson's hawk nest sites on the Piñon Canyon Maneuver Site, Colorado, 1984–87.

Species	Year				Total	
	1984	1985	1986	1987	Number	%
Birds						
Western meadowlark (*Sturnella neglecta*)	2	1	1	3	7	11.7
Horned lark (*Eremophila alpestris*)	6	0	0	0	6	10.0
Mourning dove (*Zenaida macroura*)	1	0	0	2	3	5.0
Scaled quail (*Callipepla squamata*)	0	1	0	0	1	1.7
Lark bunting (*Calamospiza melanocorys*)	0	0	0	1	1	1.7
Unidentified birds	1	8	1	2	12	20.0
Total Birds	10	10	2	8	30	50.0
Mammals						
Pocket gophers (Geomyidae)	3	9	9	0	21	35.0
Spotted ground squirrel (*Spermophilus spilosoma*)	1	0	1	0	2	3.3
Ord's kangaroo rat (*Dipodomys ordii*)	0	2	0	0	2	3.3
Desert cottontail (*Sylvilagus audubonii*)	0	1	0	1	2	3.3
Total Mammals	4	12	10	1	27	45.0
Reptiles						
Eastern fence lizard (*Sceloporus undulatus*)	0	0	1	0	1	1.7
Texas horned lizard (*Phrynosoma cornutum*)	0	0	1	0	1	1.7
Unidentified snake	0	0	1	0	1	1.7
Total Reptiles	0	0	3	0	3	5.0
Total	14	22	15	9	60	100.0

as windbreaks, and one in a pinyon pine. When I compared the proportion of territories where different nest structures were used, Swainson's hawks predominantly used territories with junipers (73% of 34 territories) and cottonwoods (12%) as nest sites (2 [6%] additional territories had nests in both junipers and cottonwoods in different years). Nearest-neighbor distances between nests ranged from 3.4 km in 1987 to 9.2 km in 1984, and averaged 5.6 km over the 5-yr study period. On average, nesting attempts were located in territories 55% of the years that they were monitored when including the year that territories were first identified, and 31% of years subsequent to the year they were first identified.

Food Habits. A total of 60 prey remains was collected from 20 nest sites on 12 breeding territories from 1984 through 1987 (Table 2). No prey remains were encountered at nests in 1988. Fifty percent of prey items encountered were birds, 45% were mammals, and the remaining 5% were lizards and snakes. Excluding reptiles ($N = 3$), the relative frequencies of birds and mammals in prey remains were not independent of year ($\chi^2 = 13.41$, df = 3, $P < 0.005$) and diet breadth for all years combined was relatively high (B = 6.52).

Home Range and Movements. Six Swainson's hawks were captured and fitted with radio transmitters. Two of those individuals returned to the study area the year following capture with functioning radios, and were radiotracked during two breeding seasons. The remaining individuals were tracked during one breeding season (Table 3). Individual hawks were monitored for an average of 6.5 tracking periods per season, resulting in an average of 57 locations per bird. Locations were obtained based on direct visual observation (30.4%), extrapolation from an immediately preceding or subsequent direct visual observation (18.7%), extrapolation within a tracking period where the bird was observed at least once (28.3%) but not immediately preceding or subsequent to the fix, or only on reception of a telemetry signal (22.6%).

Combining MCP estimates from both males and females, home range size averaged 21.3 km^2 in 1985 and 27.3 km^2 in 1986 ($t = -0.74$, df = 5, $P = 0.49$). Males ($\bar{x} = 31.7$ km^2) tended to have larger home

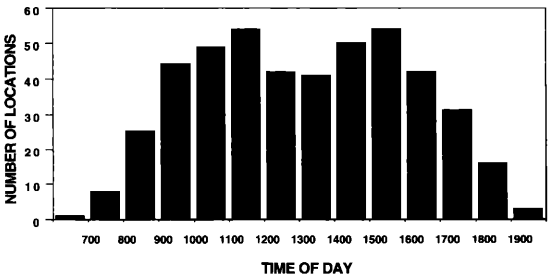

Figure 2. Radio-telemetry locations for six Swainson's hawks captured and monitored in southeastern Colorado from 1986–87 as a function of time of day.

ranges than females ($\bar{x}$ = 19.9 km^2), both when MCP area for each breeding season and each year were treated as independent observations (t = 1.69, df = 6, P = 0.15), and when I calculated an average MCP home range size for the two females that were tracked in both 1985 and 1986 (t = 2.21, df = 4, P = 0.16).

The proportions of locations obtained in each 1-hr time interval from 0800–1800 H when all locations from all tracking periods were combined, were not distributed significantly differently from random (χ^2 = 14.08, df = 9, $P > 0.05$). Sampling intensity prior to 0800 and after 1800 was not comparable to intensity during that time interval (Fig. 2). During the periods that radio-marked birds were monitored, both males ($\bar{x}$ = 83% of locations) and females ($\bar{x}$ = 72% when calculated as independent observations and $\bar{x}$ = 71% when based on between-year averages), spent the majority of their time flying.

DISCUSSION

Reproduction. Swainson's hawks nesting in shortgrass prairie habitat in southeast Colorado from 1984 through 1988 exhibited moderate nesting success and stable productivity. The number of nesting attempts located annually was highly variable. These results are comparable to descriptions of reproductive parameters from other portions of the breeding range of Swainson's hawks, where the mean number of young fledged per successful nest ranged from 1.19–2.00, and the mean number of young fledged per breeding pair ranged from 1.11–1.85 (Olendorff 1972, Dunkle 1977, Fitzner 1978, Bednarz and Hoffman 1988). As has been noted in other raptors (e.g., tawny owls [*Strix aluco*; Southern 1970]; great horned owls [*Bubo virginianus*; Rusch et al. 1972, McInvaille and Keith 1974]; ferruginous hawks [Smith et al. 1981]), the most highly variable reproductive parameter for Swainson's hawks on the PCMS appeared to be the proportion of pairs that attempted nesting.

Table 3. Tracking history, behavior, and post-fledging season home range size of adult radio-equipped Swainson's hawks on the Piñon Canyon Maneuver Site, Colorado 1985–86.

	Identification		No. of Tracking Periods	Total No. of Locations	% of Locations Flying	MCP Home Range (km^2)
Year	Number	Sex				
1985	8	F	8	64	78	24.4
	17	M	7	67	87	23.8
	10	F	4	31	84	6.8
	18	M	7	62	92	30.0
1986	8	F	7	69	55	12.1
	10	F	7	63	81	34.2
	26	M	6	52	71	41.3
	30	F	6	52	63	21.7

It is not clear from this study, however, whether all territories were occupied annually, even in the absence of a nesting attempt, or whether the PCMS population of Swainson's hawks tracked local prey populations, as has been suggested elsewhere (Schmutz and Hungle 1989). Similar to other temperate-zone raptors, the number of young fledged per successful nesting attempt was relatively stable over the 5-yr period (Newton 1979), suggesting that breeding conditions in territories that fledged young were relatively constant among years, or that successful breeders adjusted to changing conditions. There was no evidence for brood reduction, observed in other areas in response to low prey availability (Bechard 1983).

Food Habits. Based on frequency of prey remains collected at nest sites from 1984 through 1987, Swainson's hawks on the PCMS preyed heavily on ground-nesting birds and small mammals (Table 2). These food habits differ from those reported in most other published studies in that birds comprised a high proportion of the diet, compared to the reported predominance of small and medium-sized mammals

in other locations. In Wyoming, Dunkle (1977) reported that 68% of prey items were small mammals and lagomorphs and in Utah, Smith and Murphy (1973) reported that only 17% of prey items were birds. In North Dakota, Gilmer and Stewart (1984) found that ground squirrels and pocket gophers constituted the majority of prey items of nesting Swainson's hawks. Similarly, Schmutz et al. (1980) reported that prey items of nesting Swainson's hawks in Alberta consisted of 85% mammals, 67% of prey items removed from Swainson's hawk nests in Montana were mammals (Restani 1991), and small mammals were the predominant prey of Swainson's hawks in Washington (Bechard 1983). In Mexico, Thiollay (1981) observed lizards and small rodents as the primary prey species of nesting Swainson's hawks, and in New Mexico, nesting Swainson's hawks preyed predominantly on insects and lagomorphs (Bednarz 1988, Bednarz and Hoffman 1988). In contrast, in California, Swainson's hawks have been observed to include birds as the predominant prey in the breeding-season diet (Estep 1989).

Although sample size (60 items from 20 nest sites over 4 yr) was small, Swainson's hawks on the PCMS appeared to have a relatively broad diet. Diet breadth of Swainson's hawks on the PCMS compares with that of red-tailed hawks in Idaho, the species with the most general diet of three large breeding raptors studied by Steenhof and Kochert (1988). High diet breadth of Swainson's hawks on the PCMS is in large part attributable to high variability in food items collected among years (Table 2).

Home Range and Movements. Estimated home range sizes of adult Swainson's hawks during the late-nestling and post-fledging periods on the PCMS were similar to home ranges reported from other comparable studies. Radio-equipped male Swainson's hawks in Washington exhibited an average home range size of 8.9 km^2 (Bechard 1982). In California, Estep (1989) observed home ranges averaging 27.6 km^2 for 12 radio-marked Swainson's hawks during the breeding season. On the PCMS, Swainson's hawks had relatively large home ranges, similar in size to those reported in California, and spent the majority of their time budget flying.

Two potential sources of error in calculating home range size were present in data collected in this study. First, because Swainson's hawks on the PCMS spent the majority of their time flying, estimating fixes precisely, even when birds were observed, was difficult. Second, 22.6% of fixes were obtained via sequential triangulation from the ground by one observer. I was unable to estimate the magnitude of the error associated with either of these two sources. However, neither of these sources of error likely introduced bias into estimates of average home range size of Swainson's hawks on the PCMS. Rather, these sources of error probably increased the variance associated with average home range size estimates, reducing the power of statistical comparisons.

Breeding Season Ecology. Ecology of Swainson's hawks breeding in shortgrass prairie habitat in southeast Colorado may be characterized as intermediate between raptors that are territorial year round, and those that are nomadic and exhibit numerical responses to temporary prey abundance in localized areas. Swainson's hawks return to the breeding grounds after potential competitors for nest sites (e.g., red-tailed and ferruginous hawks and great horned owls) have already initiated nesting. They establish territories that are defended against conspecifics and may defend these territories against other species of raptors (Rothfels and Lein 1983, Janes 1984, Bechard et al. 1990, Restani 1991), or alternatively, nest in association with other raptors (Schmutz et al. 1980, Thurow and White 1983). On the PCMS, late-nestling and post-fledging period home range (and possibly breeding territory) size appears to be relatively large, and there is a moderate rate of breeding territory reoccupancy and high variability in the number of nesting attempts initiated among years. Reproductive success is moderately variable, and productivity of successful nests is relatively high and stable.

This reproductive strategy may in large part be explained in terms of annual variability in prey resources. Prey availability that is unpredictable and highly variable may result in birds establishing or reoccupying territories annually, but only breeding in years in which prey availability is above a minimum threshold (Southern 1970). Above this threshold, nest success may be influenced by density-independent factors (e.g., weather), which cause failure of the nesting attempt rather than reducing brood size. Whether this reproductive strategy was typical of Swainson's hawks across the breeding range prior to extensive human-induced changes in landscape patterns is not clear. However, reproductive ecology of Swainson's hawks on the PCMS can serve as a basis for comparison for other populations of Swainson's hawks in areas where grasslands have in part or in whole been converted to crop production.

ACKNOWLEDGMENTS

Support for this study was provided by the U.S. Army, Directorate of Environmental Compliance and Management, Fort Carson, Colorado, through the U.S. Fish and Wildlife Service (Colorado Fish and Wildlife Assistance Office and the Wisconsin Cooperative Wildlife Research Unit). Support was also provided by the College of Agricultural and Life Sciences, the Graduate School, and the Department of Wildlife Ecology at the University of Wisconsin-Madison. I thank W.R. Mytton, T.S. Prior, S.R. Emmons, A. Pfister, B.D. Rosenlund, and T.L. Warren, who helped coordinate the project on military property and O.J. Rongstad for invaluable guidance and assistance. Field assistance was provided by W.R. Mytton, S.R. Emmons, G.M. Hughes, W.P. Fassig, E.H. Valentine, T.R. Laurion, A. Doroff, and D.J. Grout. The comments of M.N. Kochert and an anonymous reviewer improved the manuscript considerably.

LITERATURE CITED

ANDERSEN, D.E. 1991. Management of North American grasslands for raptors. Pages 203–210 *in* B.A. Giron Pendleton, D.L. Krahe, M.N. LeFranc, Jr., K. Titus, J.C. Bednarz, D.E. Andersen and B.A. Millsap [EDS.], Proceedings of the midwest raptor management symposium and workshop. Natl. Wildl. Fed. Sci. Tech. Ser. No. 15, Washington, DC U.S.A.

———. 1994. Longevity of solar-powered radio-transmitters on buteonine hawks in eastern Colorado. *J. Field Ornithol.* 65:122–132.

——— AND O.J. RONGSTAD. 1989. Home-range estimates of red-tailed hawks based on independent and systematic relocations. *J. Wildl. Manage.* 53:802–807.

ARMSTRONG, D.M. 1972. Distribution of mammals in Colorado. Mus. Nat. Hist., Univ. Kansas, Monogr. No. 3.

BECHARD, M.J. 1982. Effect of vegetative cover on foraging site selection by Swainson's hawk. *Condor* 84: 153–159.

———. 1983. Food supply and the occurrence of brood reduction in Swainson's hawk. *Wilson Bull.* 95:233–242.

———, R.L. KNIGHT, D.G. SMITH AND R.E. FITZNER. 1990. Nest sites and habitats of sympatric hawks (*Buteo* spp.) in Washington. *J. Field Ornithol.* 61:156–170.

BEDNARZ, J.C. 1988. A comparative study of the breeding ecology of Harris' and Swainson's hawks in southeastern New Mexico. *Condor* 90:311–323.

——— AND S.W. HOFFMAN. 1988. The status of breeding Swainson's hawks in southeastern New Mexico. Pages 253–259 *in* R.L. Glinski, B.A. Giron Pendleton, M.B. Moss, M.N. LeFranc, Jr., B.A. Millsap and S.W. Hoffman [EDS.], Proceedings of the southwest raptor management symposium and workshop. Natl. Wildl. Fed. Sci. Tech. Ser. No. 11, Washington, DC U.S.A.

BLOOM, P.H., J.L. HENCKEL, E.H. HENCKEL, J.K. SCHMUTZ, B. WOODBRIDGE, J.R. BRYAN, R.L. ANDERSON, P.J. DETRICH, T.L. MAECHTLE, J.O. MCKINLEY, M.D. MCCRARY, K. TITUS AND P.F. SCHEMPF. 1992. The *dho-gaza* with great horned owl lure: an analysis of its effectiveness in capturing raptors. *J. Raptor Res.* 26:167–178.

BURT, W.H. AND R.P. GROSSENHEIDER. 1976. A field guide to the mammals. Houghton Mifflin Co., Boston, MA U.S.A.

COSTELLO, D.F. 1954. Vegetation zones in Colorado. Pages iii–x *in* H.D. Harrington. Manual of the plants of Colorado. Sage Books, Denver, CO U.S.A.

DUNKLE, S.W. 1977. Swainson's hawks on the Laramie Plains, Wyoming. *Auk* 94:65–71.

ESTEP, J.A. 1989. Biology, movements, and habitat relationships of the Swainson's hawk in the Central Valley of California, 1986–87. Calif. Dept. Fish and Game, Nongame Bird and Mammal Sec. Rep., Sacramento, CA U.S.A.

——— AND S. TERSA. 1992. Regional conservation planning for the Swainson's hawk (*Buteo swainsoni*) in the Central Valley of California. Pages 775–789 *in* D.R. McCullough and R.H. Barrett [EDS.], Wildlife 2001: populations. Jones and Stokes Assoc., Inc., Sacramento, CA U.S.A.

FITZNER, R.E. 1978. The ecology and behavior of the Swainson's hawk (*Buteo swainsoni*) in southeastern Washington. Ph.D. dissertation, Washington State Univ., Pullman, WA U.S.A.

FRIEDMAN, P.D. 1985. Final report of history and oral history studies of the Fort Carson Piñon Canyon Maneuver Area, Las Animas County, Colorado. Powers Elevation Corp., Denver, CO U.S.A.

GIBBONS, J.D. 1985. Nonparametric methods for quantitative analysis. Am. Sciences Press, Inc., Columbus, OH U.S.A.

GILMER, D.S. AND R.E. STEWART. 1984. Swainson's hawk nesting ecology in North Dakota. *Condor* 86:12–18.

GREENE, H.W. AND F.M. JAKSIĆ. 1983. Food-niche relationships among sympatric predators: effects of level of prey identification. *Oikos* 40:151–154.

HAMMERSON, G.A. 1982. Amphibians and reptiles in Colorado. Colo. Div. Wildl. Denver, CO U.S.A.

JANES, S.W. 1984. Influences of territory composition and interspecific competition on red-tailed hawk reproductive success. *Ecology* 65:862–870.

———. 1987. Status and decline of Swainson's hawks in Oregon: role of habitat and interspecific competition. *Oreg. Birds* 13:165–179.

JOHNSGARD, P.A. 1990. Hawks, eagles, and falcons of North America: biology and natural history. Smithsonian Inst. Press, Washington, DC U.S.A.

JOHNSON, D.H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* 96:651–661.

KENDEIGH, S.C. 1961. Animal ecology. Prentice-Hall, Englewood Cliffs, NJ U.S.A.

KNIGHT, R.L., D.E. ANDERSEN, M.J. BECHARD AND N.V. MARR. 1989. Geographic variation in nest-defence behaviour of the red-tailed hawk *Buteo jamaicensis*. *Ibis* 131:22–26.

LEVINS, R. 1968. Evolution in changing environments. Princeton Univ. Press, Princeton, NJ U.S.A.

LITTLEFIELD, C.D., S.P. THOMPSON AND B.D. EHLERS. 1984. History and present status of Swainson's hawks in southeast Oregon. *Raptor Res.* 18:1–5.

MAYFIELD, H. 1961. Nesting success calculated from exposure. *Wilson Bull.* 73:255–261.

———. 1975. Suggestions for calculating nest success. *Wilson Bull.* 87:456–466.

MCINVAILLE, W.B. AND L.B. KEITH. 1974. Predator-prey relations and breeding biology of the great horned owl and red-tailed hawk in central Alberta. *Can. Field-Nat.* 88:1–20.

NATIONAL GEOGRAPHIC SOCIETY. 1983. Field guide to the birds of North America. Natl. Geographic Soc., Washington, DC U.S.A.

NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, SD U.S.A.

OLENDORFF, R.R. 1972. The large birds of prey of the Pawnee National Grassland: nesting habits and productivity, 1969–1971. Tech. Rep. 151, U.S. Internat. Biome Program, Grassland Biome, Fort Collins, CO U.S.A.

PETERSEN, L.R. AND D.R. THOMPSON. 1977. Aging nestling raptors by 4th primary measurements. *J. Wildl. Manage.* 41:587–590.

RESTANI, M. 1991. Resource partitioning among three *Buteo* species in the Central Valley, Montana. *Condor* 93:1007–1010.

RISEBROUGH, R.W., R.W. SCHLORFF, P.H. BLOOM AND E.E. LITTRELL. 1989. Investigations of the decline of Swainson's hawk populations in California. *J. Raptor Res.* 23:63–71.

ROTHFELS, M. AND M.R. LEIN. 1983. Territoriality in sympatric populations of red-tailed and Swainson's hawks. *Can. J. Zool.* 61:60–64.

RUSCH, D.H., E.C. MESLOW, P.D. DOERR AND L.B. KEITH. 1972. Responses of great horned owl populations to changing prey density. *J. Wildl. Manage.* 36: 282–296.

SCHMUTZ, J.K. 1984. Ferruginous and Swainson's hawk abundance and distribution in relation to land use in southeastern Alberta. *J. Wildl. Manage.* 48:1180–1187.

———. 1987. The effect of agriculture on ferruginous and Swainson's hawks. *J. Range Manage.* 40:438–440.

———. 1989. Hawk occupancy of disturbed grasslands in relation to models of habitat selection. *Condor* 91· 362–371.

——— AND D.J. HUNGLE. 1989. Populations of ferruginous and Swainson's hawks increase in synchrony with ground squirrels. *Can. J. Zool.* 67:2596–2601.

———, S.M. SCHMUTZ AND D.A. BOAG. 1980. Coexistence of three species of hawks (*Buteo*. spp.) in the prairie-parkland ecotone. *Can. J. Zoology* 58:1075–1089

SHAW, R.B. AND V.E. DIERSING. 1990. Tracked vehicle impacts on vegetation at the Pinyon Canyon Maneuver Site, Colorado. *J. Environ. Qual.* 19:234–243.

SMITH, D.G. AND J.R. MURPHY. 1973. Breeding ecology of raptorial birds in the eastern Great Basin Desert of Utah. Brigham Young Univ. Biol. Ser. 18:1–76. Provo, UT U.S.A.

———, J.R. MURPHY AND N.D. WOFFINDEN. 1981 Relationships between jackrabbit abundance and ferruginous hawk reproduction. *Condor* 83:52–56.

SNEDECOR, G.W. AND W.G. COCHRAN. 1980. Statistical methods. W.H. Freeman and Co., New York, NY U.S.A.

SOUTHERN, H.N. 1970. The natural control of a population of tawny owls. *J. Zool., Lond.* 162:197–285.

STEENHOF, K. 1987. Assessing raptor reproductive success and productivity. Pages 157–170 *in* B.A. Giron Pendleton, B.A. Millsap, K.W. Cline and D.M. Bird [EDS.], Raptor management techniques manual. Natl. Wildl. Fed. Sci. Tech. Series No. 10, Washington, DC U.S.A.

——— AND M.N. KOCHERT. 1982. An evaluation of methods used to estimate raptor nesting success. *J. Wildl Manage.* 46:885–893.

——— AND ———. 1988. Dietary responses of three raptor species to changing prey densities in a natural environment. *J. Anim. Ecol.* 57:37–48.

THIOLLAY, J. 1981. Ségrégation écologique et pression de prédation de deux buses sympatrique dans un désert mexicain. *Gerfaut* 71:575–610.

THUROW, T.L. AND C.M. WHITE. 1983. Nest site relationship between the ferruginous hawk and Swainson's hawk. *J. Field Ornithol.* 54:401–406.

U.S. DEPARTMENT OF THE ARMY. 1980. Draft: Environmental impact statement for acquisition of training land in Huerfano, Las Animas and Pueblo Counties, Colorado. U.S. Army Corps of Engineers, Omaha District, Omaha, NE U.S.A.

WOFFINDEN, N.D. 1986. Notes on the Swainson's hawk in central Utah: insectivory, premigratory aggregations, and kleptoparasitism. *Great Basin Nat.* 46:302–304.

Received 12 December 1994; accepted 30 May 1995