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FOOD SUPPLY AND THE OCCURRENCE OF BROOD REDUCTION IN SWAINSON'S HAWK

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The adaptive significance of hatching asynchrony has received considerable attention over the past two decades (Ingram 1959; Ricklefs 1965; Lack 1966; Skutch 1967; Bryant 1975; Proctor 1975; Newton 1977, 1979). Arguments, based primarily on Lack's (1966) food-limited hypothesis, suggest that it gives species dependent on irregular or unpredictable food sources a means of adjusting reproductive effort to prevailing food supplies. The consensus is that hatching asynchrony gives older, more developed nestlings a survival advantage during periods of limited food by increasing the chances they will eliminate late-hatched chicks through starvation or fratricide and thereby prevent their own demise. The hypothesis has been criticized for its apparent wastefulness (Ricklefs 1968, Hussel 1972, Proctor 1975, O'Connor 1977), but if one considers the inclusive fitness of all nestlings, it may have adaptive value (O'Connor 1978, Stinson 1979).

Food-related incidences of brood reduction supporting the theory have been reported in a number of species (Ricklefs 1965, Nisbet and Cohen 1975, Parsons 1975, Proctor 1975). Although brood reduction has been observed at many raptor nests (Ingram 1959, 1962; Heintzelman 1966; Clevenger and Roest 1974; Meyburg 1974; Stinson 1979), data linking its occurrence with limited food supply are lacking. Possible and confirmed records of fratricide and cannibalism have been reported at nests of Swainson's Hawk (*Buteo swainsoni*) (Pilz 1976; Parker 1976, 1979; Pilz and Seibert 1978; Newton 1979), for example, but none have been linked with food supply. Here, I use nestling weight as an index of nestling food supply to demonstrate the relationship between limited food availability and the occurrence of brood reduction in this species.

STUDY AREA AND METHODS

The study was conducted in southeastern Washington in an approximately 4200-km^2 area of Whitman and Garfield counties (Bechard 1980). The native habitat once consisted of shrub-steppe vegetation (Daubenmire 1970). Because of agriculture, only small patches of native habitat remain in creek bottoms and on steep terrain, and large expanses of cropland planted in wheat, peas, barley, and lentils now dominate the landscape.

The climate is characterized by moderately cold, wet winters and hot, dry summers. Mean temperature for the coldest month (January) ranges from −5.5–1.5°C while the hottest month (August) ranges from 18.5–24.5°C. Rainfall averages from 35.5–63.5 cm per year. During the study, precipitation was average in 1978 and 1979, but a drought occurred in 1977 when monthly precipitation was well below average from January through April. The drought reduced vegetative cover in cropland and yeilds were as much as 50% below average.

The study area was searched from 1976 through 1979 for Swainson's Hawk nests. Information concerning nest-sites was also obtained from a survey of local Audubon Society members and Washington State Department of Game personnel. Nests were considered active if a pair of Swainson's Hawks were present and if there was evidence of nest-building activity. Each nest was classified as being in either grazed or cultivated habitat by using the dominant form of land use in surrounding habitats.

Three weeks after the start of incubation, I determined clutch-size using a mirror attached to a telescoping 12-m aluminum pole. After hatching was completed, nest trees were climbed every 5 days to determine brood-size at hatching, nestling mortality, and nestling weight gain. Nestling weight was obtained to the nearest 5 g using a 1000 g Pesola spring balance.

Forty-one of the 87 nestlings studied were found either while hatching or obviously within their first 24 h of life; these were therefore of known age. Other nestlings were aged by back-dating from the average hatching interval of 2 days (Bent 1961; Parker 1976; Pilz and Seibert 1978; Fitzner 1980; Bechard, unpubl.) using known-age nestlings as references. I considered this aging method to be accurate within 1 day. To identify young in nests, I used fingernail polish to mark the talons of very young chicks, later substituting individually numbered U.S. Fish and Wildlife Service leg bands.

To determine nestling diets, castings and prey remains were noted and/or collected from each nest. Remains were identified using skull fragments, lower jaws, claws, hair, and feathers. Relative percent frequency estimates were calculated for each prey taxon based on the total number of individuals identified (Curtis and McIntosh 1950).

RESULTS

I observed 87 nest attempts at 44 Swainson's Hawk nests during the 4-year study and obtained data for an additional nine nests observed in 1975 (Fitzner 1977). Some of the nests were in habitats grazed by livestock, but most occurred in areas of crop cultivation. Over 75% were in black locust (*Robinia pseudoacacia*) at an average height of 9.9 ± 4.7 m (range 3.5–27.1 m). Nests contained an average of 2.66 ± 0.47 eggs (range 2.37–2.9, N = 33) (Table 1). Ninety-three percent of the eggs hatched to produce broods averaging 2.36 ± 0.11 (range 2.0–3.15) nestlings per nest. Fledging success averaged 1.11 ± 0.06 (range 0.67–2.21) young per active nest. Compared to averages of 1.5–2.0 young per nest reported by Olendorff (1973), Smith and Murphy (1973), Keir (1976), Dunkle (1977), and Fitzner (1977), my data indicated a relatively low level of nesting success.

Estimates of clutch-size, brood-size, and fledging success varied from year-to-year. Kruskal-Wallis 1-way ANOVA, however, showed that only estimates of fledging success varied significantly ($\chi^2 = 4.82$, df = 4, $P \leqslant 0.05$). All three estimates also tended to be smaller in cultivated than grazed habitats, but only the differences in fledging success were significant (Wilcoxon two-sample test, $U_s = 1105$, $N_1 = 56$, $N_2 = 31$, $P \leqslant 0.05$).

Decreased fledging success in 1978 and 1979 resulted from high nestling mortality, particularly in cultivated habitats (Fig. 1). Mortality occurred

TABLE 1

PRODUCTIVITY OF SWAINSON'S HAWK NESTS IN GRAZED AND CULTIVATED HABITATS IN SOUTHEASTERN WASHINGTON

Year	Habitat	$\bar{x} \pm$ SE clutch-size	$\bar{x} \pm$ SE brood-size	$\bar{x} \pm$ SE no. young per active nest
1975[a]	Overall	—	—	0.67 (9)[b]
1976	Cultivated	—	2.0 (2)	0.66 (3)[c,d]
	Grazed	—	2.0 (2)	1.0 (2)[c]
	Overall	—	2.0 (4)	0.83 ± 0.20 (5)[c]
1977	Cultivated	2.72 ± 0.13 (11)[b]	2.54 ± 0.12 (11)[b]	2.41 ± 0.12 (12)
	Grazed	3.15 ± 0.17 (6)	3.15 ± 0.17 (6)	2.00 ± 0.24 (7)
	Overall	2.90 ± 0.11 (17)	2.76 ± 0.14 (17)	2.21 ± 0.12 (19)
1978	Cultivated	2.30 ± 0.17 (9)	2.11 ± 0.11 (9)	0.63 ± 0.18 (19)
	Grazed	2.42 ± 0.19 (7)	2.28 ± 0.19 (7)	0.88 ± 0.20 (9)
	Overall	2.37 ± 0.12 (16)	2.18 ± 0.10 (16)	0.75 ± 0.16 (28)
1979	Cultivated	2.57 ± 0.13 (14)	2.35 ± 0.13 (14)	0.95 ± 0.11 (22)
	Grazed	3.00 ± 0 (7)	2.85 ± 0.11 (7)	1.30 ± 0.20 (13)
	Overall	2.71 ± 0.10 (21)	2.52 ± 0.11 (21)	1.12 ± 0.15 (35)

[a] Taken from Fitzner (1977).
[b] Number of nests observed.
[c] Annual means significantly different (Kruskal-Wallis 1-way ANOVA, $P \leq 0.05$).
[d] Means in grazed and cultivated habitats significantly different (Wilcoxon two-sample test, $P \leq 0.05$).

when nestlings were from 15–30 days of age and was most frequent when they were between 20 and 25 days old. I could not determine if deaths resulted from starvation or fratricide at all nests, but the bloody heads of live birds indicated that fratricide may be a common cause of death. Partially eaten young were found in 10 of 16 nests in 1978 and in 15 of 26 nests in 1979. In all of these cases it was the youngest nestling that died; at two of four nests in 1978 and 4 of 10 nests in 1979 that started with broods of three young, further brood reduction occurred when the second youngest nestling died. Only four incidences of brood reduction occurred in 1977. All involved the deaths of youngest nestlings and all but one took place in cultivated habitats.

Diets of nestling hawks consisted primarily of small rodents (Table 2). Northern pocket gophers were the most frequently consumed prey, especially in grazed habitats. In cultivated habitats, gophers were the most common dietary constituent in 1978, but in 1977 and 1979 deer mice and voles were more common dietary items. Columbian ground squirrels and birds were consumed but they remained of minor dietary importance throughout the study.

Assuming that the survival of nestling Swainson's Hawks would be high-

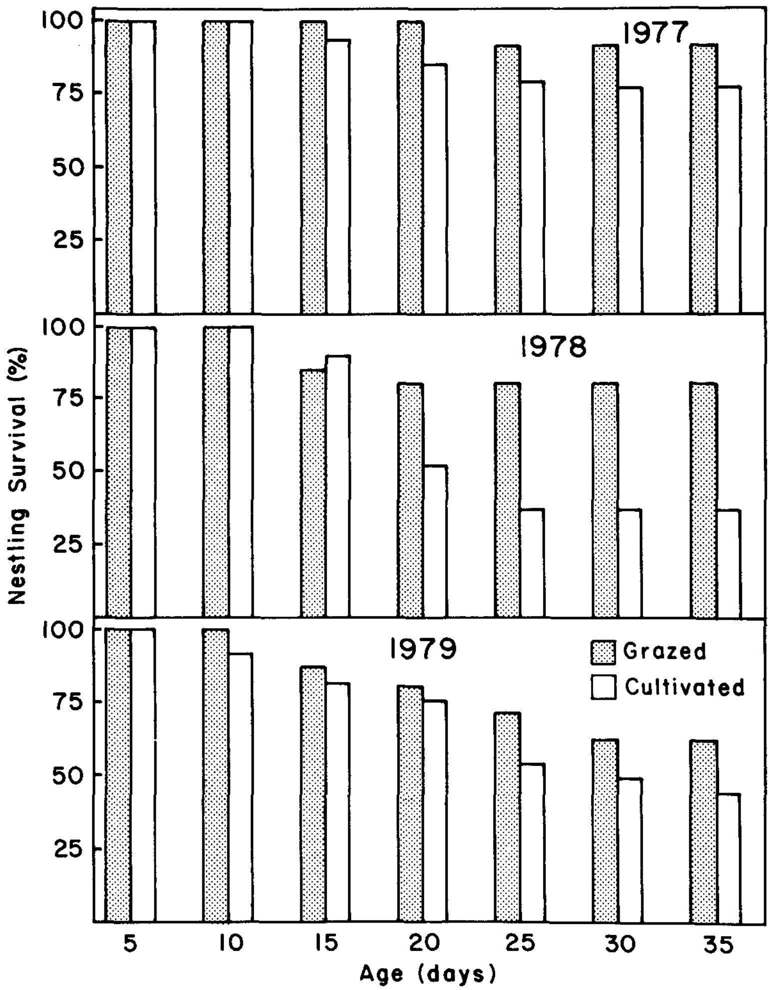

FIG. 1. Nestling survival in grazed and cultivated habitats of southeastern Washington during 1977, 1978, and 1979; same sizes as indicated in Fig. 2.

ly correlated with food supply, I weighed nestlings to obtain an index of the amount of food fed to them (Fig. 2). Twenty-nine, 21, and 37 nestlings were weighed at the start of brood periods in 1977, 1978, and 1979, respectively. Nestling weights were similar in grazed and cultivated habitats in 1977 when fledging success was high, but when success was low in 1978 and 1979, weights were lower in cultivated habitats. Decreased weight was

TABLE 2

THE DIETS OF NESTLING SWAINSON'S HAWKS IN GRAZED AND CULTIVATED HABITATS OF SOUTHEASTERN WASHINGTON, 1977–1979

Prey species	Grazed habitat % frequency[a]			Cultivated habitat % frequency		
	1977	1978	1979	1977	1978	1979
Small mammals	86	67	61	90	76	72
Northern pocket gopher (*Thomomys talpoides*)	46	72	65	33	57	33
Mountain vole (*Microtus montanus*)	19	11	9	21	16	12
Deer mouse (*Peromyscus maniculatus*)	31	11	9	46	22	47
Columbian ground squirrel (*Citellus columbianus*)	—	6	15	—	4	7
Desert cotton-tail rabbit (*Sylvilagus audubonii*)	—	—	2	—	1	2
Long-tailed weasel (*Mustella frenata*)	4	—	—	—	—	—
Birds	11	26	30	10	23	25
Ring-necked Pheasant (*Phasianus colchicus*)	—	72	88	60	54	95
Hungarian Partridge (*Perdix perdix*)	25	—	—	—	4	5
Black-billed Magpie (*Pica pica*)	75	14	6	40	14	—
Western Meadowlark (*Sturnella neglecta*)	—	—	—	—	10	—
Horned Lark (*Eremophila alpestris*)	—	—	—	—	4	—
House Sparrow (*Passer domesticus*)	—	14	—	—	4	—
Eurasian Starling (*Sturnus vulgaris*)	—	—	—	—	10	—
Short-eared Owl (*Asio flammeus*)	—	—	6	—	—	—
Reptiles	3	7	9	—	1	2
Gopher snake (*Pituophis melanoleucus*)	100	100	100	—	100	100
Insects	—	—	—	—	—	1
Grasshopper (*Melanoplus* sp.)	—	—	—	—	—	100

[a] Percent frequency based on the total number of individuals identified.

particularly evident when nestlings ranged from 15–25 days old, the period when mortality was highest. Comparison of the decrease in survival with the decrease in nestling weight yielded a significant Spearman Rank correlation ($r_s = 0.57$, $N = 21$, $P \leq 0.01$) and indicated that food supply affected nestling survival in cultivated habitats.

Sibling weights were similar when survival was high, but during years of low nestling survival, younger siblings weighed less than their older nest mates did at the same age (Fig. 3). I compared the decrease in survival of youngest siblings with the difference in their own weight and the weight of their oldest siblings at the same age. Again, I obtained a highly significant correlation ($r_s = 0.81$, $N = 21$, $P \leq 0.01$) which indicated that competition in nests decreased the food available to younger nestlings and lowered their chances of survival.

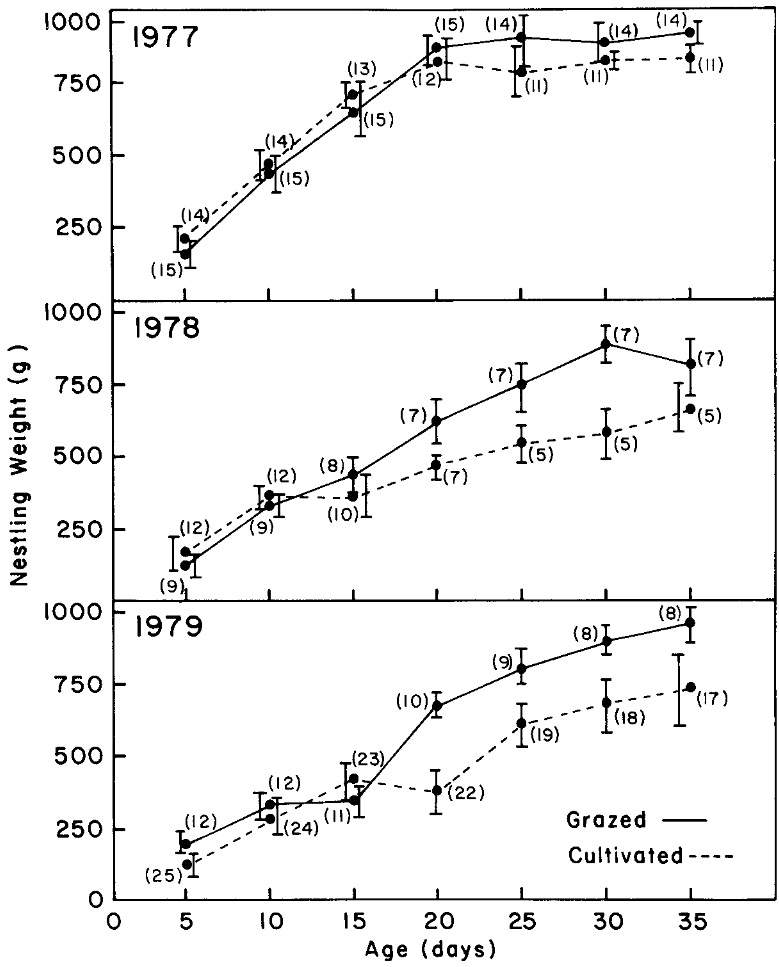

FIG. 2. Mean weights (±1 SE) of nestling Swainson's Hawks in grazed and cultivated habitats of southeastern Washington during 1977, 1978, and 1979; nestling weight based on the number of observations given in parentheses.

DISCUSSION

Nestling weight has frequently been used as an index of food supply (Owen 1960; Ricklefs 1965; Blaxter 1968; Southern 1970; Seel 1970; Perrins 1970; Spaans 1971; Dunn 1973, 1975; Bryant 1975). If this is valid, the nestling weight data I report support the food-limited hypothesis for hatching asynchrony and brood reduction in Swainson's Hawk. The cor-

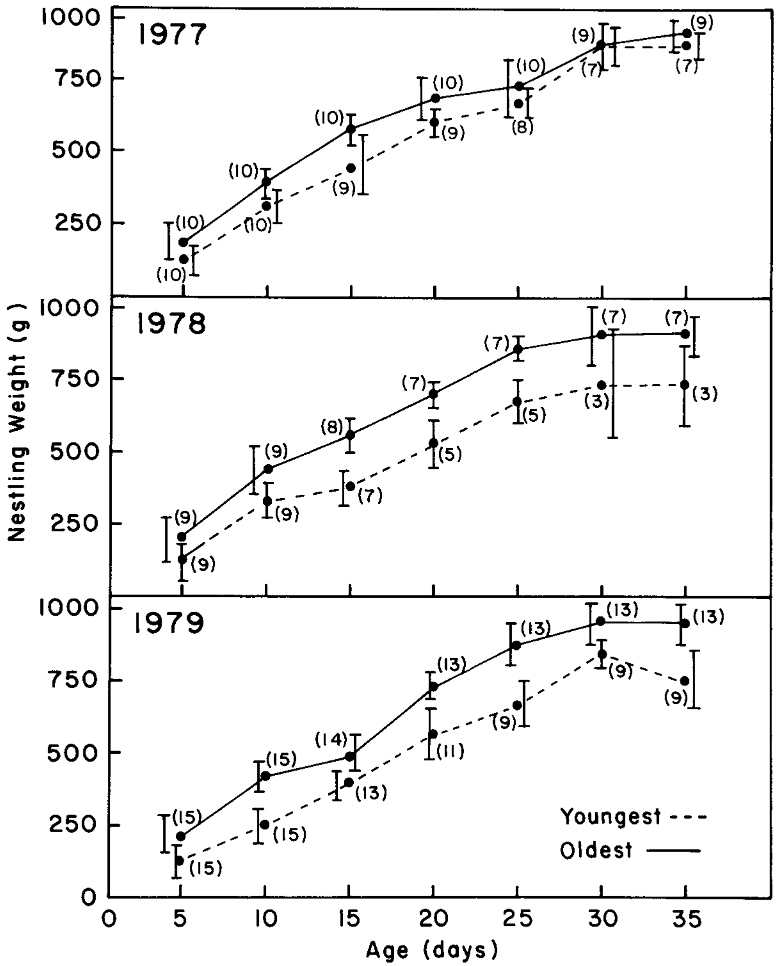

FIG. 3. Mean weights (±1 SE) of youngest and oldest nestlings of Swainson's Hawks nesting in southeastern Washington during 1977, 1978, and 1979; nestling weights based on the number of observations given in parentheses.

relation linking poor nestling survival with decreased weight suggests that limited food supplies increase the incidence of brood reduction. Also, the correlation between poor survival of youngest nestlings and the difference between sibling weights indicates that hatching asynchrony gives older nestlings a survival advantage by increasing their portion of the food supply. Weight differences between youngest and oldest nestlings of Great Reed Warblers (*Acrocephalus arundinaceus*), House Martins (*Delichon ur-*

bica), and House Sparrows (*Passer domesticus*) have also been reported and related to food supply (Seel 1970, Dyrcz 1974, Bryant 1978). Proctor (1975) has found weight differences between siblings of South Polar Skuas (*Catharacta maccormicki*) and that increases in this difference resulted in poor survival of younger nestlings because of attacks from their larger, hungrier, older siblings. Weight differences I observed between nestling Swainson's Hawks were greatest at 25 days of age and coincided with the period when brood reduction was most common. At 25 days of age, oldest nestlings had reached approximately 75% of their adult weight, a period in development when metabolic needs reach a maximum (Ricklefs 1974). The occurrence of fratricide at this time indicated that oldest nestlings were not being fed enough food and that hunger and competition resulted in the deaths of younger nest-mates.

Vegetative cover and weather affect the hunting success of many raptors including Swainson's Hawks (Craighead and Craighead 1956; Southern and Lowe 1968; Wakeley 1978; Bechard 1980, 1982; Stinson 1980). In view of this, one would assume that it is difficult for these birds to "predict" food supply during a breeding season and that adjustments in reproductive effort would out of necessity be made via hatching asynchrony and brood reduction. My observations support this hypothesis. Apparently, unable to adjust clutch-size to annual changes in prey availability, Swainson's Hawks laid the same number of eggs each year. By hatching them asynchronously, however, adults insured that, if food became critical, brood reduction would adjust reproductive effort by eliminating younger nestlings. In so doing, they prevented the starvation of all nestlings and total failure of the nesting attempt.

SUMMARY

Clutch-size, brood-size, and fledging success were observed at 96 Swainson's Hawk (*Buteo swainsoni*) nests in both grazed and cultivated habitats in southeastern Washington. Except in 1977, nests in cultivated habitats fledged fewer young. Decreased fledging success resulted from high mortality of youngest and next youngest nestlings. Using nestling weight as an index of food supply, decreases in nestling weight and increases in weight discrepancies between youngest and oldest nestlings in cultivated habitats indicated that a dearth of food increased the incidence of brood reduction. These data supported the food-limited hypothesis for the adaptive significance of hatching asynchrony in this species.

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LITERATURE CITED

BECHARD, M. J. 1980. Factors affecting nest productivity of Swainson's Hawks (*Buteo swainsoni*) in southeastern Washington. Ph.D. thesis, Washington State Univ., Pullman, Washington.

———. 1982. Effect of vegetative cover on foraging site selection by Swainson's Hawk. Condor 84:153–159.

BENT, A. C. 1961. Life histories of North American birds of prey, Pt. 1. Dover Publ., New York, New York.

BLAXTER, D. L. 1968. The effect of the dietary energy supply on growth. Pp. 329–344 *in* Growth and development of mammals (G. A. Lodge and G. Lamming, eds.). Butterworths, London, England.

BRYANT, D. M. 1975. Breeding biology of House Martins *Delichon urbica* in relation to aerial insect abundance. Ibis 117:180–215.

———. 1978. Establishment of weight hierarchies in the broods of House Martins *Delichon urbica*. Ibis 120:16–26.

CLEVENGER, G. A. AND A. ROEST. 1974. Cannibalism in Red-tailed Hawk. Auk 91:630.

CRAIGHEAD, J. J. AND F. C. CRAIGHEAD, JR. 1956. Hawks, owls and wildlife. Stackpole Co., Harrisburg, Pennsylvania, and Wildl. Manage. Inst., Washington, D.C.

CURTIS, J. T. AND R. P. MCINTOSH. 1950. The interrelations of certain analytical and synthetic phytosociological characters. Ecology 31:434–455.

DAUBENMIRE, R. 1970. Steppe vegetation of Washington. Washington Agric. Exper. Stat., Tech. Bull. No. 62.

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

DUNN, E. K. 1973. Changes in fishing ability of tern associated with wind speed and sea surface conditions. Nature 244:520–521.

———. 1975. The role of environmental factors in the growth of tern chicks. J. Anim. Ecol. 44:743–754.

DYRCZ, A. 1974. Factors affecting the growth rate of nestling Great Reed Warblers and Reed Warblers at Milixz, Poland. Ibis 116:330–339.

FITZNER, R. E. 1977. Behavioral ecology of Swainson's Hawk (*Buteo swainsoni*) in southeastern Washington. Ph.D. thesis, Washington State Univ., Pullman, Washington.

———. 1980. Behavioral ecology of the Swainson's Hawk (*Buteo swainsoni*) in Washington. U.S.D.O.E. Rept. No. PNL–2754.

HEINTZELMAN, D. S. 1966. Cannibalism at a Broad-winged Hawk nest. Auk 83:307.

HUSSELL, D. J. T. 1972. Factors affecting clutch-size in Arctic passerines. Ecol. Monogr. 42:317–364.

INGRAM, C. 1959. The importance of juvenile cannibalism in the breeding biology of certain birds of prey. Auk 76:218–226.

———. 1962. Cannibalism by nesting Short-eared Owls. Auk 79:715.

KEIR, J. R. 1976. Observations of Swainson's Hawk nesting in northeastern Illinois. Wilson Bull. 88:658–659.

LACK, D. 1966. Population studies of birds. Oxford Univ. Press, London, England.
MEYBURG, B.-U. 1974. Sibling aggression and mortality among nestling eagles. Ibis 116: 224–228.
NEWTON, I. 1977. Breeding strategies of birds of prey. Living Bird 16:51–82.
———. 1979. Population ecology of raptors. Buteo Books, Vermillion, South Dakota.
NISBET, I. C. T. AND M. E. COHEN. 1975. Asynchronous hatching in Common and Roseate terns *Sterna hirundo* and *S. dougalli*. Ibis 117:374–379.
O'CONNOR, R. J. 1977. Growth strategies in nestling passerines. Living Bird 16:209–238.
———. 1978. Brood reduction in birds: selection for fratricide, infanticide and suicide? Anim. Behav. 26:79–96.
OLENDORFF, R. R. 1973. The ecology of the nesting birds of prey of northeastern Colorado. Grassland Biome, U.S. Int. Biolog. Prog., Tech. Rept. No. 211.
OWEN, D. F. 1960. Nesting success of the Heron (*Ardea cinerea*) in relation to the availability of food. Proc. Zool. Soc., Lond. 133:597–617.
PARKER, J. W. 1976. Growth of the Swainson's Hawk. Condor 78:557–558.
———. 1979. Evidence for fratricide in Swainson's Hawk. Southeast Nat. 24:533–534.
PARSONS, J. 1975. Asynchronous hatching and chick mortality in the Herring Gull *Larus argentatus*. Ibis 117:517–520.
PERRINS, C. M. 1970. The timing of birds' breeding season. Ibis 112:242–255.
PILZ, W. R. 1976. Possible cannibalism in Swainson's Hawk. Auk 93:838.
——— AND L. K. SEIBERT. 1978. Fratricide and cannibalism in Swainson's Hawk. Auk 95:584–585.
PROCTOR, D. L. C. 1975. The problem of chick loss in the South Polar Skua *Catharacta maccormicki*. Ibis 117:452–459.
RICKLEFS, R. E. 1965. Brood reduction in the Curve-billed Thrasher. Condor 67:505–510.
———. 1968. On the limitation of brood size in passerine birds by the ability of adults to nourish their young. Proc. Natl. Acad. Sci. 61:847–851.
———. 1974. Energetics of reproduction in birds. Pp. 245–252 *in* Avian energetics (R. A. Paynter, ed.). Symposium on avian energetics. Nutt. Ornithol. Club, Princeton, Massachusetts.
SEEL, D. C. 1970. Nestling survival and nestling weights in the House Sparrow and Tree Sparrow *Passer* spp. at Oxford. Ibis 112:1–14.
SKUTCH, A. F. 1967. Adaptive limitation of the reproductive rate of birds. Ibis 109:579–599.
SMITH, D. G. AND J. R. MURPHY. 1973. Breeding ecology of raptors in the eastern Great Basin of Utah. Brigham Young Univ. Sci. Bull., Biol. Sci. 18:1–76.
SOUTHERN, H. N. 1970. The natural control of a population of Tawny Owls (*Strix aluco*). J. Zool. (London) 162:197–285.
——— AND V. P. W. LOWE. 1968. The pattern and distribution of prey and predation in Tawny Owl territories. J. Anim. Ecol. 37:75–97.
SPAANS, A. L. 1971. On the feeding ecology of the Herring Gull (*Larus argentatus*) in the northern part of the Netherlands. Ardea 59:75–188.
STINSON, C. H. 1979. On the selective advantage of fratricide in raptors. Evolution 33: 1219–1225.
———. 1980. Weather-dependent foraging success and sibling aggression in Red-tailed Hawks in central Washington. Condor 82:76–80.
WAKELEY, J. S. 1978. Factors affecting the use of hunting sites by Ferruginous Hawks. Condor 80:316–326.

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