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GENERAL NOTES

Observation of a brood of Sharp-shinned Hawks in Ontario, with comments on the functions of sexual dimorphism.—The Sharp-shinned Hawk (*Accipiter striatus*) exhibits the greatest "reversed" sexual dimorphism in size of any North American bird, with males averaging 100 g and females 170 g (Mueller and Berger, Auk 87:452–457, 1970). Of the several, controversial hypotheses to explain the extent of sexual dimorphism in raptors, that of Snyder and Wiley (Ornithol. Monogr. 20, 1976) is perhaps most amenable to verification. Snyder and Wiley have suggested that food stress late in the period of dependency of the young has acted to select for adults of greatly different body sizes, and thus different feeding niches. This increases the range of size of prey available to maintain the adults and their rapidly growing young. Casual observations of breeding Sharp-shinned Hawks and small bird populations in Ontario led us to question this hypothesis and served as the inspiration for this study.

The senior author is preparing an extensive discussion of the hypothesis of Snyder and Wiley. The purpose of this paper is simply (1) to present our intensive observations of 1 brood of Sharp-shinned Hawks, (2) to compare our results with those of 3 nests studied by Snyder and Wiley, and (3) to offer alternative explanations for some of the data. Our observations are unique in the amount of time and effort expended in observations during the post-fledgling period and in that ours is the first detailed study from eastern Canada, which appears to be the center of abundance of the species (Bent, U.S. Natl. Mus. Bull. 167, 1937).

We found a brood of 4 Sharp-shinned Hawks (3 females and 1 male) near their nest in Burpee Township, Manitoulin Island, Ontario, on 22 July 1977. We began observations on the brood that afternoon and continued daily until noon on 8 August when we had to depart. Two to 5 observers (usually 3) watched for 6.7 ± 2.67 (SD) h per day with the least observation (1.95 h) on 2 August, when it rained most of the day. The nest was about 11 m up in a white spruce (*Picea glauca*) in a grove dominated by both this species and northern white cedar (*Thuja occidentalis*), with scattered small groups of quaking aspen (*Populus tremuloides*) and an occasional balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*) and white pine (*Pinus strobus*). The nest was in the southwest corner of the grove about 35 m from the western edge and 30 m from the beach of Lake Huron. The grove extended about 130 m north and 200–350 m east of the nest, the edge was irregular, and a narrow strip of trees connected the grove to 2 larger forests to the east and north. The area surrounding the grove is locally called a "prairie," an open parkland covered with lichens, sparse grasses and some bare dolomite rock. Individual and small groups of trees, scattered through the prairie, formed 5–20% of the vegetative cover.

At least 1 observer remained near the young; the other observers were stationed at points which offered the best view of approaching adults. The young habituated to our presence rapidly and would tolerate approach to within less than 5 m after the second day of observations. The adult female also habituated rapidly. She perched quietly near us on a number of occasions. The adult male flew within 10 m of us several times, but was not observed perching near us. The young usually occupied rather exposed perches, either in aspens or dead trees of various species, although well-fed young were occasionally found on secluded perches. The center of activity of the young, as they grew older, moved northward from the nest and we moved our observation posts accordingly.

On 28 July, the young appeared to have achieved full feather growth and flight skills comparable to those of the adults; identification of age was possible only if we saw the plumage or heard begging calls. Camp (*in* Platt, unpubl. M.S. thesis, Brigham Young Univ., Provo, Utah, 1973) indicates that full feather growth is attained at an age of 38–40 days. We

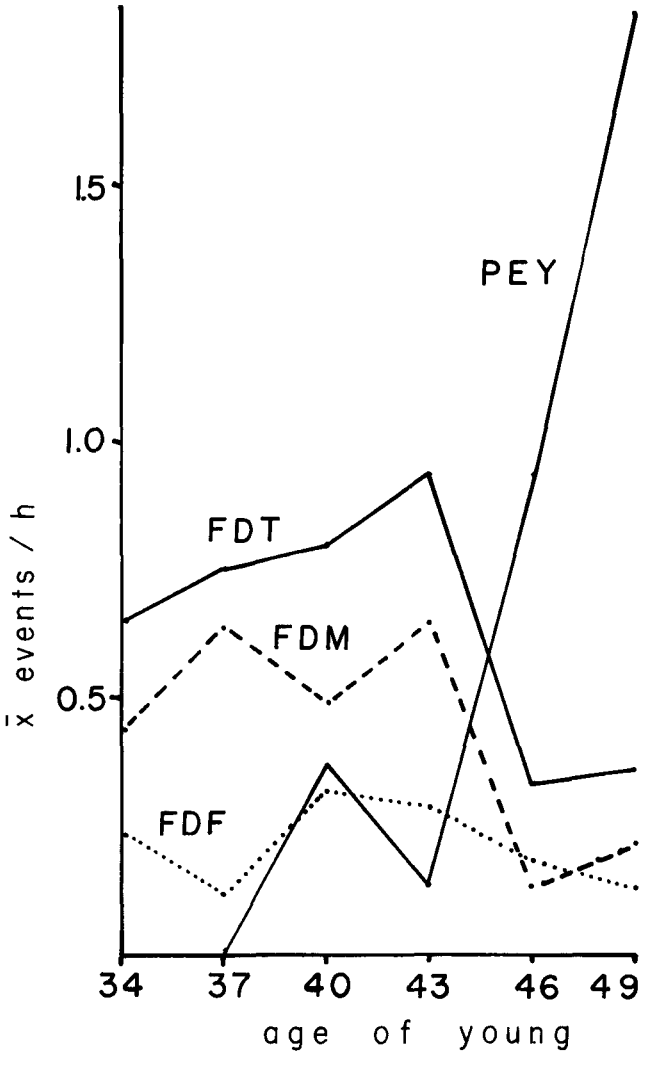

FIG. 1. Mean prey deliveries per h by the adults and mean "predatory episodes" per h involving young. FDF: food deliveries by the female. FDM: food deliveries by the male. FDT: sum of food deliveries for both sexes. PEY: predatory episodes involving young (see text).

thus estimated the age of our birds as 33 days when we discovered them on 22 July and that the females had left the nest about 6 days and the male about 9 days before we began observations.

Identification of prey items was rarely possible, particularly since most prey items were

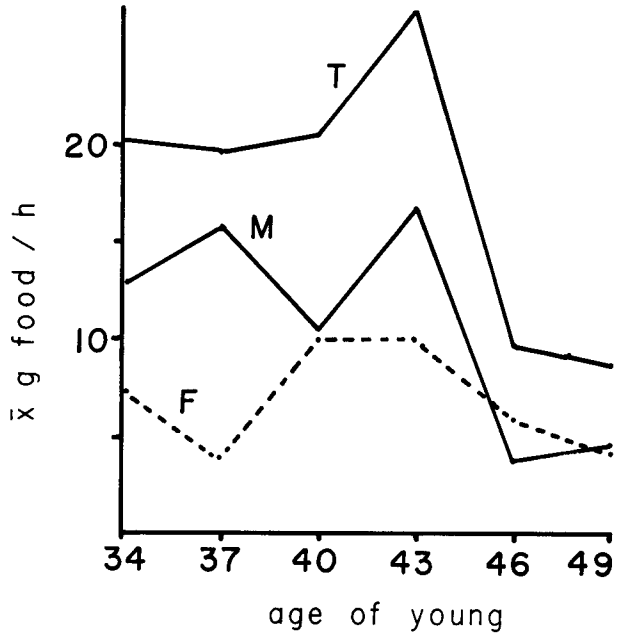

FIG. 2. Mean estimated g of food delivered per h by the adults; F: delivered by female, M: delivered by male, T: sum of the 2.

delivered plucked and remains were rarely found. If we obtained a sufficiently good look at the prey as it was being carried by the adult, we estimated its size and weight.

We did not attempt to census prey-bird populations in the range of the hawks, but a subjective judgement is that the populations were about the same as on 2 previous visits to Manitoulin at the same time of year.

Food deliveries and behavior of the adults.—In our 120.5 h of observation, there were 73 deliveries of food by the adults, 40 by the male, 23 by the female and in 10 cases we could not determine the sex of the adult. In 34 of the 73 deliveries (male 22, female 10, unknown sex 2), the prey item was seen sufficiently well, or sufficient remains were found to permit estimation of size. The 22 such prey items delivered by the male had a mean weight of 26 ± 14.8 g (range 10–80 g). The 10 items delivered by the female had a mean weight of 35 ± 21.5 g (range 10–90 g). The difference in weight of prey delivered by the sexes was not statistically significant (t-test, $P > 0.26$, 1-tailed).

To examine changes in the feeding rates by the adults, we divided our 18 days of observations into 6 three-day intervals, thus insuring a reasonable amount of observation time per interval (mean 19.9 h, range 14.0–25.9 h). Within a 3-day interval, food deliveries by adults of unknown sex were assigned to the sexes in proportion to the deliveries by adults of known sex. Weights of prey items not seen were assigned to the mean weight of prey delivered by that sex. The male made 0.53/h food deliveries during the first 12 days of study and only 0.18/h during the last 6 days (Fig. 1). The female showed less temporal change in food

deliveries: 0.24/h for the first 12 days and 0.16/h for the last 6 days. The estimated weight of food delivered per h shows similar trends: 13.6 g/h by the male and 7.7 g/h by the female during the first 12 days and 4.2 g/h by the male and 5.0 g/h by the female during the last 6 days (Fig. 2). There was a precipitous decline in total food deliveries between the end of the sixth week of age of the young and the beginning of the seventh week: 65% fewer deliveries per h and 63% fewer g/h. Daily mean deliveries/h for this 6-day period, when the young were 42 through 47 days old were: 1.05, 0.63, 1.54, 0.42, 0.25, 0.32. The dramatic drop from 1.54 deliveries per h to 0.42/h is further intersting because the latter day (3 August) marked the first easily noticeable influx of migrant passerines (mostly warblers) into the area.

The adult female was observed to loiter in the nest grove on 13 occasions for a mean of 0.83 ± 0.67 h. These 13 occasions of loitering occurred throughout our period of observation and as late as 7 August. The female may have spent even more time in the nest grove. She usually flew below canopy for some distance before relinquishing food to the young and then exited the grove at low altitude, sometimes unobserved. The male either dropped prey to the young above canopy, or dipped briefly below the treetops. The male was known to loiter in the grove on only 3 occasions for a mean duration of 0.15 ± 0.08 h. Neither adult showed any behavior which appeared defensive of the young in our presence.

We observed the female apparently hunting on 2 occasions, about 0.7 and 1.3 km from the nest. She was once observed carrying food 1.2 km from the nest. The male was never observed hunting. On the basis of our observations, we suspect that most of the hunting was done more than 1.5 km from the nest, although prey appeared to be abundant in the immediate vicinity. Chipping Sparrows (*Spizella passerina*), Yellow-rumped Warblers (*Dendroica coronata*) and American Redstarts (*Setophaga ruticilla*) were observed with fledged young within 20 m of the nest.

Behavior of the young.—The first predatory efforts by the young were observed on 29 July, when they were 40 days old and food deliveries by the adults were quite frequent (Fig. 1). Of the 80 "predatory episodes by young" depicted in Fig. 1, 52 were stoops or obvious pursuit flights at prey hidden from our view by vegetation. Of these 52, 23 were definitely unsuccessful, and for the other 29 cases we could not determine the outcome. During the last few days of our observations, young would often disappear for several hours, apparently hunting. Our efforts to follow and find such young were rarely successful, probably because of the extremely cryptic behavior of the birds. Distress calls of potential prey birds account for 16 episodes. In 2 episodes, young birds were seen apparently eating a tiny item (grasshoppers were extremely abundant in the prairie surrounding the nest grove). On 1 other occasion, 3 young were flushed from the ground by one of us twice in 3 minutes. The young remained together and their behavior strongly suggested that one had food but the dense vegetation prevented us from confirming this. No food delivery by an adult had occurred during the previous 3.13 h. On 9 occasions, we saw the bird at which the young hawk stooped. These included 4 pursuits of Gray Jays (*Perisoreus canadensis*), 2 stoops at small passerines, 1 at an unidentified warbler, 1 at a Yellow-rumped Warbler and 1 at a Common Flicker (*Colaptes auratus*). The most spectacular pursuit of prey occurred on 7 August, when we saw the young male suddenly leave a perch about 15 m up in a dead white pine. Accelerating rapidly with flicking wing-beats, he intercepted a flying warbler about 80 m away, missing by less than 30 cm as the warbler dived. The hawk wheeled and plunged after the warbler which disappeared into a spruce. We did not observe any successful capture of prey by the young, but the hawks had ample opportunities when they were not under surveillance by us. During the last few days of our observations, known positions of individual young were sometimes more than 1.5 km apart and on our last day 1 young disappeared 2 km to the north, flying high, and did not return during our last 40 min of observation. It is possible that we witnessed the departure of 1 young.

On 8 August, our last day of observations, all 4 young were under surveillance for only 0.7% of the 5.05 h of observation. Three young were under surveillance 29.7% of the time, 2 young 40.1%, 1 young 37.0% and 12.3% of the time no young were seen.

Discussion.—The 65% decline in food deliveries by the adults that occurred between 42–44 and 45–47 days of age of the young is far too sudden to be explained by a decline in prey availability or vulnerability. Furthermore, we noted a marked influx of migrant passerines into the area on day 44, just when the decrease in prey deliveries began. The decrease can be explained by a reduction in hunting by the adults. Sharp-shinned Hawks become independent of the parents at an age of about 7 weeks (Platt 1973, Snyder and Wiley 1976). A reduction in food deliveries by the adults 6 days before the young become independent and the continued begging of the young is consonant with the parent-offspring conflict hypothesis of Trivers (Am. Zool. 14:249–264, 1974). During the "weaning" period the attempts of the offspring to maximize their inclusive fitness come into conflict with that of the parents. The young selfishly demand more care than the parents, selfishly, should provide. Davies (Ibis 120:509–514, 1978) has suggested that if parents time the decline in feeding rates in response to cues from the young, they are open to being "cheated" in the conflict of maximizing fitness. If, on the other hand, the adults feed for a fixed period irrespective of the performance of the young in feeding themselves, young would be lost in times of food scarcity. The optimal strategy would involve flexibility in the behavior of the adults with parental care being prolonged when food is scarce. Davies presents the results of several studies which indicate that the length of the parental care period in birds is affected by the availability of food. We believe that this is the key to the understanding of the differences in feeding behavior of adults observed at various nests.

Newton (J. Zool. London 184:465–487, 1978), in summarizing his observations of the Sparrowhawk (*A. nisus*), suggested that the male usually brings as much food to the young as it can and that the female is induced to hunt chiefly when the efforts of the male do not meet the needs of the young. Newton noted that female *A. nisus* often loiter in the vicinity of the nest, a phenomenon observed by us, and by Platt (1973) in *A. striatus*. The available data on the Sharp-shinned Hawks are in complete agreement with Newton's hypothesis. The male Puerto Rican Sharp-shinned Hawk of Snyder and Wiley (1976) was able to provide adequate food for his family, and the female did no hunting (at least not to provide food for the young). For the spruce-fir brood of Snyder and Wiley and our Manitoulin Island brood, the male could not provide all of the needs of the young, and the female did some hunting. In the case of the riparian canyon brood of Snyder and Wiley, which we readily agree was under conditions of food stress, the female had to do considerable hunting to help feed the young. The same was possibly true of the oak-juniper brood of Snyder and Wiley, although the data are limited.

The peak in food deliveries to the Puerto Rican brood of Snyder and Wiley occurred during week 5 (the week after fledging) with a sharp drop in week 6 and little further decline in week 7. The spruce-fir brood of Snyder and Wiley showed a peak in week 4, with a considerable and steady decline through week 5 and weeks 6 and 7 (the 2 weeks were lumped because of limited observations). However, if we look at the amount of food delivered per young, the spruce-fir brood also shows a peak during week 5 (1 young disappeared at the end of the fourth week, cause unknown). A recalculation of the data shown in Fig. 2 into weekly intervals shows that our Manitoulin Island brood received the same amount of food during the last 3 days of week 5 (21.2 g/h) as they did in week 6 (21.3 g/h) with a sharp drop to 11.5 g/h in week 7. The lack of a peak in week 5 for our brood might possibly be due to the fact that we did not begin observations until the last 3 days of that week. Another possible partial explanation for the differences observed between nests in the temporal pattern of food deliveries is in the sex ratios of the brood. Newton (1978) found no difference in the

TABLE 1

PER CENT DISTRIBUTION OF SIZE CLASSES OF PREY TAKEN AND PREY AVAILABLE

			Size class[a]					
		N	1	2	3	4	5	6
Prey taken	♂	124	11.3	33.1	40.3	11.3	0.8	3.2
(Storer 1966, Table 5)	♀	125	1.6	21.6	37.6	23.2	1.6	8.0
Spruce-fir nest (Snyder and Wiley 1976)								
Prey taken	♂	68	0	48.5	47.1	4.4	0	0
(Table 5)	♀	8	0	50.0	50.0	0	0	0
Prey available (Table 17)			14.3	61.0	12.3	5.6	2.9	3.8
Riparian canyon nest (Snyder and Wiley 1976)								
Prey taken	♂	36	22.2	58.3	16.7	2.7	0	0
(Table 5)	♀	15	0	20.0	6.7	26.7	26.7	20.0
Prey available (Table 17)			22.0	44.9	7.1	9.5	7.3	9.3
Oak-juniper nest (Snyder and Wiley 1976)								
Prey taken	♂	19	0	36.8	63.2	0	0	0
(Table 5)	♀	4	0	25.0	25.0	0	25.0	25.0
Prey available (Table 17)			14.3	40.7	20.5	12.1	5.1	7.2
Manitoulin Island	♂	22	0	18.2	50.0	22.7	4.5	4.5
Prey taken	♀	10	0	10.0	40.0	10.0	30.0	10.0

[a] The size classes are those of Storer (1966): 1 = 3.4–8 g, 2 = 8–15.6 g, 3 = 15.6–27 g, 4 = 27–42.9 g, 5 = 42.9–64 g, 6 = 64–91.1 g.

food consumption of nestling male and female Sparrowhawks and attributed the high food consumption of the smaller males to more rapid development than the larger females. It is unlikely that equal food consumption by the sexes persists for very long after fledging; we suspect that males soon consume less than females. Our Manitoulin Island brood consisted of 3 females and 1 male, the spruce-fir brood of Snyder and Wiley consisted of 2 males and 1 female (after the loss of 1 male), and the Puerto Rican brood consisted of 2 males. Assuming that the adults were responding to the needs of the young, the sex ratio of the broods thus relates rather well with changes in food deliveries after the fifth week. If we take the above factors into consideration, the temporal patterns of food deliveries to the 3 broods discussed above are basically similar.

In contrast, the riparian canyon brood of Snyder and Wiley showed a slight increase in food deliveries between week 5 and weeks 6 and 7 (the last 2 weeks were lumped because of limited observations). This high rate of food delivery at the end of fledgling dependency, and the considerable participation of the female in providing food, suggest that this brood

was suffering from food stress and that the parents were responding in accord with the hypotheses of Davies (1978) and Newton (1978). The riparian canyon nest was studied in 1971 during the worst drought in 50 years, and bird populations were judged to be low (Snyder and Wiley 1976). Our results show a precipitious drop in food deliveries early in the seventh week. It is possible that a similar, sudden decline occurred in most of the broods studied by Snyder and Wiley (1976) but was not recognized because of the very limited observations conducted during week 7.

Newton's (1978) hypothesis suggests that the relatively meager participation of the female in delivering food to the spruce-fir brood of Snyder and Wiley (1976) was due to adequate provisioning by the male. Snyder and Wiley suggest ". . . both sexes of adult accipiters hunt pretty much full time toward the end of the breeding cycle . . ." and suggest that the relatively low contributions of the female to the provisioning of the spruce-fir brood was due to her bringing relatively small prey. She also brought fewer prey items (11% of the total) than did the riparian canyon female (29% of the total). Snyder and Wiley attribute the difference in the feeding behaviors of the females at the 2 nests to a greater abundance of prey in the size range preferred by females in the riparian canyon habitat than in the spruce-fir habitat. We interpret the data in another way. A shortage in prey of the size classes preferred by the male in the riparian canyon habitat resulted in inadequate food deliveries by the male and increased participation by the female, while in the spruce-fir habitat, a reasonable abundance of prey in the size classes preferred by the male resulted in reasonable food deliveries by the male and the female was not induced to hunt regularly.

We feel that the data of Storer (Auk 83:423–436, 1966) offer the best estimate of prey-size preferences in sharp-shins. Storer examined the gut contents of 223 sharp-shins of which 82% were taken during migration, a period when one might reasonably expect random availability of the various size classes. The analysis of 249 prey items reveals that males prefer size classes 2 and 3 (73% of the total) and females prefer size classes 3, 4 and 2 (82% of the total). The preference of females for size class 4 is only very slightly greater than for size class 2 (Table 1).

An examination of Table 1 suggests that the male at the spruce-fir nest of Snyder and Wiley (1976) was taking larger prey than expected either in comparison to Storer's (1966) data or the prey available. The female took few prey, and it is not surprising that none were from the presumably few individuals available in larger size classes. The riparian canyon male took considerably smaller prey than the males of Storer (1966) or those of any other brood studied. We believe this is strong evidence of food stress. It appears that the male was doing the best he could during this "worst drought in 50 years," low bird populations and probably limited breeding by prey-birds. The riparian canyon female brought a larger proportion of the prey during the fledgling period than at any other nest: 53% (Manitoulin 37%, spruce-fir 22%, Puerto Rico 0%). In view of the high participation in feeding by the riparian canyon female, and the apparent scarcity of prey, the high proportion of large-sized prey taken is not surprising. It is possible that the male considerably depressed populations of smaller birds early during this unusually bad year. The limited data from the oak-juniper nest suggest that the male was preying on relatively large prey. The 4 prey items taken by the female are insufficient for comment. The Manitoulin Island male took larger prey than predicted on the basis of Storer's data and the same is true, to a lesser extent, for the female.

We believe that our intensive observations on Manitoulin Island, and our interpretation of the data of Snyder and Wiley, suggest that food stress late in the period of dependency of the young in Sharp-shinned Hawks is an exceptional phenomenon. We believe it occurred only in the riparian canyon brood of Snyder and Wiley (1976) during an unusually unfavorable year. We therefore conclude that food stress during breeding, ameliorated by separate feeding niches of the adults, is an unlikely explanation for the remarkable reversed dimorphism

in size exhibited by Sharp-shinned Hawks. It appears that, under most conditions, the female could contribute whatever prey is needed by the brood without having to be 1.7 times as large as the male and capturing slightly larger prey.

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Food deprivation and temperature regulation in nestling Ferruginous Hawks.—Nestling deaths from heat prostration may occur regularly in some falconiform species (e.g., Fitch et al., Condor 48:207–237, 1946; Nelson, pp. 64–72 *in* Peregrine Falcon Populations, Their Biology and Decline, Hickey ed., Univ. Wisconsin Press, Madison, Wisconsin, 1969; Olendorff, U.S.I.B.P. Rep. No. 211, 1973; Beecham and Kochert, Wilson Bull. 87:506–513, 1975). Beecham and Kochert (1975) concluded that 41% of Golden Eagle (*Aquila chrysaetos*) nestling mortality in their Snake River, Idaho, study area was caused by overheating and observed that young birds in nests with a southern or western exposure are most vulnerable to heat stress.

The Ferruginous Hawk (*Buteo regalis*) nests in the semi-arid regions of southern Canada and the western United States (Olendorff 1973; Tomback and Murphy, unpubl.). Throughout the breeding range Ferruginous Hawks nest primarily on rocky outcrops, tops of trees (especially junipers [*Juniperus* spp.] and cottonwoods [*Populus* spp.]) and occasionally on sagebrush (*Artemisia* spp.) or the ground (Smith and Murphy, Brigham Young Univ. Sci. Bull. 18:1–76, 1973; Oldendorff 1973; Woffinden, Ph.D. diss., Brigham Young Univ., Provo, Utah, 1975; Howard and Wolfe, J. Range Manage. 29:33–37, 1976; Lokemoen and Duebbert, Condor 78:464–470, 1976; Fitzner et al., Condor 79:245–249, 1977). Despite the high temperatures encountered in the latter stages of the nesting cycle (e.g., Smith and Murphy 1973; Fitzner et al., 1977), apparently shade availability is not a nest-site requirement for the species. In the Great Basin west of Utah Lake, Woffinden (1975) examined 56 nests of Ferruginous Hawks on rocky outcrops, on the ground, and in trees. Almost half of these nests were unshaded throughout the day. The nests on steep slopes received some shade only in morning or afternoon, depending on slope aspect.

Here, we present field data suggesting that underfed Ferruginous Hawk nestlings are especially vulnerable to heat stress. We predict that combined effects of inadequate food provisions and high temperatures may cause much nestling mortality in years when prey populations are low.

On 15 June 1977, we surveyed Cedar and Rush valleys, Utah Co. and Tooele Co. (elev. 1760–1895 m; 40°00′N, between 111°55′W and 112°35′W), for Ferruginous Hawk nests (for detailed description of study area see Smith and Murphy 1973). Thirteen light phase nestlings between ca 5 and 7 weeks old remained in 5 nests, including 2 tree nests in Utah juniper (*Juniperus osteosperma*), 2 nests on rocky outcrops on steep (ca 40°), west-facing slopes, and