NESTING BEHAVIOR AND FOOD HABITS OF GOSHAWKS IN THE SIERRA NEVADA OF CALIFORNIA

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This study deals with nesting and food habits of Goshawks (*Accipiter gentilis*) with special reference to the adaptive behavioral mechanisms of large avian predators. The scope of the paper has been limited because of delay in finding a suitable nest for observation. By June 16, 1956, when the nest was located, the eggs had hatched and the nestlings were about a week old. Unfortunately, only limited information was obtained after the young had left the nest. This was due in part to the difficulty of following the fledglings and in part to lack of time for continuance of the study. Thus few data were obtained on territory size and behavior outside the nest area.

The literature contains little information on behavior or food habits of the Goshawk in North America. The accounts that have been published, although lacking in detail, have been helpful in understanding the various phases of the nesting cycle that were not followed in the present investigation. Zirrer (1947) presents observations on courtship and nest-building activities in northern Michigan. Siewert (1933) gathered valuable information on incubation behavior. Dixon and Dixon (1938), Gromme (1935), and Sutton (1925) also present informative observations on nesting activities. Sulkava (1956) studied seasonal variations in the diets of Goshawks in Finland.

My efforts were focused on continuous observation of a pair of nesting Goshawks at Donner Lake, Nevada County, California. A blind, erected approximately 50 feet south of and five feet above the level of the nest, afforded an unobstructed view of activities about the nest. The identification of prey was aided by use of a 20X telescope. A consistent schedule of observations was followed in the blind. Continual watch was maintained from 5:00 a.m. to 8:45 p.m. This was followed on alternate days for a period of five weeks or a total of 19 observation days. On days not spent in the blind, pellets were collected and plucking posts were examined for prey remains. The study involved a total of 408 hours, 294 spent in the blind and 114 hours in field activities. Field excursions in some instances entailed the collection of prey species by the use of snap traps. Specimens thus obtained were used throughout the study period for reference in identification during observations at the blind. Weight and feather measurements of the developing young were taken at approximately 11:00 p.m. every four days. Individual nestlings could be identified while in the nest by marks of colored lacquer which were applied to the head region.

A new technique was tried for one observation day toward the end of the study. This consisted of removal of the food item immediately after delivery to the nest; the prey was identified, weighed, and then returned. Such a procedure could not be continued because disturbance of normal activity was too great.

Daily activity charts were constructed for the 19 days of observation. These were constantly used both in the organization of material and when a particular behavioral event needed special interpretation. Each delivery of food to the nest was individually entered on a mimeographed form and its type classified. Prey identification, prey condition, and amount of prey consumed, together with other significant events associated with delivery, were entered on this form. Pellets collected below the nest were analyzed in several instances where prey identifications from the blind were uncertain.

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THE NEST AREA

Donner Lake is situated in a basin which drains to the east. Its shores are fairly precipitous banks and there is little shallow water. The nest under observation (fig. 1) was located on a slightly elevated bench which extends on a level plane southward from the east end of the lake for perhaps three quarters of a mile. Two old Goshawk nests were found in the immediate area, and it is probable that nesting occurred here annually over many years. Records go back 34 years, to August 9, 1923, when a streaked juvenal male, attended by its parent, was collected at this point by Alden H. Miller.

The zonal distribution of breeding Goshawks in California according to Hall and Grinnell (1919:62) and Miller (1951:534) is the Canadian Life-zone. However, the area studied was not clearly assignable to this zone. The presence of faunal and floral representatives from both Canadian and upper Transition zones indicated that it is intermediate between the two. There are published records for the western United States of nests in the Canadian Zone (Dixon and Dixon, 1938; Rowley, 1939) and the upper Transition Zone (Ingles, 1945), and there is one from the Upper Sonoran Zone (Bond, 1940). Nests are usually placed in a lodgepole pine (*Pinus contorta*), as were five nests discovered by me. However, there are records of nests in red fir, *Abies magnifica* (Grinnell and Storer, 1924:287), aspen, *Populus tremuloides* (Rowley, 1939:247), and the narrow-leaved cottonwood, *Populus angustifolia* (Bond, 1940:101). The species of tree chosen obviously depends on what is available, but conifers are preferred when present.

The study nest was located in a dense lodgepole pine forest (fig. 1) which had a canopy approximately 40 to 80 feet in height. Subcanopy layers were poorly represented or entirely absent. Pine needles covered the ground to depths of six inches. During the early phases of the nesting season, the forest floor is interspersed with impoundments of snow-melt water.

The nest proper was placed in a lodgepole pine at a height of 35 feet (fig. 1). Nests found by Rowley (1939:247) and Ingles (1945:215) were at heights of 15 and 45 feet, respectively, and represent extremes.

At the periphery of the nest area to the east, south, and west, the forest becomes less dense and the canopy somewhat discontinuous. In these areas, fallen and arched trees were used as plucking posts. These were perches where prey items, brought into the nest area by the adults, were plucked of some of the larger feathers or defurred on certain portions of the body. They were marked by prey remnants immediately below the perching structure. Not all likely perches were used for plucking purposes; height, accessibility, and sturdiness of structure appeared to be important factors influencing choice. The average distance from the nest of ten perches found in the area was 225 feet with a maximum of 425 and a minimum of 100 feet (fig. 4). It was learned that perches were not extensively utilized for plucking purposes during the nestling and early fledgling stages of the young Goshawks. This can be explained by the fact that principally nestling birds were fed to the young hawks and plucking was therefore unnecessary. It is postulated that most plucking activities occur in the course of the courtship

and incubation phases of the nesting cycle when nestling prey are not abundant. Sulkava (1956), who studied variations in Goshawk food habits during six nesting seasons, found that adult avian prey was abundant in the diet throughout the nest building and

Fig. 1. Study nest of Goshawks (*Accipiter gentilis*), located about 35 feet from the ground in a lodgepole pine (*Pinus contorta*).

incubation stages, while young birds were largely represented in the diet after the hatching of the young Goshawks. A plucking perch in the nest area is shown in figure 2.

It became evident after several days of observation that set patterns of approach and departure were adhered to by the adult Goshawks as they flew through the dense lodgepole stand. Certain flyways were evidently dictated to the birds by the limits of their structure and maneuverability. Dixon and Dixon (1938:8) state that the birds they watched seemed to be creatures of habit in that they always approached the nest from the same side and always lit on the edge of the nest in almost the same spot.

ACTIVITY PATTERNS

Before discussing some of the more specific aspects of Goshawk behavior, a general picture of nesting activities will be presented.

Daily pattern.—As the nest area becomes illuminated at approximately 5:00 a.m., Goshawk activity begins. The female, if brooding the young, becomes alert and looks keenly at the ground or surrounding area. Her head turns abruptly from one fixed posi-

tion to another between periods of concentration. Should the nestlings become active, the female is momentarily distracted. She rises slightly and allows the nestlings to move more freely. When they cease to struggle, the female settles again into the brooding position and arranges her breast feathers over the nestlings by a side-to-side rocking motion. By arching her neck slightly over her breast and lifting her body backward, the female was often observed to nudge a protruding nestling lightly with her beak. When the brooding position is regained, the female again becomes alert and watches the sur-

Fig. 2. Plucking perch of Goshawks at position 1 (see fig. 4). Photograph taken April 15, 1957.

rounding area. After perhaps 15 minutes, if no further distractions occur, she may ruffle her feathers, causing her head to lose its sleek, alert appearance, and then close one or both eyes for short periods of time.

The female was observed to continue brooding and scanning the area without changing position for periods ranging up to three hours. More frequently, she would re-orient herself on the nest at intervals or stand on the rim or branch nearby while perching, stretching, and preening activities were performed. The female was observed to remain perched for from two minutes to an hour and 35 minutes before returning to the brooding position. Before settling once more on the nest, an activity which I have termed "excavation" was often performed by the female. This seemed to be a modified nest-building action which apparently functioned to prevent food decay on the floor of the nest.

Any of the foregoing activities were discontinued if the male called in the nest area. In this event, the female would move slowly to the nest rim, step around the nestlings and, while calling, fly to the position of the male. This maneuver resulted in the transfer of prey from male to female. After such a "transfer," the female returned to feed the young and the male left the area. Usually the entire carcass was fed to the nestlings. If, in the course of the meal, they reacted slowly in taking the food from the female and if they ceased to beg vigorously, feeding was discontinued. With the partly eaten carcass grasped in one foot, the female would leave the nest and store the food somewhere in the area to be used for future feedings.

After the young had been fed and brooding or perching had been resumed for a short period, the female would often engage in sprig-collecting activities. Fresh sprigs of lodge-

pole pine were removed from the canopy up to distances of 50 feet from the nest and then dropped on the nest platform, but usually no immediate effort was made to incorporate them in the nest structure. Replenishment of pine sprigs was continued throughout most of the nestling stage of the breeding cycle (fig. 3).

In the blind at 5:00 a.m., the average temperature for 16 observation days was 40.6°F. with a minimum of 32°F. and a maximum of 50°F. At noon, temperatures rose as high as 95°F. in direct sunlight. The temperatures were usually not above 65°F. at dusk, and they dropped rapidly after the sun had set.

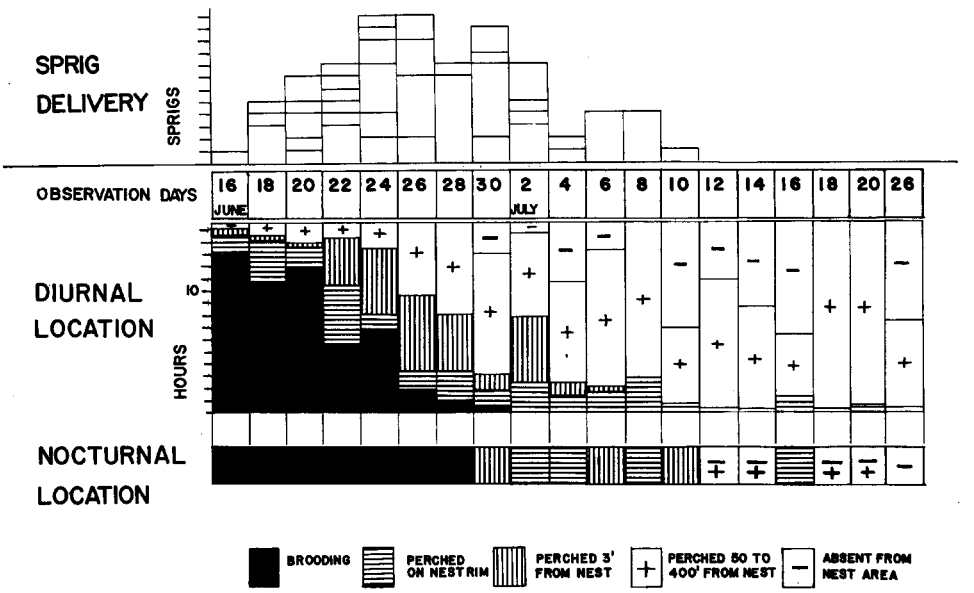

Fig. 3. Activity of female Goshawk. In Sprig Delivery histogram, the total height of each bar equals the total number of sprigs brought to the nest. The number of horizontal lines in each column equals the frequency of sprig-collecting activities for each day. The chart below (Diurnal Location) indicates the activity of the female during each day of 15½ hours of daylight. Nocturnal Location was determined by the location of the female when observations terminated at the blind at dusk.

In the morning, when the temperatures became approximately 52°F. (between 8 and 10 a.m.), insects began to swarm around the nest. These most likely were ceratopogonid flies, which are blood feeders. Insects were observed to pester the nestlings and the female incessantly. The female engaged in fly-catching activities whenever she brooded or perched near the nest. She would watch intently when a gnat or fly landed nearby and then move her head slowly forward until within striking distance. A sudden stab with the beak secured the insect. On one occasion, an insect was swallowed. Black flies (*Simulium* sp.) often crawled in and over the down of the sleeping nestlings. If the female was watching, she would move to the young and gently pick off any visible insects.

Prey species often passed through the nest area unaware of the female and the young Goshawks. The female was observed to locate immediately any movement in the area, and she would often concentrate intently on Oregon Juncos (*Junco oreganus*) moving about on the forest floor. If an animal or bird was close at hand or otherwise readily available, the female would drop from the nest rim to make the capture.

There is considerable division of labor between the male and female resulting from

the differences in their behavior. The male is almost entirely responsible for supplying the family with food, whereas the female performs a more sedentary role. Of 88 prey items brought to the nest, the male brought 75 items, or 85 per cent; the female brought 13 items, or 15 per cent. Never did the male share in actual feeding of the young. This was done entirely by the female. Several times the male was subjected to stimuli which, in the female, would have induced feeding of young, but no response was evoked in him. The male was observed several times to drop food into the nest, stand rigidly on the rim and look curiously at the begging nestlings. Dixon and Dixon (1938:11) report that the male Goshawk tried to get the nestlings to help themselves by half-heartedly picking at exposed pieces of raw meat. I have never observed the male picking at meat while on the nest. He usually left the rim several seconds after depositing the prey item.

Sprig collecting was performed entirely by the female, except in one instance when the male brought a dead twig to the nest.

Goshawk activity ceased at sunset, approximately 8:45 p.m.

Seasonal patterns.—In the present study, no observations were made during the nest building or incubation stages of the breeding cycle. Zirrer (1947) describes what appeared to be the nuptial flight of a pair of nesting Goshawks in northern Wisconsin. He observed nest-building activities in the same pair. He states that the female builds the nest alone, breaking twigs from prostrate young trees or collecting them from the ground. She takes considerable time to select each individual branch and to incorporate the twigs into the nest structure.

Siewert (1933:53) describes behavior of *Accipiter gentilis marginatus* during the incubation period (translated from the German): "On May 3, I observed from 8:15 a.m. to 4:45 p.m. The male brooded in the eight and a half hour period from 1:45 p.m. to 3:30 p.m., or one and three quarter hours. On May 10, the male brooded on the nest during a ten hour period of observation from 7:02 a.m. to 8:10 a.m. and from 1:40 p.m. to 3:40 p.m."

The activities discussed previously under "daily pattern" are subject to modification in some instances as the nesting season progresses. Such changes in the activity of the female are presented in figure 3. As may be seen, the incidence of brooding diminishes. The nestlings increase in size and activity, physically preventing the female from continuing to brood. She is still motivated, however, to stay close to the nest, as is evidenced in the increased time spent on the rim or on a nearby branch (fig. 3: barred portions of the individual columns). Eventually this motivation wanes and more and more time is spent away from the nest. At first distances of 50 to 400 feet were involved (blank portions of bars marked +), but as the season progressed, the nest area was left entirely for varying periods (blank portions of bars marked −).

The nocturnal position of the female showed similar changes (fig. 3). In the early phases of the study, the female returned to the nest to brood the young at night. On June 17, it was evident that the female was strongly motivated to return and brood the nestlings. After being flushed from the nest in the course of weighing activities at 11:00 p.m., she was present at the nest at 5:00 a.m. the next morning, evidently having returned some time during the night. After this date she did not return to brood the young the same night after being flushed from the nest.

In figure 3, sprig-collecting activity has been graphed in relation to the brooding activity of the female. Two modes are discernible—one in the total number of sprigs brought daily, and the other in the total number of sprig-collecting activities each day (indicated by the number of horizontal lines in each daily column). These modes fall in the period of waning of brooding. A possible explanation for them is that the female

is obviously under the influence of estrogen while brooding and that because brooding is physically prevented due to the size and activity of the nestlings, a displacement activity consisting of twig gathering is evoked by the continuing influence of estrogen.

When the female perceived the male in the nest area, she flew to him to obtain the prey item. The male remained perched and the exchange usually occurred when the birds were stationary. On one occasion, Gromme (1935:19) observed the meeting of a pair of Goshawks in flight near the nest. Most likely food was exchanged, but this was not determined. In the present study, there is some evidence to indicate that aerial exchange was occasionally attempted although this was never actually observed. After the "transfer" had been performed, the female fed the young and the male left the area. The female uttered a distinctive call when the male appeared in the nest area. This was used by the investigator throughout the study as an indicator of the male's presence.

An element of hostility was discernible in the "transfer" phenomenon that cannot be accounted for solely by the inherent disposition of falconiforms. The female tolerated the presence of the male in the nest area and often waited expectantly for him to bring food for the young. However, after food was delivered, she would not begin to feed the nestlings until he had left the area. This the male did when the female uttered the "dismissal call."

It is postulated that this phenomenon is a mechanism whereby the male increases his foraging rate so that the food demands of the young can be met. If the male was not expelled from the nest area by the female, he would remain perched near the nest and would not hunt. This was observed on several occasions when the female was absent from the area. The male did not leave until she returned and uttered the "dismissal call." Later in the study, the sight of the female was enough to expel the male.

Transfers of food between male and female continued throughout the study (see table 3: column "T"). Whether the hostility mentioned earlier occurred in this pair during nest-building and incubation periods is unknown. Siewert (1933:53, 56) observed that during incubation the male came to the periphery of the nest area, called, and was met by the female. The male then flew to the nest to incubate the eggs. The female did not return to resume incubation for an hour or so. From these observations, it seems reasonable to conclude that the male is not expelled from the nest area during incubation nor probably during the nest-building period. It may be that when the young hatch, the disposition of the female changes and her actions cause the male to leave the nest area. In the present study, the male flew to the nest immediately after "transfers" for the first four days of observation (table 3: column Tmn). It would appear that this is a carry-over behavior from the incubation period when the male flew to the nest to brood immediately after a "transfer."

BEHAVIOR OF THE FEMALE

Most of the data gathered on Goshawk behavior relates to the female. It was impossible to study in detail the activities of the wide-ranging male. The members of the pair at Donner Lake could not be readily distinguished on the basis of size alone, unless they were observed together at the nest. On closer examination through the 20X telescope, it was found that in this pair the female had wider cross-barring and wider mesial streaks on the breast feathers than did the male, which gave an overall darker appearance to the under parts. These differences were of little use for quick sex determination in observations from the blind. But as I became familiar with activities, differences in behavior afforded unfailing criteria for distinction between male and female.

Defense of the nest area.—The female Goshawk is extremely aggressive in her actions when attempting to drive intruders from the vicinity of the nest. Investigators

Table 1

Numbers and Weights of Prey Items Fed to the Young

	Total numbers	Per cent	Total weight (in gms.)	Per cent
Robin	27	30.7	1285	21.4
Steller's Jay	22	25.2	1356	23.1
Citellus lateralis	6	6.8	700	12.0
Chickaree	5	5.7	594	10.2
Eutamias sp.	5	5.7	226	3.9
Tanager (nestling)	4	4.6	89	1.6
Citellus beldingi	3	3.4	575	9.8
Mallard ducklings	3	3.4	185	3.1
Audubon Warbler	1	1.1	12	.2
Snowshoe Hare	1 (leg)	1.1	100	1.8
Scapanus latimanus	1	1.1	67	1.4
Weasel	1	1.1	45	.8
Williamson Sapsucker	1	1.1	42	.7
Pigeon	1	1.1	140	2.4
Mountain Quail	1	1.1	26	.4
Unknown				
Mammals	5	5.7	399?	6.8
Birds	1	1.1	25	.4
Totals	88	100.0	5866	100.0

who have had only casual experiences with nest sites have been duly impressed by the persistence and abandon displayed in her swooping attacks. Clothes have been torn and wounds inflicted on persons attempting to climb to blinds near the nest (Dixon and Dixon, 1938:5; Gromme, 1935:16, 19). The female may inflict injury in two ways. She may swoop on the intruder and deliver a stunning blow with the feet or she may rake exposed portions of the body with the large hind claw (Sutton, 1925:196).

It was noted in the present study that attacks were less frequent if several persons were in the nest area. In this event, the female's aggression may be limited to several close swoops or merely to aggressively cackling in the tree tops. After each swoop, the female usually takes a position out of sight of the observer and will again move to a hidden position if she is brought into view. Diving attacks are usually accompanied by the aggressive cackle, but in one instance a silent swoop was made on me. Aggressiveness diminishes if the intruder becomes motionless or remains in the area for long periods. The female became more aggressive when I moved to a position between her and the nest. If a white cloth or sheet of paper was raised above the head and waved vigorously, it was possible to frighten the female away from the vicinity of the nest. On such occasions, climbing to the nest or the cackling of the young did not induce the female to return. Aggressive behavior was observed only when humans entered the area. This particular nest was near a camp ground, but human intrusions, other than my own, were noticed only on four occasions.

Call notes.—The female utters a high-pitched note at rapid intervals when defending the nest. The call has been described as *ca, ca, ca, ca* by Sutton (1925:196). These notes are of short duration, three or four being uttered per second. Series of these notes were uttered at varying intervals depending on the aggressive attitude of the female. When the female cackles from a stationary perch, she often turns the head slowly from side to side, causing the sound to seem to change direction.

The second type of call given is totally different from the defense cackle. It is a long, plaintive scream lasting from one to two seconds, first rising and then falling in pitch. This call was given when the male entered the nest area. Three modifications of the call were noted. These have been named (1) the recognition scream, (2) the transfer scream, and (3) the dismissal scream. The names serve merely to distinguish the three types and may only partly reflect functions of the calls. When the male is first sighted or heard in the nest area, the female leaves the nest, uttering the recognition scream, but it consists of shorter, more intense notes which frequently end in a harsh-sounding falsetto tone. It would seem that these occur when the two birds meet for food exchange, but this exchange was never observed. Possibly the male in some instances does not relinquish the food immediately to the female, causing her to call excitedly. A third modification of this call was heard when the male remained in the nest area after the food transfer. The female in this instance would return with the prey item to the rim of the nest and utter the dismissal scream. This call resembles the recognition scream but is given with less vigor. It is uttered in succession with periods of approximately one half second between each call. The first note was usually one half the length of the others. This produced a choked, cut-off scream and a longer pause between the first and second notes than between the second and the third or the third and fourth. In one instance, the female uttered dismissal calls for 10 minutes after the transfer, presumably until the male left the area. Only then was feeding of the young undertaken.

Feeding of the young.—Feeding was performed entirely by the female. She insisted on feeding the young even after they were capable of tearing flesh for themselves, and she would portion out food whenever she brought or found prey at the nest. This behavior could have survival value because when the female feeds aggression among the nestlings ceases and the food is more evenly distributed.

The female held the prey tightly with the inner toes of both feet. The outer toes were used for support and their contact with the nest platform afforded the balance needed while she was tearing the prey. The hooked beak was closed into the flesh and portions of meat were torn away with an upward pull and a simultaneous twist of the head. The food was then held out to the begging nestlings, who struck forcefully at the female's beak, removing the portions of meat. The female's head was often twisted slightly so as to facilitate the nestlings' removal of the food from the closed mandibles.

The length of time involved in feeding depended on the size of the prey and was found to vary considerably. Of 79 feedings, the average period per carcass was 11.5 minutes. The range was 15 seconds to 61 minutes. Sixty-one feedings occupied 15 minutes or less. Usually the entire carcass was fed to the nestlings, exclusive of a few hard parts such as legs, beak, and tail, which were eaten by the female.

If the prey was whole when brought to the nest, the female would usually begin to tear at the head. Only once was feeding observed to be initiated at the posterior end. In one instance, plucking of the prey on the nest rim preceded feeding of the carcass to the nestlings. The item was usually entirely consumed except for the intestine. A special "dislike" was noticed for the intestinal portions of the alimentary tract in most prey items. Other viscera were ravenously eaten, but when the intestine was torn loose from the body, the female would hesitatingly pass a portion of it in and out of the beak several times without swallowing it. It would then be laid aside and later taken from the nest. A somewhat similar attitude was noted when the stomach of a Steller's Jay (*Cyanocitta stelleri*) was torn open. The female put her beak into the exuding contents and scattered them over the nest platform with sideward motions of the head before feeding was continued.

Post-feeding activities.—At the termination of feeding, the female would search for

particles of food which had fallen to the nest platform in the course of the meal. These when recovered would be presented again to the nestlings or eaten by the female. After these "clean up" actions the female often assumed a perching position. This was followed by cleaning the talon on the second toe and wiping the beak on the perch. Cleaning the talon was accomplished by gripping it with the beak and pulling upward. As the claw passed between the maxillary and mandibular tomia, removal of blood and flesh particles was accomplished.

Excavation.—This term has been given to an activity performed by the female at the nest. At times she would stand in the center of the nest cup, extend the beak and head out of sight into the matrix, and then pull and push vigorously at the structure. When she lifted her head, pine needles and debris held in her beak were discharged with a sideward motion of her head. The material was scattered on the surface of the nest platform. Occasionally, objects cleared the nest rim and fell to the forest floor, but this was not a common occurrence. Excavation activities diminished as the season progressed. Like brooding, sprig collecting and some other activities of the female (see fig. 3), excavation activities are probably influenced by the estrogen level.

Sprig collecting.—The method of twig collection was observed in detail. Before leaving the nest the female was often seen to raise and lower the head with "rapid peering" motions as described by Grinnell (1921). She would fly from the nest and alight on a lodgepole pine branch perhaps 50 feet away from the nest and at about the same level. From this position, she walked or flew toward the distal portion of the branch until suitable live twigs were encountered. A twig was gripped with the beak at a place close to its attachment on the branch. It was pulled upward with the same motion used when tearing prey, although the vectors involved differed slightly. In tearing prey, a direct line of pull existed between the feet and the neck muscles. In sprig collecting, the beak, being closed over the twig, was in a slightly more forward position and the line of pull was not directly from the feet. To compensate for this, the female leaned backward and, bracing both feet against the limb, pulled with abrupt movements until the sprig came free. The wings were used to regain an upright posture after each backward thrust and to maintain balance when the twig snapped off. It was then grasped in the beak and delivered to the nest. When the female arrived at the nest rim, the sprig was occasionally placed at a definite spot, but more commonly it was dropped wherever the female happened to land, and even on the nestlings themselves. In this event, utterances of pain were heard and escape reactions were elicited. Once dropped on the platform, no immediate effort was usually made to incorporate the sprig into the nest structure. On one occasion, when a sprig was dropped over the nestlings, the female was observed to push it between them forcefully.

Of 39 sprig deliveries, 18 involved only one sprig and 21 involved two or more sprigs. In figure 3, sprig-collecting activity has been graphed.

Stimuli evoking sprig deliveries were found hard to isolate as several activities were associated with this phenomenon. Sixteen delivery activities were initiated from a brooding position after the female preened or after movement of the young; three followed "excavation" or nest-building activities; eight were not preceded by any identifiable event, and in two the preceding activities were unobserved.

Perching.—While perched, the female was often observed to stand on one leg with the other drawn close to the breast between the feather tracts. This position was assumed frequently during perching activities by both male and female. Such a one-legged stance was preceded by a set pattern of actions. From a two-legged posture, the right leg is lowered until the "heel" joint meets the perch. Then with the toes clenched, the right leg is raised and lowered, striking the perch several times until it is abruptly retracted against the breast feathers.

Stretching.—Immediately after perching, or occasionally before reaching a perched position, a standard stretching activity was performed. The right side of the tail was spread sideward and held rigid. The right leg was then extended stiffly backward and held parallel under the tail. Finally, the right wing was extended downward and back, causing a spreading of the primaries and partial coverage of the fanned tail. Balance was maintained by a slight shift to the left. The tail, leg, and wing were tensely held in this position for from three to five seconds. After relaxation, the normal perching position was again attained. The left side of the body was stretched infrequently.

Table 2

Caching Activity of the Female

Species	Date	Total time food item was cached	Time elapsed since last feeding of the young
Citellus lateralis 160 gms.	June 16	3 hr. 20 min.	3 hr. 20 min.
Citellus lateralis 82 gms.	June 16	4 hr. 40 min.	2 hr. 40 min.
Robin (nestling) 50 gms.	June 18	3 hr.	47 min.
Scapanus latimanus 67 gms.	June 20	9 hr. 20 min.	1 hr. 10 min.
Citellus lateralis 86 gms.	June 24	1 hr. 6 min.	1 hr. 6 min.
Citellus beldingi 103 gms.	June 30	1 hr. 13 min.	1 hr. 13 min.
Chickaree 222 gms.	July 2	6 hr. 25 min.	2 hr. 57 min.
Chickaree 93 gms.	July 6	2 hr. 56 min.	59 min.
Citellus lateralis 42 gms.	June 16	Remained over night.	
Citellus lateralis 176 gms.	June 28	Remained over night.	

Caching of food.—Food items were cached during the early phases of the study when the nestlings were too young to consume large amounts of food at single feedings. The female ceased to cache prey after July 6 when the nestlings were approximately one month old. The female was also seen to cache prey items if a human intrusion occurred while she was feeding the young at the nest. Immediately after the carcass was cached, the female would return to attack the intruder. The caching behavior apparently takes preference over defense of the nest area.

As can be seen in table 2, ten definite instances were noted where prey items were stored in the nest area. Eight of these items were returned to the nest later in the day to be entirely consumed by the nestlings; two were left stored over night and presumably were recovered and eaten on the following day. It was evident that cached items were returned to the nest because the female left the nest and returned within short periods of time with prey. It is doubtful that she had time to forage away from the nest, and her actions when leaving the nest did not indicate that she had sighted live prey within the nest area. Cache returns were not entered in table 2 unless caching of prey was observed earlier in the day. The condition of retrieved items always correlated with descriptions in the notes of items cached earlier in the day. As far as could be determined the female never fed on the cached items while away from the nest.

Carcasses were not always stored at the same location. Direction of departure from the nest indicated at least three storage locations. Six caches were made in an easterly

direction, three were made to the south, and one was made to the west. In three instances where data are available on the directions of cache retrieves, two were from the same direction as that of the original cache.

For seven known instances where the female cached a prey item, she spent an average of 2.7 minutes away from the nest. The average time spent away from the nest in retrieving cached items was 4.1 minutes.

A letter from Dr. John J. Craighead, dated April 18, 1957, describes his observations of a Goshawk caching its food as follows: "The caches were made as close as 100 feet away from the nest and others were several hundred yards away. In every instance the hawk simply wedged the kill in the crotch of a tree, generally one of the smaller limbs. Most of the caches were made in lodgepole pine. Frequently these caches were left for four or five days."

The question arises as to what stimulates the female to retrieve the prey from its storage location. Hunger signs in the young or a timing mechanism in the female could be postulated. If the former stimulus is involved, the time elapsed between the previous feeding and the cache return would be expected to remain fairly constant or to diminish as the season progressed and the food capacity of the young increased. If the latter stimulus is involved, the total time that each item is cached would be expected to remain fairly constant. In table 2, it can be seen that neither of these two postulates holds conclusively, although there is a slight tendency for the times elapsed since the last feedings to diminish. It is quite possible that the hunger level of the female also influences the time of recovery of cached prey.

Foraging.—As already mentioned, the female was occasionally observed to dive from the nest to capture birds or mammals. One mammal and four birds were caught in this manner. A California mole (*Scapanus latimanus*) which apparently came above ground was captured near the nest. An Audubon Warbler (*Dendroica auduboni*) was captured near the ground, approximately 50 feet from the nest. Three young Mallards (*Anas platyrhynchos*) were captured approximately 200 feet from the nest.

This latter event was observed in detail. At 4:15 p.m. the female was perched on a branch three feet from the nest, facing east. She turned around and looked intently toward a partly dried impoundment some distance to the west. The hawk left the nest and swooped to the grassy plot. Immediately the alarmed quacking of an adult Mallard was heard plus the sound of flapping wings. This continued sporadically for about three minutes. Then the Mallard left the pond but continued to quack from a distance. After the hawk landed in the grassy plot, she was observed to walk and hop through the ground vegetation. "Rapid peering" motions were performed and occasionally she would seek a vantage point such as an upraised log or stump. Eventually the entire pond area (approximately 75 by 150 feet) was searched for the hidden ducklings. At 5:26 p.m. the female brought back a partly eaten duckling to feed to the young. The time away from the nest was not spent entirely hunting in the meadow. Twice the female was observed flying to the nearly woods, probably to eat or cache a duckling. Three ducklings in all were fed to the nestling hawks. They were delivered 17 and 34 minutes, respectively, after the first duckling. The female's breast feathers appeared moist and she was observed on several occasions to wade into the shallow water in search of the ducklings.

A similar foraging incident was related to the investigator by a ranger at Donner Memorial Park. He had observed a Goshawk on the ground near his house attempting to flush prey from around brush and logs.

Another observation not exactly pertinent to the discussion of foraging behavior will be injected here. In the early phase of this study, when the female remained close to the nest, a freshly skinned carcass of a *Citellus beldingi* was thrown from the blind. It was sighted by the female and after two minutes of "rapid peering" at the fallen object, she dropped from the nest, retrieved it, and began to feed the young. This incident is not surprising in view of the fact that the female was once observed to recover a prey item

which had fallen from the nest during feeding of the young. It seems highly unlikely that the Goshawk would forage for carrion under normal circumstances.

The female occasionally left the nest area late in the day to hunt. This was evidenced by the fact that she was away from the nest for long periods prior to each of her food deliveries. Seven instances, as listed below, were observed when the female hunted and brought food to the nest.

Species	Time away from nest
Citellus beldingi	2 hr. 42 min.
Chickaree	1 hr. 11 min.
Steller's Jay (nestling)	2 hr. 17 min.
Chickaree	3 hr. 30 min.
Chickaree	5 hr. 56 min.
Chickaree	5 hr. 56 min.
Weasel	8 hr. 26 min.
Chickaree	2 hr. 20 min.

The female often fed on the carcasses that she captured while absent from the nest area. This was proved by the partly eaten condition of the prey delivered and by the gorged state of the female upon her return to the nest.

BEHAVIOR OF THE MALE

The male usually entered the nest area only to bring prey items to the female or to the nestlings. After each delivery, he left the area and was not seen until he again returned with food. During the 19 days of observation, the male delivered food 75 times, an average of 3.9 times per day. Each food delivery was completed in from one to two minutes. Consequently observations on the male are fewer than those on the female.

Defense of the nest area.—Aggressive behavior in defending the nest area is not characteristic of the male. Several observations made in the course of the study support this statement. On one occasion as I entered the nest area and proceeded toward the nest, the male was discovered perching approximately 40 feet from it in a lodgepole pine. He remained in a perched position and watched my approach with unalarmed curiosity. After one minute, he took flight and disappeared. In a second instance, the male remained perched and undisturbed when I made an appearance at the top of the blind, approximately 30 feet from him. A third instance occurred when the male was delivering food to the nest. Before the food was deposited, he discovered my position on the ground below and, clutching the prey, flew off into the surrounding woods. He did not return and attempt to drive the intruder from the nest area as the female would have done. On one occasion, however, the male was heard to give the defense cackle. This occurred after the female had been cackling in a confer above my head for three minutes. The male suddenly came to perch below her and uttered the cackle. It seems likely that this was provoked by the female's actions. When the female heard the cackle of the male, she uttered the "dismissal call" and he left. Other authors (Dixon and Dixon, 1938:4; Bond, 1940:103) have noted aggressive behavior in the male when he accompanied the female around the nest at times of human intrusion. Sutton (1925:194), however, describes the shyness and lack of aggression in the male.

Call notes.—The male is capable of uttering a special note not given by the female (Sutton, *op. cit.*; Siewert, 1933:56). It is an unmusical sound, having somewhat the tone produced by a person snapping the tongue away from the roof of the mouth. In uttering this sound, the male holds the beak wide open and thrusts the head up and forward. When the sound is emitted, the head is brought abruptly downward toward the throat. This is repeated at intervals of five seconds and is audible at distances up to 300 or 400

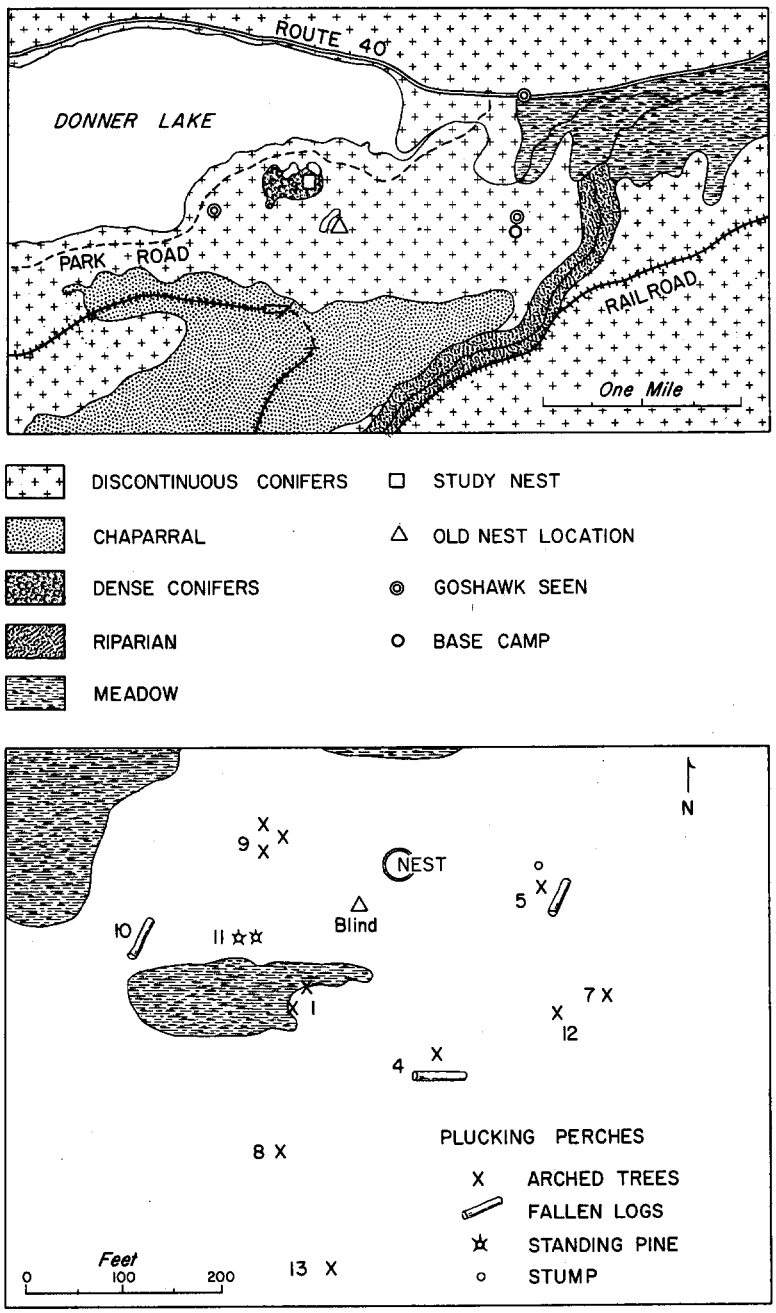

Fig. 4. Upper: map showing location of study nest of Goshawks near Donner Lake, California. Lower: plucking perch locations of Goshawks (see fig. 2).

feet. This call was heard when food was brought to the periphery of the nest area. In this instance, the call indicated the male's presence and his position with regard to the female. A "transfer" usually resulted. The same call was given when the male encountered the female at close range. In this instance, the call appeared to have a social or "conversational" function. The observations of Siewert (*op. cit.*) support these conclusions.

The plaintive scream is often uttered in place of the "guck" call (just described) when the male brings food to the periphery of the nest area. The two calls function in the same way in this situation. The scream never served the function of a social note.

The defense cackle of the male has a throaty quality, is weaker, and is uttered less rapidly than the female's cackle.

Sprig collecting.—One observation was made of the male delivering nesting material to the nest. On July 10, at 11:45 a.m., the male brought food to the nest. The female was absent from the area and consequently the male was able to remain near the nest. Forty-nine minutes later he brought a bare, dead twig, dropped it on the nest rim with a sideward cast of the head, and then left immediately.

Foraging.—On July 7, the male captured a pigeon which I had kept in captivity at the base camp, about one mile from the nest (see fig. 4). When I discovered this kill, a portion of the skull remained, indicating that the hawk had eaten at least the head of the pigeon at the plucking site. On July 8 at 6:26 p.m., 32 hours and 26 minutes after the kill, the male delivered the carcass to the nest. In the interval, the head, shoulders, wings, and breast had been eaten. The male had evidently cached the pigeon on or before July 8 and had continued to hunt for smaller prey during the day. It would appear that the presence of prey cached by the male had some effect on his foraging activities. The total number of deliveries of the male on the 8th were fewer in comparison with those of previous days (see table 3). Possibly the hunger level of the male influences his foraging effort.

It seems unlikely that small prey is similarly retained for such long periods before being delivered to the nest. Two prey items, a nestling Steller's Jay and a Belding ground squirrel, were delivered still alive. Larger prey may be cached and then eaten at intervals by the male. This explains an earlier observation (June 16) when the male delivered only the hind leg of a snowshoe hare to the nest. It is obvious that the male's foraging activities, in some instances, are more complex than merely catching the prey and delivering it to the nest.

Demandt (1938) states that male hawks hunt far from the nest area whereas females hunt somewhat closer. Observations in the present study somewhat support this. The male was seen twice foraging at distances greater than three-quarters of a mile from the nest. Out of 11 prey items brought by the female, five were caught in the immediate vicinity of the nest area, and six were caught outside of a 300 to 400 foot radius from the nest. How far they were captured beyond this point was not known.

I was fortunate to witness the capture of a fledgling robin (*Turdus migratorius*) at the Sagehen Creek station by a male (?) Goshawk that was not a member of the pair studied. The young robin was seen on a dirt road following its parent which was foraging in some scattered sagebrush (*Artemisia tridentata*) about 20 feet away. The Goshawk suddenly burst from concealment, shooting out of a bordering stand of conifers on the uphill side of the sagebrush vegetation. Immediately the adult robin uttered several alarm notes, but before the fledgling could take cover it was captured by the swooping Goshawk. With the fledgling clutched in its talons, the hawk dropped behind a small pile of boulders at the side of the road. Two adult robins continued to call excitedly. I attempted to bring the hawk into view, but in so doing flushed him into the nearby

conifers. The robins followed and continued to call excitedly, thus making the position of the hawk quite obvious. He was standing on the ground about 200 feet from the initial place of the capture, under the trunk of a conifer, and was plucking the carcass.

It seems evident that a male Goshawk returns to nests where more than one nestling have been discovered. This is done immediately after delivering prey nestling to his young. On June 22, two Steller's Jays of the same age were delivered within 21 minutes, and on July 6 two robin nestlings of the same age were brought to the nest within 36 minutes. It seems unlikely that the male could have located two separate nests in either of these instances.

DEVELOPMENT OF THE YOUNG

Growth and age.—Growth curves of the nestling Goshawks were constructed from weight measurements taken from June 25 to July 23 (fig. 5). It was impossible to construct a complete growth curve from these weights because weighing of the young commenced well after the time of hatching. An attempt was made to project the curve in order to establish a hatching date for the nestlings. This was done by calculating the weight at hatching from the egg-weight formula developed by Bergtold (1929) and by superimposing the growth curve of the Golden Eagle, *Aquila chrysaëtos* (Sumner, 1933: 281) onto the Goshawk weights determined in this study. When this was done, the hatching date was estimated to be June 4. The length of time the young spend in the nest is probably from 42 to 47 days (Dixon and Dixon, 1938:11; Siewert, 1933:93). This would place the date of hatching in the present study in the period from June 5 to June 10. To facilitate further discussion, the mid-point of June 7 was taken as the date of hatching of the nestlings at Donner Lake. All ages have been based on this date.

It would seem that two of the nestlings were of the same age and one was younger. This is shown by the weights of the nestlings when they were first weighed. Two weighed 410 grams and 400 grams, respectively, and the other weighed 236 grams. Siewert (1933:92, 93) states that eggs are laid 48 hours apart and brooding begins with the laying of the second egg. If this is so, the smallest nestling was probably two days younger than its nest mates.

In altricial birds, three main stages of nestling growth can be recognized. There is (1) an initial period of rather slow gain in weight, (2) a period of maximum increase in weight, and (3) a final protracted interval of minor fluctuations (Sumner, 1933:284). The growth curves of nestling 1 and nestling 2 leveled off, and that for the male (2) reached the fluctuation stage at a lighter weight than that for the female (1) (see fig. 5). This was probably caused by inherent differences in growth of male and female. The curve form of nestling 3 is not normal. Due to the lack of nourishment, the period of maximum growth was protracted. It would appear that competition for food with the older nest mates commenced at least as early as June 25 (16 days of age), as the weight of the youngest nestling at this time deviated from expected normal growth (see fig. 5). It seems evident that insufficient nourishment from this time on never allowed the growth curve of the youngest nestling to assume its proper form during the period of maximum weight increase. This resulted in a weakened condition and probably was the ultimate cause of death of July 19.

During periods of feeding, the youngest nestling was not receiving as much food as his larger nest mates. This was due to the greater strength of the older nestlings and the inability of the smaller nestling to consume food as fast in a given period of time. After feedings, the youngest was often observed to show signs of hunger while the older nestlings were well satisfied. Throughout the study it was noticed that nestling 3 was listless and slept almost continually.

Behavior.—Behavioral changes in the young were evident from one observation day

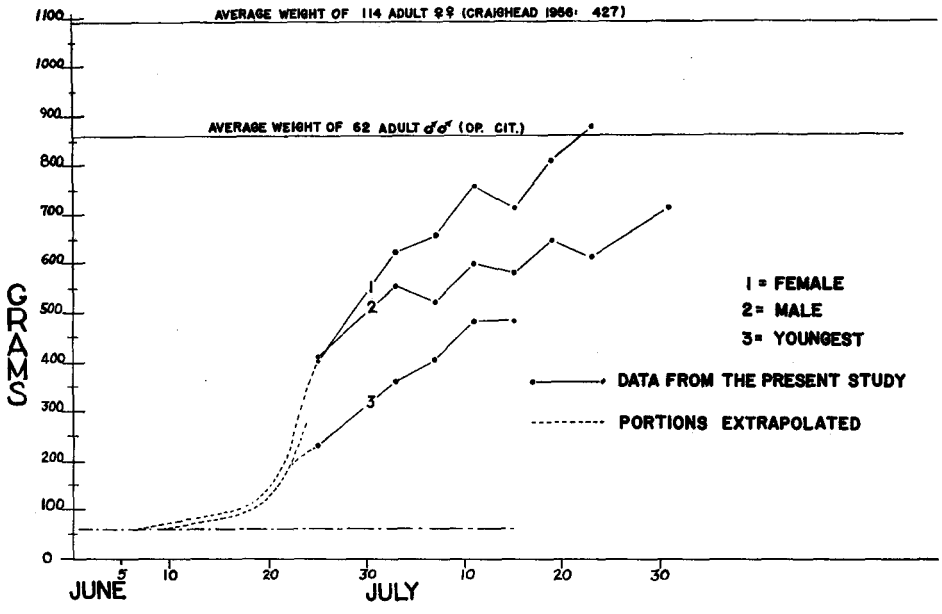

Fig. 5. Growth curves of young Goshawks.

to the next (a period of two days). It was thus necessary to consider nestling behavior on each observation day. The presentation describes for each day of observation only the behavioral events that were observed then for the first time. These activities are not usually mentioned in the succeeding days of observation, althought they may continue to be evident.

The young were color marked on June 25. The discussions for each observation day were drawn mostly from the actions of the older nestlings because they displayed behavior traits sooner and were more active.

Nine days old.—The female brooded the young almost the entire day. At 5:54 a.m. she flew from the nest, leaving the young uncovered. The nestlings were all facing inward in contact with each other. Their heads swayed with uncontrolled, thrashing motions, and in a few instances the beaks of adjacent nestlings came into contact. When this happened one nestling was observed to thrust and poke vigorously at the beak of another. This stimulus and reaction probably directs the movements of the nestlings toward the food held in the female's bill immediately after they hatch.

Call notes were uttered by the nestlings when the female fed them. The sound was a squeaky whistle, lasting about one second, and was barely audible at the blind, 50 feet away. These begging whistles were uttered throughout the meal.

The time that the nestlings spent under the female was related to temperature. In the morning, if one of the nestlings attempted to crawl outside, the female would nudge it gently back under with the beak, or it would crawl back of its own accord. In the afternoon, the nestlings crawled out and slept on the nest platform. One remained out for thirty-five minutes. As the nestlings slept, the female removed insects that alighted on them.

Greater activity was shown from 1:00 p.m. to 8:45 p.m. than from 5:00 a.m. to 1:00 p.m. In the morning, only one defecation was recorded for the three nestlings; in the afternoon three or four were recorded. Increased environmental temperature with a consequent increase in activity of the nestlings explains this difference.

When the female brings food, the nestlings "whistle-beg" and stand unsteadily under the female as she tears at the carcass which is gripped in her talons. She holds food about one and a half inches above the nestlings and waits for them to strike at it. At this age, the young react to a specific

pattern of stimuli when feeding. They will not peck at the carcass nor will they pick up fallen portions of red meat that are lying on the nest floor. Often the nestlings would strike at the female's beak when it was lifted from the carcass whether it contained food or not. The nestlings sometimes strike at the meat held in the beak of one of their nest mates and attempt to snatch it away. The weaker nestling often had food stolen in this manner. If the portion of food received by a nestling was small, it was easily swallowed. A larger piece of meat was only successfully swallowed after a series of contortions. The head was thrown back and the beak pointed upward. With a continuous motion, the head was brought downward to the neck and then extended toward the floor of the nest. These motions were repeated until the food was finally forced into the crop.

Eleven days old.—On June 18, the young were noticeably larger. Coordination was essentially as poor and uncontrolled as at nine days of age. Some improvement was noted during the warmer parts of the day. A general increase in activity was noticeable in comparison with the nine-day-old nestlings. No contour feathers were as yet visible on the nestlings, but a rudimentary "preening" motion was observed. This action was an awkward nibbling at wing, side of neck, and back. Each "preening" attempt lasted only from two to three seconds.

A call note was uttered whenever the nestlings were in pain. On one occasion, it was uttered when the adult female stepped on a nestling. In another instance, the call was given when a nestling became caught between two twigs. The sound is a rapid, high-pitched twitter, resembling the note of a domestic chick when caught and picked up.

The two older nestlings began to display interest in their surroundings. They pecked "inquisitively" at each other and one was observed to pull weakly at a twig in the nest platform from time to time. The youngest nestling did not engage in these activities and slept most of the day.

Thirteen days old.—On June 20, during feeding, the nestlings were observed to strike at the red meat held in the female's talons as she stood on the nest rim and tore at the carcass. This was the first evidence of a change in feeding reactions. However, the young did not pick up fallen particles of food from the floor of the nest.

A reflex motion was used by the nestlings to dislodge insects from their bodies as they slept. The motion was not directed at any particular part of the body and was performed regardless of where the insect caused the discomfort. In this action, the head is thrown violently upward and back against the shoulders. One side of the head, usually the left, is rubbed rapidly back and forth between the shoulders. The entire movement lasts only about two seconds, but it is enough to dislodge a crawling insect. The female performs this same movement when dislodging insects from the head region.

The defecating mechanisms which enable falconiforms to eject the feces outside of the nest are well known. This behavior trait is innate and appears early in the behavior of the nestlings. At nine days of age the nestlings were observed to orient themselves while remaining in prone position so that the trajectory of the feces was directed over the side of the nest. At 13 days, due to the increased development of muscular coordination, the feces were ejected from a standing position. Intention movements could be detected five to seven seconds before the actual ejection of the feces. The nestling would rise and awkwardly maneuver to a position near the rim, facing toward the center of the nest, whereupon the feces would be ejected.

Fifteen days old.—On June 22, the nestlings appeared to be more active and to move about the nest with more facility. They still remained in a crouched position and took unsteady steps when moving from one place to another, often using the wings to maintain balance. Defecation, feeding, preening, and fly-shaking movements had become more ritualized. During feeding, the nestlings continued to strike at red objects. In three instances, the nestlings pecked at the red-orange eye of the female. The nestlings became increasingly aware of objects in the nest. One nestling was observed to peck hesitatingly at a branch and later at its own outstretched toe.

Seventeen days old.—Activities on June 24 were not essentially different from those of the preceding observation day, although one nestling was observed to stand erect for the first time. It took four unsteady steps across the nest and remained standing for about five seconds. All activities prior to this, except feeding and defecation, had been performed from a prone position. The wings of one nestling were extended upward, in a stretching motion. This was the first time that wings were used for any activity except balance while moving in the nest.

Intention movements of defecation were evident 26 seconds before the actual ejection of feces.

Apparently muscular coordination is better developed than at 13 days of age when intention movements were detected 5 to 7 seconds before actual defecation.

Differences in the behavior of individual nestlings became evident. Of the two oldest, one was decidedly more advanced. The youngest was considerably retarded. It was observed to preen for the first time on this date—six days after preening was first observed in the older nestlings. One of the larger nestlings performed mature preening motions on newly emerged pin feathers. It reached back and preened under the wing, using a "nibbling" movement of the beak to slough off scales from the feathers sheaths. It also preened the wing along the ulnar tract.

An awareness of objects away from the nest was noticed on this day. One of the older nestlings watched the motions of the female perched on a branch about three feet away from the nest.

Nineteen days old.—On June 26, the nestlings could be distinguished because color dopes had been placed on their heads the night before. For purposes of brevity, the nestlings will henceforth be referred to by number. The female, the male and the youngest are numbers 1, 2 and 3, respectively.

Behavioral events that were observed for the first time were: (1) Nestling 3 pecked at a twig. This action had been observed eight days previously in the older nestlings. (2) Nestling 1 pecked forcefully at a twig. Pecking activities previous to this observation had been performed in an "inquisitive" fashion. The motion observed on this day was a forceful biting and a twisting of the head from side to side. (3) Nestling 1 peered over the nest rim to the ground below. Improved visual perception was evident. (4) The nestlings uttered a "contentment twitter." The call given was somewhat like the sound of the "pain twitter" but the individual high-pitched, staccato notes were spaced farther apart and the rhythm was uneven. As each note was uttered the body of the bird would bounce. This note is probably analogous to the "conversational chipper" described by Sumner (1934:347) in Golden Eagles. In the Goshawks, the note was often given by the nestlings when they had been well fed and the female was perched nearby.

Twenty-one days old.—On June 28, the nestlings were observed to associate the female's "recognition" and "transfer" scream with the bringing of food to the nest. When the female called as she left the nest, the nestlings uttered food-begging calls. These had been previously associated only with food brought to the nest or with the tearing of the carcass on the nest rim by the female.

Visual perception continued to improve. Nestling 2 was observed to watch the approach of the female when she brought twigs to the nest. Use of the talons was observed in nestling 1. After vigorously pecking at a twig for a short time, it suddenly grasped a twig with its foot. This action is probably a precursor of the "stabbing" reaction which is performed at a later age.

Striking at insects with the beak is evidently a deep-seated response. Nestling 2 was observed to peck at black flies crawling on the head of nestling 3 on this day.

The motions used to regurgitate pellets were observed. From a prone position, the head and neck were thrown from one side to the other. The pellet was seen to be lodging in the crop. After perhaps two minutes, during which time the sideward head motions were continued, the pellet was worked up to the top of the throat. In preparation for its ejection, the head and neck were lowered and pointed into the nest matrix. A final dislodgement of the pellet was effected by vertical pumping motions of the head and neck.

Nestling 1 was seen to peck vigorously at nestling 3. Pecking activities previously had usually been directed to inanimate objects. Such aggressiveness was rarely recorded in the nestling period except at times of feeding.

Twenty-three days old.—On June 30, in the absence of the female, the nestlings (2 and 3) attempted to tear flesh from a prey item. At 2:50 p.m., the male left a nestling robin in whole condition at the nest. Nestling 2 at first pecked inquisitively at the yellow areas at the gape of the beak. Nestling 3 joined in. Most unexpectedly a change occurred in nestling 2. It aggressively attacked nestling 3, uttering a sound resembling the female's cackle in rhythm and tone. Nestling 3 immediately moved to a remote portion of the nest and faced away from the attacker. This call elicited an apparently innate response in both nestlings 1 and 3. They stood up, faced away from nestling 2 and moved to positions on the edge of the nest rim. Their heads and necks were pointed down, almost touching the nest structure. The rumps were above the level of the head and were pivoted toward the attacker. This posture has been named the "defense stance." The function of this posture becomes evident when the method of the feeder's attack is observed. The attacker attempts to strike at the head or neck with

the beak. This is seldom possible if the individual being attacked holds the head low and pivots the rump to block the attacker. Such a reaction would appear to have survival value for the species, permitting weaker nestlings to survive the attacks of larger nest mates during feeding activities.

After attacking the other nestlings, nestling 2 tore small pieces of flesh from the neck of the robin. It was not yet able to feed from a standing position but it managed to tear at the carcass while resting on its abdomen and heel joints and holding the prey in front with both feet. The other nestlings were not able to remain standing for long periods. When they sank to a prone position, the activity caused the feeder to again utter the "aggressive cackle." The "defense stance" was immediately resumed by the attacked nestlings.

When the female arrived and retrieved the carcass from nestling 2, all the young birds clustered below her and their aggressive actions ceased.

On this date, all the nestlings were able to perceive objects away from the nest. They observed the female as she flew to and from the nest.

Twenty-five days old.—On July 2, activities were essentially unaltered from those of June 30. Events observed for the first time were: (1) Nestling 2 used the "rapid peering" motion in sighting away from the nest. (2) Nestling 2 scratched the top of the head with one toe. (3) Nestling 3 was observed to nibble lightly at the head of nestling 1.

Twenty-seven days old.—On July 4, nestling 1 was observed to pivot the tail with a movement identical to that of the female when she was perched or settling on the nest. Although the tail feathers had just begun to emerge from the quills, muscular reflexes responsible for tail movement were evident.

Nestling 3 was observed to grasp the prey left at the nest by the male and give the aggressive feeding call. This caused the others to assume the "defense stance" as was observed on July 30.

Experimental flight motions were first noticed. Nestling 2 initiated the beating motions and was immediately mimicked by nestling 3. Nestling 1 watched closely. Its head was twisted at right angles to its usual position, with one eye pointing toward the nest floor. This has been interpreted by Sumner (1934:349) as a curiosity activity. He believes that it is a method for the attainment of a better perspective. He states: "In the evolution of the habit the youngster [*Haliaeetus leucocephalus*] had gradually come to tip its head more and more until it was rotated nearly 180°."

The nestlings remained prone throughout most of the day. In one instance, the three nestlings were observed to remain standing for an interval of one minute. In the weighing activities at 11:00 p.m. on July 3, the nestlings were seen for the first time to grip the nest tightly when lifted.

The awkwardness previously connected with defecation movements had disappeared. The nestling preparing to defecate stood facing the center of the nest and at the same time moved backward until the edge of the rim was reached. About two to three seconds before the ejection of the feces, the head was lowered, the neck stretched forward, the hind quarters raised, and the wings extended sideward.

Nest-building actions were performed on this day. Nestling 1 picked up a fascicle of pine needles, carried it in the beak across the nest and dropped it on the rim. A vigorous tugging at the nest floor was also observed which might possibly be a precursor of "excavation" activities.

Twenty-nine days old.—On July 6, the "stabbing reaction" (Bond, 1942:84) was seen for the first time. The nestlings while standing erect would suddenly strike out with one foot and grasp a twig that protruded from the nest platform. The twig would be grasped for a few seconds and then released. These reflex actions in adult life enable the hawks to subdue the prey, but at the immature stages the significance and the motivating stimulus of such behavior is not fully understood. Cade (1953:28–30) presents an excellent discussion of the subject. He quotes Rand (1951:525) who states that attacks on inanimate objects may be "at times the attack on an enemy; at times a response to a strange object; at times the result of over-belligerence; and at times play." It would seem that a certain twig configuration elicited a "stabbing response" in the two nestlings. Nestling 2 struck at a sprig lying in the nest; twenty minutes later nestling 1 struck at the same sprig, and after 33 minutes nestling 2 again grasped the same sprig.

Nestlings were now able to maintain a standing position when moving about in the nest, although balance was still uncertain.

In feeding activities, the nestlings had become less dependent on the female. During one feeding, nestling 2 persisted in tearing flesh from the prey held in the female's talons rather than snatch portions which were disarticulated and held in her beak.

Thirty days old.—On July 7, at the time of weighing and measuring, the fear reaction was first observed in the nestlings. When they were brought to the ground, they sat erect with head held back and beak open; the wings were lifted and extended laterally.

Thirty-one days old.—On July 8, no essential differences in nestling behavior were evident. The prey carcass was often snatched away from the female in the course of feeding activities. The nestlings were apparently motivated by conflicting responses. One pattern of reaction was to snatch the food from the female's beak; this created a disposition of docility in the nestling. Another was to tear flesh from the carcass grasped in the female's talons; this caused an aggressive disposition in the nestling. These "conflicting" dispositions were evident when the female fed the young birds.

Sight was well developed at this age. Flying birds and objects dropped from the blind were immediately perceived by the three nestlings. Vigorous attempts at flight were made by nestling 2. The wings were flapped several times and the talons were closed into the nest matrix to prevent the bird from rising from the platform.

Thirty-three days old.—On July 10, fairly skilled nest-building actions were observed. Nestling 2 took a twig in its beak and pushed it with a wiggling motion of the head into the nest rim.

The nestlings exercised the wings more frequently. They were able to raise their weight slightly off the nest platform for periods of one to two seconds. The wings were flapped vigorously and the legs were momentarily retracted as they raised from the nest.

The inquisitive head-twisting motions previously discussed were again observed. In this instance, the head was rotated completely at 180°. This motion appeared to be used as a method for obtaining a better perspective of a strange object (Sumner, 1934:349).

Nestling 1 while feeding on a carcass was observed to swallow a portion of the intestine. The nestling did not show the hesitancy that the adult female had shown in eating intestinal material.

Thirty-five days old.—On July 12, the nestlings were more skillful in using their wings to lift themselves from the nest platform. They were observed to flap vigorously and leap from one location to another as they moved about the nest. These flight actions often took on the appearance of play activities. After a short flight, a nestling would often run back and forth across the nest, playfully.

On this day, nestling 1 was observed to discard a piece of intestine when it was first encountered. Later, however, after the prey was consumed, the intestine was swallowed hesitatingly.

Intense aggressive behavior was observed when nestling 1 was tearing at a carcass on the nest platform. Usually the nestling that was feeding gave the aggressive call, *ke,ke,ke.* This caused the nest mates to assume the defense position and was enough to discourage the others from attempting to snatch the carcass. However, nestling 2 in several instances was observed also to snatch at the carcass. This caused the feeder, nestling 1, to chase after nesting 2 and strike out with the foot.

On this day a nestling first left the nest and perched on a branch about one foot away. It had been chased there by another nestling in the course of feeding.

Thirty-seven days old.—On July 14, a new observation method was attempted from a blind on the ground. Behavior of the young could not be observed in detail. Nestling 2 was seen to perch on one leg and draw the other up against the breast in a similar fashion to that of the female (p. 387).

Thirty-nine days old.—On July 16, observations were resumed in the blind in normal fashion. The stretching movements performed by the female (p. 387) were performed by nestling 2 on this day. The female fed the nestlings once during the day. Large portions of the carcass were given to the young. When each nestling received food, it would turn away from the others to assure retaining possession of the meat. No cackling or other aggressive behavior was shown, however.

Forty-one days old.—On July 18, nestling 1 was observed to walk awkwardly to a branch beside the nest and assume a perched position. The begging call note usually given by the nestlings had become modified and sounded somewhat like the plaintive scream given by the female when she sighted the male in the nest area.

Forty-three days old.—On July 20, only two nestlings remained in the nest; nestling 3 had died on July 19 and apparently had been eaten by his nest mates.

Nestling 1 performed the instinctive spreading reaction, well known in hawks. The wings were lowered and spread and the head was held low. The action occurred when the female returned to the nest and the nestling was feeding on a carcass. Sumner (1934:350) interprets the spreading reaction as functioning to keep the food from the other nestlings and to maintain balance while the feet are

utilized in subduing the prey. In the instance I observed, it would seem that the spreading of the wings and tail obstructs the view of the challenging hawk and usually prevents further aggression.

The nestlings continued to perch on the branches beside the nest throughout the day. Their ambulations to and from the nest were performed with more agility.

Forty-nine days old.—On July 26, the young birds left the nest and were observed to move about through the branches, reaching distances of 50 feet from the nest. Certain "pathways" through the canopy were used. Whether this was because one bird followed the other or because limitations of strength and agility dictated patterns of movement through the trees could not be determined.

When the young birds perched in the branches, most of their time was spent in preening and sleeping with head lodged under the scapulars. They were also observed to remove strips of bark with their beaks from portions of the perch directly beneath them. These actions were often preceded and succeeded by inquisitive head-rotation movements.

Occasionally begging calls were uttered. These calls resembled the "recognition scream" of the female. Such periodic sounds probably enable the adults to locate the young birds when they range to greater distances from the nest later in the season. The "twitter" call, previously uttered only when the nestlings were in pain (p. 394), was given at the initiation of flight or when the fledglings climbed about in the branches.

The fledglings remained away from the nest most of the day except when prey was delivered. The female persisted in feeding the young. On one occasion she captured a chickaree (*Tamiasciurus douglasi*) and fed it to the fledglings. On other occasions, the male brought food to the nest.

Whenever food was brought to the nest by the male or female, the fledglings would immediately return to obtain the prey. At first the return flight was awkward and often several separate flights from one branch to another would be necessary to cover the distance. Later in the day, single flights were accomplished. Such flights were simple glides initiated from a higher level than the nest, resulting in a loss of altitude. Flights of 20 to 30 feet were made. The first nestling to arrive at the nest snatched the prey and usually consumed the entire carcass, attacking the other nestling if it intervened. At first, landings on the nest were awkward, with the fledgling landing in a heap on the top of the prey item. Later, however, more agility was developed and landings were smooth and accurately performed. "Rapid peering" motions preceded each flight or movement from one branch to another.

Nestlings 1 and 2 spent the night perching at points 40 and 60 feet from the ground, respectively.

FEEDING HABITS

The data reported here were amassed entirely by distant observations, with a 20X telescope, of food deliveries, except in three instances when prey items were retrieved by me from the nest. Eighty prey items were definitely identified, three were tentatively named, and three could only be placed in the categories of "bird" or "mammal." Identification of the prey mammals was occasionally hindered when a head was missing or when fur had been plucked from the body.

Several methods were used to determine the weights of prey items brought to the nest. If the prey item was an adult in whole condition, it was assigned an average weight value for the species. These were determined for each species from specimens caught in the area and from data in the collections at the Museum of Vertebrate Zoology. Hall's data (1946) were used in a few instances.

If the prey item delivered to the nest was partly eaten, it was assigned an estimated percentage of the total weight. These estimates were aided by trial removal of various parts of an animal type and by expressing the remainder as a percentage of the total original weight. A *Citellus beldingi* was used to calculate the percentage values for the small mammals, and a Hairy Woodpecker (*Dendrocopos villosus*) and an Oregon Junco were used for determination of the percentage values for birds.

It was often necessary to make allowance for variations in weight due to age in items brought to the nest. For mammals, weight assignments for young individuals presented no problems. Few young mammals were brought to the nest and those that were brought

matched specimens that had been collected in the course of the study. Nestling robins and Steller's Jays of all ages were brought to the nest. Consequently a method was required for the determination of weight for various ages. From study skins of robins and Steller's Jays, age-weight curves were plotted. Wing feather lengths of prey items brought to the nest could be estimated through the telescope and a weight figure could be assigned to each individual by reference to the age-weight curve.

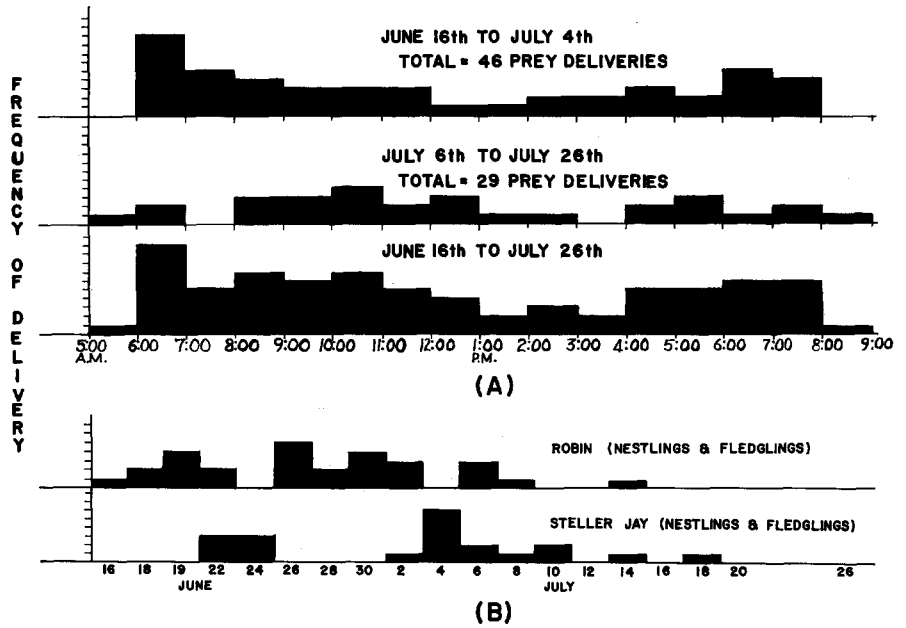

Fig. 6. (A) Daily prey deliveries by male Goshawk.
(B) Seasonal variations in diet of Goshawks.

In instances where the prey could not be identified, the foregoing methods were useless for weight determination. Weight assignments were made in these instances by timing the length of feeding and multiplying by a figure calculated for the amount of food consumed by the nestlings per minute. This figure was determined by recording the length of time taken by the nestlings to consume a prey item of known weight. Small mammals were consumed at an average rate of 5.2 grams per minute, and nestling birds were consumed at a rate of 8.2 grams per minute.

The work of Sulkava (1956) shows that the food habits of nesting Goshawks are best divided into two parts: (1) the prey taken during nest building and incubation, and (2) the animals caught during the period of juvenal development. Adult birds are captured in the first period and nestlings are preyed upon predominantly during the second period. Most probably the shift in the diet is due to the change in abundance of the prey species. If this is true, it would appear that the nestling Goshawks at Donner Lake capitalize on the peak nesting populations of two principal prey species, the American Robin and the Steller's Jay. In view of data gathered from prey deliveries to the nest, it would appear that the robin population reaches a peak slightly earlier than the jay population (fig. 6B). Both peaks occurred when the nestling Goshawks were consuming large amounts of food. A list of food items for breakdown of prey numbers and weights is presented in table 1. From this table it can be seen that the numbers of nestling

birds (60.5 per cent) and the weights of nestling birds (46.1 per cent), account for the largest part of the diet.

Of 87 deliveries of food to the nest, the male accounted for 74 or 85 per cent and the female accounted for 13 or 15 per cent. Of the total weight of prey items brought to

Table 3

Food Deliveries to the Nest[1]

Date	Total	Female	Male	F(ex)	F(in)	Fc	T	Tmn	M[2]	Mt[2]
June 16	5	2	3			2	3	2		
18	6	2	4		1	1	2	2		2
20	7	3	4		2	1	2	1		2
22	6	0	6				4	1		2
24	5	1	4			1	3			1
26	5	0	5				3			2
28	7	3	4		3		1		1	2
30	7	2	5	1		1	1		3	1
July 2	7	2	5	1		1	3?		1	1
4	7	1	6	1			4		2	
6	7	2	5	1		1	3			2
8	4	1	3			1	1		2	
10	6	1	5			1	1		4	
12	3	0	3						3	
14	3	0	3				3?			
16	5	2	3	1		1	2		1	
18	1	0	1				1			
20	3	1	2	1			1		1	
26	5	1	4	1					4	
	99	24	75	7	6	11	38	6	22	15

[1] Key to symbols at column heads: F(ex), female catches prey outside the nest area; F(in), female catches prey in the nest area; Fc, cache retrieve, female returns stored food to nest; T, "transfer," male exchanges food with female; Tmn, "transfer," then male flies immediately to nest; M, male alone delivers food to the nest; Mt, male gives food to the female at the nest.

[2] Columns M plus Mt give the total number of deliveries by the male to the nest.

the nest (5866 grams), the male brought 4838 grams or 82.5 per cent and the female brought 1028 grams or 17.5 per cent.

The daily frequencies of delivery by the male show a slight tendency to fluctuate as the season progresses. Medium daily frequencies were recorded at the initial stages of observation; higher numbers of deliveries were evidenced when the nestlings were at the period of maximum growth and maximum food consumption; medium and low frequencies were again observed just before the young left the nest (table 3; fig. 6A). This increase and decrease could be caused collectively or in part by: (1) changes in prey abundance, (2) the female's behavior toward the male; this could indirectly reflect the increased food demands of the young, and (3) the hormonal state of the male.

The male delivered food to the nest at all hours of the day (fig. 6A). However, it is evident that more deliveries occurred in the early morning between 6:00 a.m. and 7:00 a.m. and in the afternoon and evening from 4:00 p.m. to 8:00 p.m. than at other times. A moderate peak is also evident from 8:00 a.m. to 11:00 a.m. In the course of the observations, 44 deliveries occurred in the morning (5:00 a.m. to 1:00 p.m.) and 31 occurred in the afternoon (1:00 p.m. to 9:00 p.m.). The pattern of daily deliveries was altered

as the season progressed. During the early period (June 16 to July 4), deliveries were more numerous after dawn and immediately before dusk. During the later period (July 6 to July 26), deliveries occurred throughout the day with a slight peak being evident from 11:00 a.m. to 1:00 p.m. (see fig. 6A).

Weight consumed by the nestlings.—The total weight of prey consumed by the nestlings for each observation day has been plotted in figure 7. A peak in the daily weights of prey consumed by the nestlings is evident, but the total rations are highly variable from one day to the next.

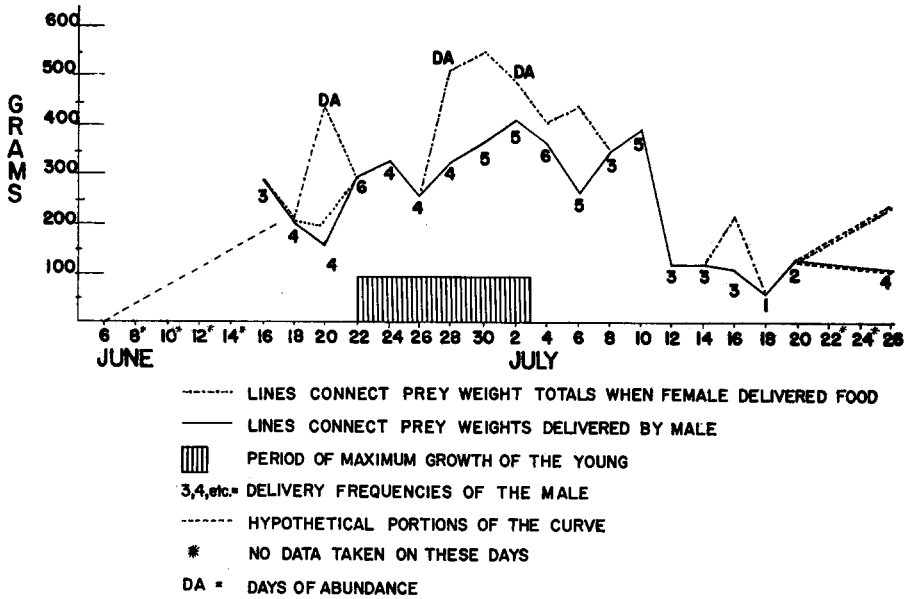

Fig. 7. Food consumption of young Goshawks. Data were not taken on June 8, 10, 12, 14, and July 22 and 24. On these days, the curve was completed by extrapolation. On June 20, dotted lines indicate the form of the curve if a carcass had not been thrown from the blind (p. 389). Days of abundance (DA above) indicate times when food brought to the young hawks was in excess of their daily needs (p. 387).

An observation day was considered one of abundance if the prey was cached and left stored over night. This occurred three times (see fig. 7). One of these days, June 20, can be explained by the fact that a carcass was tossed from the blind by me, retrieved by the female, and fed to the young. The dotted line would represent the curve if this extra item had not entered the daily ration. The two other days of abundance (June 28 and July 2) occurred during the peak period of food consumption. The question arises as to whether prey abundance influences the form of the food curve. More specifically, is the breeding season timed in the Goshawk so that maximum prey abundance occurs when the young are consuming the maximum amount of food and are in the state of maximum growth? Since "normal" days of abundance occur when daily food consumption is at its highest, one would logically conclude that the peak in the food curve is caused by prey abundance. When separate curves are plotted for prey weights contributed by each of the adults (see fig. 7), it is evident that the foraging efforts of the female are mostly responsible for the peaking of the food consumption curve, whereas the male but slightly increases the daily ration at the time of maximum consumption.

Two factors influenced the foraging activity of the female. One of these is prey

abundance in the nest area. As mentioned earlier, the female captured prey in this area; these captures were completely fortuitous and clearly were affected by prey abundance. If the animals had not entered the nest area, they would not have been captured. But after June 30, the female foraged outside the nest area. Subsequent to this date, the increase in daily rations was not necessarily due to maximum prey abundance but was caused by the addition of the female's prey items. The female foraged when the young were most in need of food.

A figure has been determined for the total weight of prey necessary for two nestling Goshawks from the time of hatching until they begin to leave the nest (49 days). Since data on daily rations are absent for two intervals of this period, it has been necessary to sketch in the missing portions of the curve and thereby derive the additional prey weight values (fig. 7). The total estimated weight of prey consumed by two nestling Goshawks during 49 days of development was then estimated to be 13 kilograms.

SUMMARY

The nest of a Goshawk was located in a dense stand of lodgepole pine near Donner Lake, Nevada County, California. Activities of the three young and parents were watched from June 16, when the young were judged to be 9 days of age, to July 26, when the young fledged. The youngest nestling died at 40 days of age, apparently from undernourishment.

Division of labor between the adult male and female was marked. During the initial stages of the study, the female remained close to the nest day and night. She left the nest only to receive food from the male, to capture prey near the nest, to cache prey items, and to collect sprigs to bring to the nest. Her activity changed as the season progressed. Brooding time per day decreased and then ceased altogether; time spent near the nest decreased. After June 30, the female left the nest area to hunt. The female's sprig collecting activity, apparently a displacement behavior, reached a peak as brooding ceased.

The male was responsible for capturing 85 per cent of the food for the brood, but only the female fed the young. She persisted in portioning out food to the nestlings even after they were capable of feeding themselves. The female aggressively defended the nest area from human intruders, but the male showed little concern.

The transfer of prey items from male to female occurred throughout the study with evidence of "hostility" on the part of the female after the food was exchanged. It is postulated that this hostility of the female toward the male is the mechanism which caused increased delivery of prey items by the male to meet the food demands of the young.

Goshawks were observed to capture prey by swooping from a hidden position and by searching in the grass of a small pond for hidden ducklings. Large animals appeared to be cached and periodically fed upon by the male before being brought to the nest; small prey apparently was delivered to the nest soon after capture. The male in foraging, evidently returned to prey nests that contained more than one nestling.

Nestling birds accounted for the largest part of the Goshawks' summer diet. Daily prey weights consumed by the nestlings in the course of the study were recorded, and the peak in daily weight rations was coincident with the period when the food demands of the young were maximum. The peak of the food-consumption curve is caused by the food items contributed by the female. Factors responsible for this increased foraging activity of the female are prey abundance in the nest area and a behavioral change causing her to hunt outside the nest area.

The total weight of prey consumed by two nestling Goshawks in 49 days of development was about 13 kilograms.

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