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FALCONIFORM REPRODUCTION; A REVIEW.

PART 1. THE PRE-NESTLING PERIOD

by

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This series, *Raptor Research Reports*, is issued by the Raptor Research Foundation, Inc., for recording materials such as literature reviews, bibliographies, translations, and reprints, to provide access to the often scattered primary sources. The series is inaugurated with the first part of a review of serial literature on falconiform reproduction.

Editor of this report: Byron E. Harrell

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INTRODUCTION

In the light of recent attempts at captive breeding of raptorial birds there has been an increasing need for an extensive review of the periodical literature concerning falconiform reproduction, organized to give experimenters a general idea of the complex biological phenomenon they are striving to harness. This paper has been written with this aim in mind.

Much detailed information has been purposely included in the hope that the basic principles of both normal and aberrant behavior of wild raptors may be better understood so that every advantage can be taken by current researchers of knowledge gained by our predecessors. It is thought that this would serve better the needs of both ornithological students desirous of specializing in avian ethology or reproductive physiology and falconers who are diligently working to "show willingness" to preserve our declining raptor populations for future ornithologists as well as the followers of their sport.

Too often, animal reproduction has been presented with little emphasis on the ethological or behavioral aspects and how these affect the general cycle. The wide differences in behavior between species of raptors, and even between different pairs of the same species, precludes the use of the term "typical" behavior. It is this reviewer's opinion, therefore, that much of the value of collected data lies in the fact that certain things have occurred. Some behavioral patterns included herein occur often enough that we expect to see them frequently; others may never be observed again. Nevertheless, in this review virtually all available behavioral information is included. This should facilitate comparison of observed captive behavior and the wild situation, with the possibility of aiding evaluation of captive breeding projects in order to improve their effectiveness in the years to come.

As with most review articles, which may be better described as integrated, annotated bibliographies, none of the information is original. Any statements or conclusions made herein are undoubtedly prompted by the literature reviewed. but extensions and analyses of the data are the responsibility of the reviewer. Apologies are given at this time for any misrepresentation or misinterpretation of the papers reviewed.

This paper was originally intended to cover the entire subject of falconiform reproduction, but due to time limitations, emphasis was necessarily placed on two general groups. hawks and falcons. Two or

three significant papers on eagles were included for comparative purposes. The papers reviewed by no means exhaust the subject, but represent the total of pertinent papers available to the reviewer between September and December, 1967. It must also be remembered that the periodical literature represents only half of the information available. Information in ornithological books and non-serial volumes has not been included, since a large part of this reviewer's intent is to aid those who do not have extensive serial listings at their disposal. Also, the most recent papers concerning captive breeding have been omitted.

The review is divided into two large parts: The first is basically a treatment of selected topics concerning falconiform reproduction up to and including hatching, while Part 2, to be finished by March, 1971, will cover the development of young raptors from their physical condition at hatching through the immediate post-fledging period. In addition to an extensive section on food and feeding, emphasis in Part 2 will again be placed on behavioral considerations as much as the literature permits, but much morphological data will also be included.

Appreciation is due Dr. Paul H. Baldwin of the Department of Zoology, Colorado State University, for his assistance in supplying understanding and reading of the manuscript. The paper is partial fulfillment of a special problems course offered by the Department of Zoology, Colorado State University. Dr. Byron E. Harrell of the Biology Department, University of South Dakota and Raptor Research Foundation, Inc., was instrumental in seeing the manuscript to press and provided welcome criticism of the logic, grammer and format of the review. My wife Sharon selflessly typed the rough draft and original manuscript.

[*Editorial Note*: Scientific names of species mentioned are listed in the Species Index. In general the common names follow the usage of L. Brown and D. Amadon, *Eagles, Hawks and Falcons of the World*. The names of Peale's Falcons and Shaheen, both races of Peregrine Falcon, are also used. Authors referred to in the text are indexed in the Papers Reviewed and Author Index. The detailed Table of Contents is used in place of a subject index.]

CHAPTER 1. ANATOMY AND MORPHOLOGY

A definitive anatomical work on the falconiform reproductive system does not exist in the serial literature and this reviewer is aware of none in other ornithological publications in English. If such a study has been printed, it should be made known to all those interested in raptor aviculture, since therein would lie the fundamental basis for all reproductive study. If our knowledge is lacking in this area, it would be well for someone to start a comprehensive anatomical inspection of the pertinent genera immediately. A stepping off point for such a study might be H. F. Gadow's volume in Bronn's *Klassen und Ordnungen des Thierreichs*, Volume 6, or perhaps M. Furbinger's anatomical monographs.

BILATERAL OVARIAN DEVELOPMENT

The only major point concerning this vital area substantially treated in scientific periodicals is the persistence of the right ovary in many raptorial species. Typically, birds have unilateral (one-sided) development of the female reproductive organs with only the left ovary and oviduct functional.

Certain falconiforms show bilateral (two-sided) development of ovaries to almost equal size. This is considered the primitive condition (187a, 188). In other species there is unequal bilateral development, the right ovary being smaller, but retained throughout life. Between these two extremes is an even gradation of the degree of development of the right ovary depending upon the species considered. There is considerable variation even within the same species. In this light some have postulated that the birds of prey represent an intermediate evolutionary stage in a direct line toward complete elimination of right ovarian development as seen in other orders of birds (187a).

In species with a persistent right ovary, however, all eggs are still produced from the left side, since the right oviduct is non-functional. The maximum development of the right oviduct in full grown birds of prey mentioned in all articles herein reviewed is a two-centimeter-long vestige (188).

Gonadal development. The establishment of significant asymmetry in gonadal development in most birds appears to take place during the migration of germ cells to their final site in the gonadal region, although slight differences in the number of germ

cells on either side may be inherent in the original blastoderm. In all species there is evidence for early equable development with respect to distribution and number of germ cells on the two sides. This is emphasized by Stanley (187a) in his work on the Cooper's Hawk and Marsh Hawk. This equality is maintained or destroyed in varying degrees, depending upon the species, during germ cell migration. In the Cooper's Hawk and Marsh Hawk where the right ovary is usually more than half the size of the left, there is little migration of germ cells across the mesentery from the right to the left side. In the Red-tailed Hawk where the right ovary is small or wanting, there is much shifting of germ cells from right to left (188).

The movement of the splanchnic mesoderm destined to be the cortex and albuginea of the gonads moves toward the inner border of the mesonephric body between this body and the dorsal root of the mesentery. This movement is essentially the same in hawks and other birds. The movement of germ cells, however, toward their position in the cortex of the future gonad begins much earlier in hawks. This was noticed by Stanley and Witschi (188) in the Cooper's Hawk where early firm investment of germ cells in the future gonadal cortex is believed to prevent exchange of germ cells from the right to the left side. Thus, a right ovary of noticeable size develops. Perhaps in those raptorial species, as with the chick, where only the left ovary persists, the movement of germ cells occurs later allowing migration of germ cells to the left side. Stanley and Witschi (188) were not able to establish this definitely.

The presence of a rudimentary right oviduct is not directly correlated with the size of the right ovary. In all birds there appears, initially, symmetrical development of the oviduct followed, secondarily, by a lag in development on the right side beginning at the 18th day of incubation in Red-tailed Hawks (8th to 9th day in the chick) (188). The right oviduct in this species ceases to increase in length by the end of 20 days of growth. After 26 to 28 days of incubation, right oviducts of Red-tailed Hawks begin to degenerate and do so until, at hatching, only a vestige remains (187a).

During the breeding season the follicles of the left ovary and those remaining in the right ovary enlarge. Since there are usually more ripe follicles in the left ovary even where there is equal bilateral development, all species show asymmetry at this time (188).

As evidence of in-season follicle development in the right ovary, Snyder (184) found enlarged bilateral ovaries which appeared functional in a Marsh Hawk collected during the breeding season. A dissection of an adult Cooper's Hawk by Fitzpatrick (76) revealed a good-sized left ovary containing many "ripe" follicles, but some of the follicles in the right ovary were larger than the smallest in the left indicating at least some follicle development on the right side. Stanley (187a) states that evidence indicates that the right ovaries of

raptorial birds can produce viable ova.

Only one case of actual ovulation in the right ovary is documented (192). This was in a female Northern Goshawk shot over her nest with three eggs. The left ovary showed evidence of two ovulated follicles, but more important was a single ovulated follicle in the right ovary. The egg from the right side apparently passed down the left oviduct, since the right duct was non-functional.

It is worth mentioning at this point that in the males of species showing redimentary or much reduced right ovaries in females, there is usually asymmetry with respect to testis size, again the left being the largest (188). Asymmetry in the male organs is usually less pronounced, however (187a).

Species considerations. Gonadal asymmetry in general is least pronounced in vultures and buzzards, most prevalent in the true hawks and intermediate in the true falcons. It has been found that closely related species found in the New and Old World show similar types of ovarian asymmetry (188).

Table 1 includes those raptorial species with confirmed bilateral development of the ovaries and literature references. It should again be emphasized that there is much variation within the species mentioned. Contrary to the listings, M. Wood (230) found individuals with right ovaries absent in the Red-tailed Hawk, Red-shouldered Hawk, Marsh Hawk and Peregrine Falcon. The Red-tailed Hawk shows the most variation having either equal or unequal bilateral development or left-side unilateral development. The European Sparrow-hawk and the Sharp-shinned Hawk of North

TABLE 1. BILATERAL OVARIAN DEVELOPMENT

Species	References
1. Northern Goshawk	(75, 76, 230)
2. Sharp-shinned Hawk	(76, 185, 187a, 230)
3. Cooper's Hawk	(74, 76, 185, 187a, 230)
4. European Sparrow-hawk	(75, 76, 177)
5. Red-tailed Hawk	(75, 76, 185, 187a, 230)
6. Red-shouldered Hawk	(187a, 230)
7. Broad-winged Hawk	(76, 185, 187a)
8. Rough-legged Hawk	(187a, 230)
9. Greater Spotted Eagle	(177)
10. Golden Eagle	(187a)
11a. Marsh Hawk	(29, 76, 185, 187a, 230)
11b. Hen Harrier	(177)
12. Peregrine Falcon	(76)
13. American Kestrel	(76, 185, 187a)
14. Common Kestrel	(75)

America show the most consistent bilateral development (187a). For complete tables listing species, plumage, sex, right and left gonad weights and right oviduct development of 67 specimens see Stanley and Witschi (188:331-332).

SEXUAL DIMORPHISM

Sexual dimorphism with respect to size, the female being the larger, is more conspicuously developed in the orders Falconiformes and Strigiformes than in any others. This subject was studied by N. P. Hill (105) to determine in what species and to what degree it is exhibited. He came to the following conclusions: First, there is very little size difference in the vultures, but the male may be only two-thirds the size of the female in falcons and accipiters; second, there seems to be no ecological explanation for the difference in size, there being a better correlation between taxonomic position and the percentage of difference; and third, this dimorphism is manifested in a decrease in the size of the male rather than an increase in the female. Experiments done by Willoughby and Cade (225) show that sexual dimorphism has no effect on the sexual behavior of captive American Kestrels.

American Kestrels, as well as a few other species, show a dual sexual dimorphism, both in size and plumage coloration. In the Kestrels the female is larger, but the male is more distinctly colored. The adult female Marsh Hawk is basically brown, the male basically gray. Other examples of color dimorphism exist even in the eagles (32).

Nonetheless, weight difference is the most marked type of sexual dimorphism. Table 2 gives comparative weights for males and females of several species. It is interesting to note the complete absence of overlap in the Sharp-shinned Hawk. Imler (112) found a similar difference in the Ferruginous Hawk where one female weighed almost twice as much as one of the males.

Cade (39) points out that sexual dimorphism is more pronounced in the larger falcons than in the smaller. Just the opposite was encountered in certain hawks by Sutton (201). For more extensive treatments of the significance of sexual dimorphism see Cade (39) and Amadon (6).

TABLE 2. SEXUAL DIMORPHISM

1. Northern Goshawk			(231)
Adult females	693 to 1500 g.	(Aver. 1082 g.)	
Adult males	668 to 1167 g.	(Aver. 861 g.)	
2. Sharp-shinned Hawk			(201)
Adult females	6 to 8 oz.		
Adult males	3 to 4-1/8 oz.		
3. Gyrfalcon			(39)
Females	1200 to 2000 g.		
Males	900 to 1400 g.		
4. Peregrine Falcon			
Females	1244 to 1597 g.	Beebe (Pacific	(14)
Males	810 to 1058 g.	Northwest)	
Females	1020 to 1320 g.	Bond (Western	(20)
Males	665 to 875 g.	North America)	
Females	750 to 1200 g.	Cade (arctic	(39)
Males	500 to 800 g.	Alaska)	
5. Merlin			(20)
Females	205 to 255 g.		
Males	191 g.		

that intraspecific tolerance in Red-tailed Hawks and Great Horned Owls is less than the interspecific tolerance between the two species. This is interesting, but not surprising if one considers territory as a repelling factor between birds of the same species.

Functions of territory. Territory in birds of prey has several possible functions. Among those proposed are sexual isolation, monopolization of the food supply, dispersion of individuals, conditioning to an area and general defense of the pair, the nest and the young. Since acquisition of mates and establishment of territory may occur simultaneously, territorial behavior may also function to bring the sexes together and to strengthen the pair bond.

Sexual isolation. The obvious advantage of sexual isolation is the reduction of competition (7). Courtship and copulation can occur without interference. Promiscuity is substantially eliminated. Perhaps more important, conflict is reduced in the aggressive, pugnacious species comprising the order Falconiformes.

Food supply. Monopolization of food supply has obvious advantages in species which establish mating, nesting and feeding territories. Conflict occurs between species with overlapping ecologies of which food supply is an important aspect. Therefore, the Golden Eagle and Harpy Eagle protect their food supply during the nesting season when their mobility is restricted (7). This has apparent survival value since the eagle is assured of exclusive use of its relatively limited number of large prey species while the young are being raised—a time when ample food has great biological significance.

Ecological familiarity. Conditioning to an area implies efficient and effective utilization of the environment. Establishment of territory probably reveals the subtlities of the surroundings, *i.e.*, produces "ecological familiarity," which, after a period of time, makes it easier for the birds to carry on their predatory existence.

Population dispersion. Dispersion of the population, if applicable as a function of territorialism, would have the effect of controlling, at least partially, the population density of the species. Ratcliffe makes this point, but continues: ". . .territorialism is not in itself an ultimate factor but has evolved in relation to food supply so that the numbers of predators are permanently balanced against this factor" (150:38). With this statement one begins to see the intricate nature of the matter at hand. A territory is both static and dynamic; it is a stationary piece of ground, but a living ecological enterprise.

Design of a territory. The final design of a territory depends both on rigid and plastic factors; some are pre-existing and unchangeable, while others fluctuate or are changed by the birds. A territory is molded from the existing conditions such as the prevailing

vegetation, general topography of the area, food supply, territorial pressure and seasonal climate.

Vegetational factors. The vegetation of a region is a vital matter. Northern Goshawks nest in forests while the desert falcons prefer open expanses; a Cooper's Hawk might be vigorously aggressive in a certain grove of trees, but ignore disturbances in an adjacent field. Fitch *et al*. consider adequate perches "the most essential feature of a territory" in Red-tailed Hawks (73:207). Plants are also important as refuge for prey and as material for nest building.

Topography. The geological features and topography of an area are important to the final design of a territory. The prime example here is the Peregrine Falcon which almost always requires rocky cliffs or steep river banks. Its distribution and therefore its territories are limited to those areas where such features exist. In addition to the above, Hickey states that these cliffs must have a suitable egg-site, since the "Peregrine appears to possess an absolute requirement in that the eggs must be laid in a hollow which is scraped out of dirt, gravel, or similar material" (102:180). Although this point is disputed below, it illustrates one of the rigid topographical factors which may be involved in territorial design.

Other topographical considerations include an apparent preference of falcons for overhung nest-sites, but this is by no means an absolute requirement. As we will see below when considering intra- and interspecific close nesting, these nests are rarely in view of each other, there always being an intervening cliff or ridge.

Some permanent features of a territory which may be used as boundaries are man made. Errington (65) confirmed the use of a fence and a ditch as absolute limits of three close-nesting pairs of Marsh Hawks.

Food supply. The importance of a fluctuating food supply in territorial design was pointed out by Hickey (102), but he suggests that this factor had very little effect on the distribution of the Peregrine in the eastern United States. He states, with caution, that this may be due in part to the effectiveness of the Peregrine as a hunter of a wide variety of bird species.

To the contrary, F. L. Beebe found that food supply did affect the design of Peale's Falcon territories with virtually every active eyrie located within easy striking distance of one or more colonies of one or more of the very limited variety (four species) of prey species. He speculates, therefore, "that territorial behavior is markedly modified by the abundance of food. . ." (14:163).

Fitch *et al*. (73) found that territories of Red-tailed Hawks are often much larger than necessary to supply the family with food and from this suggest that intraspecific intolerance appears to be more of a limiting factor in territorial design than food supply.

Territorial pressure. Intra- and interspecific intolerance, both

treated in detail below, are important faunal involvements. In the Scottish Highlands, Ratcliffe (151) found that the actual breeding density of Peregrines was reduced by a high Golden Eagle population, the limiting factors being at least nesting space and possibly food supply.

Climate. Climate is another fluctuating influence on territory or perhaps, more correctly, breeding range. Humidity, rainfall and temperature all may be factors, but it is difficult at best to determine the importance of each of these factors (102).

PEREGRINE FALCON TERRITORY.

Since the Peregrine is an extensively studied species and the captive breeding of it is of primary importance, a specific treatment of the proposed theories of its territorial behavior is warranted before going on to the interspecific manifestations of territorialism.

General description. Cade describes territory in Peregrines as follows:

> "While peregrines show extremely strong attachment for their nesting cliffs and defend them with vigor against trespassers, there do not seem to be any very clear cut bounds around the cliffs which are regularly patrolled or which are always defended against trespass by other peregrines. . . .In other words, territorial behavior of peregrines is not a simple, all-or-none aggressive response related to a specified unit of terrain; it is a variable, multifactorial response the strength of which varies with the present motivation of the resident falcon, the phase of the breeding cycle, the attitude of the intruder. . . .weather conditions, and the time of day" (39:198-199).

Hickey (102) advanced a similar theory several years earlier, at least with respect to defense of a small amount of ground. Bond mildly disagrees, stating that if a foraging area were not defended "it would be difficult to account for the fact that pairs are well spaced, even on apparently ideal cliffs with innumerable suitable potholes and enormous supplies of food" (23:106).

Breeding density theories. The major theorists on this subject mention or try to explain the breeding density of the Peregrine, partially at least, on territorial behavior. Since Cade (39) mentions that territorial aggressiveness is a density limiting factor in arctic Peregrines, F. L. Beebe (14) finds the lack of territorial or other conflict between established pairs of Peale's Falcons nesting in areas

of rather high density a "most puzzling observation."

Ratcliffe brings us back to earth again by speaking of "a repulsion effect between contiguous pairs. . .indistinguishable from that produced by territorialism" (151:63). If one narrowly defines a territory as that area defended against intruders of the same species or even certain other species, this repulsion is not likely caused by true territorialism. This follows from the fact that Peregrines apparently establish only a mating and nesting territory, not an extensive mating, nesting and feeding territory requiring defense of large boundaries. If on the other hand one accepts the broader limits of the term "territory" as set down by E. Howard (*Territory in Bird Life*, London, 1920), the subtle intolerance between pairs of Peregrines "falls within the original concept of territory. . .as serving a regulatory function" in determining breeding density (151:63).

One other theory concerning the breeding density of Peregrines, and which will be treated more thoroughly under the topic "nests and nesting," was proposed by Hickey as follows:

> "Since cliffs are so scarce, territorial jealousy is, therefore, a factor of considerable importance in restricting the density of nesting peregrines. This is especially evident where a long escarpment is the only available nesting site for twenty or more miles (32 km.) around" (102:181-182).

Historical occupancy. Another interesting aspect of Peregrine territorialism is historical occupancy. Territories gain their stability partially through continued use (7). Hickey (102) tells of 14 Peregrine eyries in eastern North America that had been occupied for over fifty years. This phenomenon is best known in European Peregrine eyries. "Through the literature, several sites can be traced back for over 100 or even 200 years, but much more remarkable, there are at least three island sites aged more than 350 years. . ." (71:154). The longest occupancy of a Peregrine Falcon territory by a single female is variously listed as between seven and thirty years (23, 91, 150).

Many other species use the same general territories from year to year, although not necessarily the same nest (10, 57, 151). Dixon (57) found seven nesting territories of the Red-shouldered Hawk in an area of California in 1907 and upon his return twenty years later found all seven areas occupied by Red-shouldered Hawks without exception. According to Tinbergen (206), European Sparrow-hawks use the same territories year after year. As nearly as he could ascertain these territories were used a minimum of 4.2 years (on the average). Cameron (40) and many other observers believe that historical occupancy is the rule for eagles.

Constancy of occupation has been speculated to result from several factors: First, attraction of the nesting cliffs as ecological magnets (102); second, survival of at least one bird of a pair which returns to occupy the territory (39, 206); and finally, return of offspring to the vicinity of their birthplace (69).

INTERSPECIFIC RELATIONSHIPS.

Conflict between species is part of molding a territory. Boundaries must be compromised between adjacent pairs of the same species and in many cases with adjacent pairs of other species with which there is ecological overlap. This conflict may or may not involve true competition for nesting sites and/or food supply.

Although Cade (39:246-254) gives well planned, concise coverage of interspecific relations particularly with respect to the Peregrine and Gyrfalcon, there is much pertinent data scattered throughout other papers.

Provocation of attack. Some of the general factors involved in provoking an attack include the mannerisms and size of the intruder and the stage of the breeding cycle of the nesting raptor.

Mannerisms of the intruder. Liversidge (120) speculates that interspecific attacks made by the African Little Sparrow-hawk near the nest were initiated mainly by the noise of the passing bird. Certain kingfishers, hoopoes and cuckoos were allowed nearer the nest if silent, but were chased off if noisy. Selous (172) observed similar behavior in another species of Sparrow-hawks. A Carrion Crow was squawking after being disturbed by the observer in the same grove of trees as the European Sparrow-hawks. Upon hearing the noise, the male Sparrow-hawk flew to the crow and struck it a good blow on the back. The incident was interesting, "for it shows that the hawk was irritated simply at the noise made by the crow. . . .had she been silent she would probably have escaped his observation altogether; nor could it in any case have been her mere presence that annoyed him, since these hawks and these crows have been fellow-denizens of this small plantation probably since early spring, their home-trees separated by but a few paces" (172:66).

Size of the intruder. Lawrence (119) believes that the size of an intruder is a factor in releasing territorial defense in Merlins. Smaller birds such as swifts, waxwings and chickadees were usually allowed free passage in the immediate nesting vicinity, but larger birds such as herons, crows, hawks and especially Golden Eagles elicit defense reactions at distances of a half-mile or more.

Stage of breeding cycle. Interspecific relations, as with territorial defense in general, are more strained during certain periods of the nesting cycle. When young Peale's Falcons are in the nest, a Bald

Eagle is attacked by the adult falcons at a greater distance from the eyrie than at any other time. In addition to this, F. L. Beebe (14) noted just the opposite when humans disturbed Peale's Falcons during the fledging period; the falcons allowing closer approach that at other times.

Other interspecific considerations. The remaining territorial observations have been broken into four categories: Relations with other raptors; relations with non-falconiform avian species; defense against non-human, non-avian species; and effects of human intrusion.

Relations with other raptors.

(A) *Intrageneric relationships.* Two species of the same genus may occupy the same general area. This type of interspecific relationship usually involves two species of drastically different size. Liversidge (120) found a pair of African Little Sparrow-hawks and a pair of African Goshawks exploiting the same area, the one preying on small birds and the latter on large birds. This may not always be a successful arrangement. In Europe, Tinbergen (206) points out that territories of Northern Goshawks and European Sparrow-hawks evidently overlap since the smaller, both as adults and nestlings, was victim of predation by its larger relative.

(B) *Interspecific cooperation.* The interspecific relationship need not be hostile. Burns (36) actually observed a pair of Broad-winged Hawks assisting a nesting Red-shouldered Hawk trying to scare an intruder from her nest. It is doubtful that a modern student of behavior would interpret this incident in the same manner, however. A better example would be Cade's (39) findings of repeated close association of Peregrines and Rough-legged Hawks on the arctic slope of Alaska to the extent that where one was found, the other could be expected. Gyrfalcons did not show the same tolerance for the hawks. Gyrfalcons seemed to have mixed reactions, nesting near them on one cliff and preying upon them at other locations.

A remarkable case of "joint feeding" (interspecific food exchanges) was observed by Lundevall and Rosenberg (121). "Joint feeding" has been recorded between various passerines, but it is quite rare in the falconiforms. The following passage sets the circumstances:

> "At one of the nests [of Pallid Harriers] we observed that a female of *Circus pygargus* [Montagu's Harrier] was watching nearby. Suddenly she flew up. At the same moment we saw a male of the Pallid Harrier arrive. The female flew to him and asked for food. To our surprise he threw the prey to the Montagu's female just as if she had been his own, and then she went down on the nest to the

> young of the Pallid Harrier. The male disappeared immediately. . . .After having delivered the prey the female stayed and flew over the nesting-place. Now the Montagu's Harrier [male] arrived and as usual among the harriers he was chased by the female to go out hunting again, which he did very unwillingly. After this the female started hunting on her own in the vicinity. . . .After one and a half hours the Pallid male came back with prey and the Montagu's female flew up as before to get it, but was this time completely ignored. The male instead went directly down and put the prey in the nest and disappeared. Later on he came twice again with prey, which he would not give to the female, who was still calling for food. Not until the fourth time did he give her the prey in the same way as before. The Montagu's male came back without prey and was again chased away by the female" (121:601).

Lundevall and Rosenberg explain this situation in the following manner: Apparently, the pair of Montagu's Harriers had lost their nest but were still living together. The Pallid Harrier male had lost his mate. In the active Pallid Harrier nest two young had fledged and one remained. Therefore the Montagu's female was able to satisfy her mother-instincts and because of the similarity in color between young female Pallid Harriers and adult female Montagu's Harriers the male Pallid was duped into reacting as if the Montagu's female was one of his fledged young. This is substantiated by the fact that the Montagu's female was fed every fourth time as if in rotation with the three young Pallids. This rotation has been observed in other harriers. Presumably the male Pallid could not count either.

(C) *Interspecific nesting relationships.*

(C1) *Interspecific exclusion.* The large falcons in Alaska and indeed throughout the world have a particular intolerance for Golden Eagles (23, 39, 150) and Bald Eagles (14). Ratcliffe (150) states that Golden Eagles in the British Isles have first choice of nesting sites, their presence nearly eliminating occupancy by Peregrines or Ravens for several miles around. In the Scottish Highlands the Golden Eagle population may be an important factor in limiting the population density of the Peregrine. One hint as to the cause of this intolerance involves strong circumstantial evidence of Golden Eagle predation on young Peregrines and Bond (23) gives direct evidence of a Golden Eagle destroying Peregrine eggs.

The exclusion of Peregrines and Golden Eagles from the same nesting area is not carried over to Bald Eagles, however. F. L. Beebe (14) found extensive breeding overlap between Peale's Falcons and Bald Eagles with nestings as close as 400 yards. This overlap did not, however, preclude conflict between the two species even at

considerable distances from an active falcon eyrie. In contrast to a lack of intraspecific territorial conflict between pairs of Peale's Falcons, there is much conflict between the falcons and the eagles. "Any eagle passing close along the shore. . . .is passed from pair to pair, and its progress can be followed by the sound of screaming falcons. . ." (14:163). Cade (39) has observed "passing" of a Golden Eagle along from Peregrine eyrie to Gyr eyrie on the Colville River in Alaska.

Before leaving the subject of one species precluding the nesting of another, it should be stated that Ratcliffe (150) also found that the presence of Peregrines or Ravens excludes Common Kestrels and Merlins, although Ravens sometimes tolerate Kestrels on the same large cliff. Another instance of competition for nest-sites between raptorial species is documented by Orians and Kuhlman (135). Of 48 Great Horned Owl nests visited, 31 were built by Red-tailed Hawks and, as the hawks often reuse their nest, some species conflict is suspected.

(C2) *Relationships involving owls*. Concerning owls, Hagar (89) also discusses territorial disputes between Red-tailed Hawks and Great Horned Owls. In 19 attempts at nesting within one-half mile of each other there were nine failures by the hawks and only two by the owls, indicating at least that the latter species is more often victorious in their disputes. Other factors are involved, however, such as the fact that the owls nest earlier and usually have established themselves in an area before the hawks arrive.

Hamerstorm and Hamerstrom (92) observed an apparent interspecific territorial conflict between a pair of Cooper's Hawks and a pair of Barred Owls nesting 200 yards apart.

Other evidence for competition between raptors for nesting sites involves eggs of two species found in the same nest. Decker and Bowles (53) found a Red-tailed Hawk egg in a nest with five Prairie Falcon eggs. Speculation is that the hawk laid the final egg of a clutch destroyed by Ravens in the falcon's nest prior to laying by the falcon or that the falcon evicted the hawks from the eyrie after they had already laid a single egg. Hanna (95, 96) records two instances of finding eggs of the American Kestrel and Screech Owl in the same nest. On the first occasion the owl evidently won possession of the nest-hole, since it was incubating four Kestrel eggs and four of its own. In the other case the opposite was true; the Kestrel was incubating two owl eggs and four of her own. F. A. Sumner (199) writes of a nest containing four nearly fledged Kestrels and a nearly fledged Screech Owl. All apparently left the nest.

The relationship between falconiforms and strigiforms is not always one of conflict. The Marsh Hawk is relatively tolerant of Short-eared Owls around its nest.

(C3) *Relationships between eagles*. For comparison, interspecific

(C7) *Semi-colonial nesting*. Semi-colonial nesting seems evident in only one large group of falconiformes—the harriers. Hecht (101) believes Marsh Hawks approach colonial nesting, tending to nest in "clumps" despite territorial disputes. His study area supported five Marsh Hawk nests within one square mile. Speculation is that this intraspecific relationship may provide nest security and augment nesting success if one of the parent birds is lost.

There is little evidence to support a notion that close proximity of harrier nests is caused by limited nesting habitat. Errington (65) found three pairs of Marsh Hawks nesting in a very small area. The closest nests were about 130 yards apart, while the third was equidistant, 400 yards away from the other two. The proximity of the nests was inexplicable, there being considerable space to spread out. Errington was afforded a great opportunity to observe the dynamic nature of territory at work. Birds carrying prey were observed taking "the long way home" to avoid trespassing on the territory of the other pairs. On one occasion all six hawks were observed in one territorial battle. The intraspecific conflicts became less frequent as the summer progressed presumably because each pair learned the extent of its territory and how to approach it without trespassing. Even human intrusion did not cause the birds to trespass. As the young fledged, territorial boundaries fell and the youngsters had free reign on all areas.

E. M. Hall (90) discovered a concentration of five Marsh Hawk nests in an area of less than five acres, although there were hundreds of acres of suitable nesting habitat close by. Reindahl (154) found five nests of this species within a radius of one-half mile.

Other raptors found nesting in small semi-colonial aggregations include the Montagu's Harrier (56) and the Red-footed Falcon. Horvath (107) found the latter species nesting in dense aggregations near the rookeries in Hungary. Rooks were not found extensively in their diet.

(C8) *Colonial nesting*. The final topic concerning the intra- and interspecific close nesting of raptors involves colonial nesting. The most conspicuous example is the Eleanora's Falcon studied by Vaughan (213, 214) in the Mediterranean Sea area. Colonies reach two hundred or more pairs with no solitary nestings being reported. One seven or eight acre islet supports 80 pairs, some nests being only a few yards apart.

Other species found nesting in colonies include the Sooty Falcon on the islets in the Red Sea (214), the Merlin in Mongolia (up to 14 pairs) (175) and the Common Kestrels in Japan (68). In the latter case Fennell found 50 nesting sites along a mile stretch of cliff. The closest nests were no more than one meter apart.

Relations with non-falconiform avian species.

(A) *Close nesting*. It is logical reasoning that the area surrounding

a raptor's nest would be deserted by all prey species of appropriate size. To the contrary, potential prey does exist near almost every eyrie or nest. Even in the concentration of nesting Marsh Hawks found by Reindahl (154) mentioned above, small birds such as Bobolinks and Marsh Wrens successfully raised young nearby.

The functions of close nesting of falconiforms and smaller birds can be viewed from two perspectives. Some hold that the non-falconiform species seek the protection of the raptor's territory, since many predatory species such as smaller hawks, crows, magpies, etc., are banished from the area. In the case of the Raven (discussed more fully below) it is speculated (14) that the falcon kill remains may attract these scavengers. In any event, this interpretation implies a one sided symbiosis whereby the non-falconiform species is benefited.

The other possibility is that the raptor nests near potential prey because of its food value to the adults or newly fledged young. Although Raven kills do occasionally appear near falcon eyries, they are not a major prey item, and thus falcon-Raven relationships are inexplicable from this viewpoint.

Undoubtedly there is a certain amount of validity in both theories. What seems clear to Cade (39) is that non-predatory species usually nest close to an established predator nest-site. This seems plausible in the view of the inherent season-to-season rigidity in most raptor territories, but the true functions are still difficult to establish. The facts that a raptor may prey on one of its neighbors, but not another or may not hunt at all in the vicinity of its nest are complicating factors which uphold one viewpoint while negating the other.

(B) *Various raptor, non-raptor associations*. Some of the observed situations between raptors and non-falconiform species follow; you may draw your own conclusions with regard to function. Cade found actual commensal nesting associations on the Colville River in Alaska between Peregrine Falcons (one pair per occurrence), Rough-legged Hawks (one pair) and Canada Geese (one to six pairs) on the same cliff. Despite the close proximity of nesting, interspecific conflict between these birds was rarely observed. Other associations with waterfowl involve an observation by Buechele and Nosler (35) of a Mallard nest within 39 inches of a Marsh Hawk nest. Eight of the Mallard eggs and one Marsh Hawk egg hatched on the same day, and the ducklings roamed throughout the area of both nests. In three days the ducklings left and a second Marsh Hawk had hatched. Hecht (101) found very little conflict between ducks and Marsh Hawks. As many as 18 waterfowl nests were found within 100 yards of a hawk nest. This suggests that Marsh Hawks and waterfowl tolerate each other to nest in close proximity, but says nothing to rule out Marsh Hawk predation on the ducklings.

Buturlin (cited by Cade, 39) found concentrations of ducks, shore birds, pipits and Snow Buntings around Peregrine eyries. Sushkin (cited by Cade, 39) writes of pigeons, Kestrels and Starlings nesting near Peregrines in the Ural Mountains.

Paradoxical nesting of medium-sized passerines in the immediate vicinity of an active Merlin nest is documented in a paper by Lawrence (119). Similarly, potential prey species nest near Northern Goshawks (58). Cameron (40) brought forth an interesting theory after observing repeated nestings of Kingbirds near or in the same tree as Swainson's Hawks. It seemed to him that the arrangement existed only for the satisfaction of the Kingbird by being able to attack the hawk every time it flew. A similar situation was observed between a pair of American Kestrels and a pair of Swainson's Hawks by the same writer.

Truly interesting observations were made by Rothshil'd (160) on communal nesting of sparrows, buteos and eagles. Over 45 percent of the sparrow nests found in the Asian study area were in the nest structures of large birds of prey. There was an average of over 13 sparrow nests per Imperial Eagle nest. He concludes that the sparrows benefited considerably from the association since they were protected from enemies and had a constant supply of food consisting of insects attracted to the predator's nest by decaying food remains.

Finally, and by no means the least interesting, Ravens are often found in association with large falcons. A major paper exploring the relationship between Peregrines and Ravens in Britain was published by D. A. Ratcliffe (150) and those interested are referred to it.

In America, conflicting reports exist concerning this relationship. F. L. Beebe (14) found nearly complete harmony between Ravens and Peale's Falcons. Decker and Bowles (53) discuss a tolerant relationship between Prairie Falcons and Ravens in the state of Washington. This association was found in about 70 percent of the Prairie Falcon nestings in their study area. Pairs of the two species even switched nest-sites after first clutches of both were collected. The lone dissenting comment found concerning falcon and Raven compatibility comes from Dawson (52) after extensive Prairie Falcon work in California. Conflict was observed on several occasions.

Defense against non-human, non-avian species. The territorial relationship between raptorial birds and other classes of animals is not as extensively documented in the periodical literature as it should be. The significance of small mammalian species is, of course, two fold; the birds use them as food and the small mammals use the eggs and young hawks for similar purposes. The latter brings forth typical nest defense in parent hawks. The few available examples of inter-class conflict or compatibility follow.

Raptors seem to recognize threatening mammalian species and attempt to run them out of the vicinity of their nest-site. Cade (39)

observed Peregrines in Alaska attacking Red Foxes. Fitch *et al.* (73) often found Gray Squirrels climbing in the nest-trees of Red-tailed Hawks. To the writers this indicated some sort of immunity to capture presumably based on the elusiveness of the adult squirrels. Lawrence (119) noted around Merlin nests that small mammals such as squirrels and chipmunks were ignored; dogs and man were attacked vigorously.

Defense of nesting territory against reptile invasion is little known, although it has been observed. Liversidge (120) witnessed an attack of a male African Little Sparrow-hawk on a three and one-half foot snake making its way up the nest-tree. The hawk attacked the snake only when its head was intwined in the branches of the tree indicating at least a little experience or instinct in defense against such an enemy.

Effects of human intrusion. This reviewer had hoped to gain a needed understanding of raptor-human relationships in the wild, so that a better approach to the captive situation could be made. In addition to the generalities in the following paragraph, only a few pertinent points seem worthy of mention, all other considerations being substantially destroyed by extreme variability. If one had to choose the most variable aspect of falconiform life, behavior, especially when threatened or disturbed, would certainly be one of the first choices.

The three major groups treated herein, falcons, hawks and eagles, represent a gradation of aggression with the falcons being the most consistent attackers. Peregrines (10, 32, 81, etc.), Prairie Falcons (53), Merlins (48, 119) and American Kestrels (159) are nearly always fierce defenders of their eyries. The Gyrfalcon may (216) or may not (39) defend theirs. The eagles, at the other extreme, and particularly the American forms, are quite shy around their nests, but Brown (32, 33) found certain African eagles somewhat defensive against human disturbance. The general reaction of hawks, admittedly a large group, lies between the two extremes with both very shy and very bold defenders averaging each other out to properly point up the moderate degree of aggressiveness characteristic of a majority of hawks. For example, the Swainson's Hawk is more often very shy than even slightly aggressive (26). Short-tailed Hawks generally only scold an intruder from a distance (27). There is a vast number of hawks, however, which almost always show moderately bold defense behavior in varying degrees, of course. Perhaps the best examples of this type are the Red-tailed Hawk (73, 142) and the Marsh Hawk (101, 212). The true hawks or accipiters are the warriors of the falconiform order, particularly the Northern Goshawk. More observers (58, 60, 61, 86, 169, 200) have commented or complained about the tenacious pugnacity of this species than about virtually all others put together.

When approached while on the nest, birds of prey simply crouch lower until all hope of escaping notice is abandoned. This is particularly noticeable when pipped eggs or very young nestlings are being covered. Bailey and Neidrach (8) observed a female Goshawk cowering down into the nest so that only the long tail stuck over the edge. She left the nest only after the tree was tapped. Dixon (57) found that the Red-shouldered Hawk often does not flush until the climber is half way up the nest-tree.

(A) *Deflection of attack.* One of the most significant aspects of human-raptor interaction, particularly in the wild falcons, is the often noticed "deflection of attack" from the intruding human to other avian species, most commonly other raptors. Bond (23) points out that probably most interspecific defense of territory in Peregrines away from the actual nest-site occurs as a result of nest disturbance, either by humans or other predators. Other species become targets of the raptor's frustration at being disturbed. Bond's most striking example of this behavior involved Prairie Falcons and Barn Owls. He flushed the owls from the Prairie Falcon nest-cliff and with single stoops the female falcon broke the female owl's wing and the male falcon killed the male owl outright.

Cade (39) found that Gyrfalcons, when their eyrie is approached, often seek out the nearest pair of Rough-legged Hawks and attack them violently. F. L. Beebe witnessed the attack and near capture of a Peale's Falcon by a Bald Eagle after the eagle's eyrie had been approached. "The presence of the observer in this instance was almost certainly the disturbing factor that caused the eagle to attack the falcon by way of substitute" (14:166).

No instances of the irate female falcon attacking the male of the pair have been recorded.

(B) *Variation in attack.* The aggressiveness of nesting raptors toward human intruders is apparently a reaction to the recognition of potential threat to the eggs, young or nest-site itself (14). This aggressiveness can be lessened or increased under different circumstances. Saunders (168) believes that a male Marsh Hawk began to recognize his field clothing and would attack him at distances up to one-mile away from the nest-site. In cliff nesting Peale's Falcons, F. L. Beebe (14) found that an eyrie was more vigorously defended if approached from below than if approached from above. This fact would be of some value to those designing new breeding pens if it were not for Hickey's seemingly contradictory statement. "As a general proposition, Peregrines appear to be little molested by the progress of what passes for civilization below their cliffs, but frequent or prolonged visits by human beings to the top of an escarpment or cutbank may bring about interruptions in the breeding cycle, and in some cases actual desertion of the eyrie" (14:193).

(C) *Aggression toward egg collectors*. Reports of aggressiveness toward egg collectors vary. From one European Sparrow-hawk nest, Davenport (51) collected 15 eggs on alternate days for a month. The significance of this will be discussed later, but the point to be made here is that the female became so accustomed to his visits that she would not leave the nest until he was level with it. On the other hand, Salter points out that "older birds [Common Buzzards] which have been much molested at the nest, become extremely bold in defense of their eggs or young" (165). Williamson (224) was struck several times by a female Red-shouldered Hawk at a nest with a history of being robbed. This trait has not been often recorded by oologists, however, so these isolated incidents may not be of importance.

(D) *Method of attack*. The method used by Peale's Falcons to attack humans was discussed by F. L. Beebe (14). Attacking raptors are often aware of being watched, preferring to attack a human intruder from behind. Of a male Peale's Falcon, Beebe states: "As long as I kept my eyes on him, he would circle and scream; but the instant I have my attention to something else, I would feel the rush of his slipstream as he zipped past" (14:164). This method is used in attacking other birds, too. This same observer and others have noted a predilection of attack to the back, particularly when large buteonine hawks or eagles are pursued by falcons.

(E) *Intimidation*. The final point concerning human intrusion into raptor nesting territories concerns the number of people in the observation party. This may have something to do with the severity of the attack. At one of Bailey's (9) Marsh Hawk nests the parents vigorously attacked a single intruder, but were intimidated by three. Similar reactions are more commonly observed in the Northern Goshawk (58, 61, 86, 169, 200). Might this indicate magnified distress when raptors are approached by a crowd?

CHAPTER 3. THE BREEDING CYCLE–GENERALITIES

GENERAL CONSIDERATIONS

All falconiforms are single-brooded (102). Some of the larger species such as the vultures and the Philippine Monkey-eating Eagle have breeding cycles lasting over a year; as much as 15 months in the latter case (102).

There is a rough correlation between the size of the bird and the total length of the cycle. A large falcon can be expected to have a longer breeding season than a small species, due more to specific differences in nestling development than differences in incubation length, the latter being a fairly constant 28 to 31 days in North American falcons. The eagles have a longer cycle than falcons due to a longer incubation period (45 days or more) and slower development of the young (up to six months or more).

When comparing birds to other classes of animals such as reptiles, amphibians and mammals, it is found that the lower classes produce many eggs most of which perish, while mammals and birds, including the falconiforms, produce highly advanced young which are carefully cared for. "Those pairs producing the best endowed young, even though few in number, will contribute more individuals to the following generations" (7:109).

Still there is variation in egg number within the falconiforms. Take for example the California Condor which raises no more than one young every other year and contrast it with the American Kestrel which may raise five or six young each year. Most eagles raise only one or two young per year. It is speculated that the longer nestlife of the larger, low productive raptors, in particular, implies a more careful raising of the young resulting in the higher level of development before fledging.

Although Cade (39) noted remarkable intraspecific constancy in the timing of separate events in the breeding cycle of arctic Peregrines, there may be much interspecific variation in the same locality. Cade lists three temporal differences in the breeding of Gyrfalcons and Peregrine Falcons in arctic Alaska. "First, the total period of the cycle is two to three weeks longer for the gyrfalcon because of the slower development of the young. Second, the timing of the cycle tends to be earlier by about a month for the gyrfalcon. Finally, there is a greater year-to-year variation in the timing of the cycle among gyrfalcons" (39:205).

TIMING

These basic differences reflect the various factors which affect the general timing of the breeding cycle of any species. Among these factors are photoperiodicity, climate, food supply, latitude and migratory status of the bird involved.

Photoperiodicity. The amount of daylight is known to be an important regulating factor of reproduction in many avian species, although precise information concerning this matter in the falconiforms is quite lacking, particularly because of the difficulty of studying them in the captive situation, and secondarily because many of the necessary physiological techniques require destruction testing. This may be a significant avenue of research subsequent to establishing captive breeding populations of raptors.

Nevertheless, non-destructive experiments by Willoughby and Cade indicate that "photoperiodic stimulation is the most important environmental factor governing the seasonal timing of the breeding cycle in North American populations of the American Kestrel" (225:95). These researchers were able to induce egg-laying (fertile at that) during the winter months, regardless of the temperature, simply by manipulating the amount of daylight.

Climate. After a mild winter, birds of prey in temperate regions may nest somewhat earlier than after a severe winter. Webster (217) believes that climatic factors may affect the beginning of breeding in successive years as much as three or four weeks. Cade (39) found that spring weather considerably affects the onset of reproduction in the Gyrfalcon. The effects of season differ for raptors in different parts of the world. Brown (32, 33) discovered that general timing of breeding season in Kenya eagles coincided with the cool seasons of the year so that it was not necessary for the parent to continually shade its young from the sun. There is much less support for the theory that the breeding season of these eagles is so timed that prey is most easily obtained by the adults and inexperienced young.

Food supply. Availability of food is considered an important controlling factor in other species. Vaughan (214) implies that Eleonora's Falcons breed relatively late, fledging their young in late September or early October in order to take advantage of the autumn migration of passerines.

The same is indicated for the Sooty Falcon of the Libyan Desert. Booth (25) found further evidence for this remarkable adaptation in the barrenness of this falcon's habitat, it being devoid of vegetation, living and dead, and as judged by Booth, insufficient in fauna to support a family of falcons earlier in the season. Cade (39) also

speculates that variation in Gyrfalcon reproduction timing depends somewhat on its food supply, the fluctuating ptarmigan population in particular.

Latitude. Cade (39) indicates that southern Alaskan Peregrines (latitudes 52° to 56° N) begin breeding a month or more before those on the arctic slope (latitudes 68° to 70° N), with a corresponding intermediate timing in central Alaska (latitudes 64° to 66° N). This is not true for the Gyrfalcon in the same area. Peregrines in southern California (latitudes 33° to 35° N) begin about 90 days before arctic slope Peregrines. Further evidence for latitudinal effects comes from Baker (10) who found that Shaheen reproduction begins in March; eggs are found throughout April depending upon the geographical location. In southern India they lay in January and February since there is no significant difference between winter and summer.

Migration. Migratory status affects the onset of reproduction. Resident birds were found by Cade (39) to begin nesting a full month before migrating Peregrines. Because of the short summers in extreme northern latitudes, migratory species must adhere to very strict timing of their breeding season lest their young be caught by the rigors of the oncoming winter. Conversely, resident species have a wider choice of times to breed, being able to start earlier in the spring and, if necessary, extend their season into the fall.

MOULT

The correlation between the onset of the moult and the timing of the breeding cycle is still open for investigation. F. L. Beebe (14) pointed out a 30-day difference in the beginning of the moult in the two sexes of Peale's Falcons, the female beginning before the male, and offers an explanation of this based on the physiological levels of sex hormones in the birds. Lundevall and Rosenberg (121) found in Pallid Harriers that the moult began during incubation in the females, but not until the young were almost fledged in the male. It is reasonable to speculate that this is due to the biological need for the male to hunt for the young. Data presented by Dementiev (55) indicates that the female Gyrfalcon begins to moult during incubation.

Amid these fairly consistent findings are several contradictions indicating that variation again prevails. Colling and Brown (47) observed a female Marsh Harrier which appeared to be moulting even before laying the first egg. Her moult continued throughout incubation and the nest-life of the young. In the male Marsh Harrier moult began at the most critical time—the latter two or three weeks

of nest life of the young when it necessarily had to do a tremendous amount of hunting. Wayre and Jolly (216) report that the female Gyrfalcon at an eyrie in Iceland containing month-old young was about half-way through the moult. Webster (217) found year-old Prairie Falcons around eyries deep in the moult several months ahead of the older birds.

BREEDING OF IMMATURE BIRDS

The initial onset of breeding in an individual bird, *i.e.*, the first production of viable eggs or sperm, is difficult to correlate with age. Moult to adult plumage does not necessarily indicate sexual maturity. Speculation concerning this matter indicates that some Peregrines attain maturity at one year of age (150). It seems fairly well established that large eagles become sexually mature at the age of four or more years (7). The field evidence is contradictory; some observers report a striking absence of immatures breeding; several examples of year-old birds at active nests, more often females, have been recorded.

Absence of young birds. With regard to the absence of immatures, Cade (39) sighted no immature Peregrines among 250 breeding pairs in the arctic, but mentions two possibilities collected by another observer. Cade also found immature Gyrfalcons very rare in the spring, seeing only one in six seasons in Alaska. F. L. Beebe (14) never observed year-old Peale's Falcons breeding during his extensive studies in southwestern Canada.

Interesting observations made by Webster (217) may explain the presence of immature Prairie Falcons at active nest-sites early in the season and their absence when most researchers are afield. At an eyrie from which partially albino birds regularly appeared, the young of the previous year returned each spring to their birthplace. After some days of imitating the adult male, they were driven away usually during the late courtship period.

To explain the absence of breeding immatures, Cade brought forth the idea that perhaps year-old birds are unable to "bring about in a single season all of the social adjustments required for successful reproduction" (39:240). These social adjustments include effective courtship and copulation to synchronize physiological readiness and insemination, and assumption of "biologically appropriate" roles during incubation to assure proper warming and during the fledgling period to assure proper development of the young (39). The implication is that year-old birds may be physiologically, but not psychologically, capable of reproduction. Observations by Hagar (89) support this theory. He found that Red-tailed Hawks in central New York abandon 40 per cent of their nests each season usually between

the time the nest is built and the eggs laid. Speculation is that these nestings involved birds too young to be sexually mature.

Immatures at active eyries. Some observations of birds in immature plumage at eyries tend to indicate that some species are able to reproduce the first summer after hatching. Lundevall and Rosenberg (121) observed one immature male and five immature female Pallid Harriers attempting to nest during an abnormal influx of this species into Sweden in 1952. This observation may involve older birds, however, since in the Pallid Harrier the females may not be in mature plumage until their third summer (121). Colling and Brown (47) believe that female Marsh Harriers breed after one year, but males take two years to mature sexually. They present a case of two immature Marsh Harriers at the same nest. The plumage of the birds, late nesting, poor nest success and near desertion of the young by the female of the pair when the young were nearly feathered were used as indications of immaturity. Additional evidence in harriers includes reports of display flights of year-old birds in four species of harriers (79, 121).

In other hawks, Abbott (2) found an immature Goshawk at a nest in New Hampshire, but the three eggs were collected and fertility not determined. Burns (36) states that the Broad-winged Hawk has been observed breeding in immature plumage on several occasions. A case which leaves no doubt that immature Cooper's Hawks are capable of producing eggs is mentioned by Brooks (31). A female carrying three eggs, one of which would have been laid the next day, was collected in immature plumage.

In Prairie Falcons Webster states that he has never seen "a juvenile male about the ledge as one of a mated pair, but it is a known fact that juvenile females are capable of raising and do raise, a healthy family" (217:611).

Hickey (102) observed three immature Peregrines at nest-sites, all failing to lay eggs. He mentions two instances where immatures were incubating clutches of two eggs, an unusually small number for the species. Fertility was not mentioned.

Brooks makes the point that breeding of immature raptors may be the "result of a female being shot and its mate rounding up an immature to help him to bring up the young, or even to hatch the eggs already laid" (31:245). His evidence of this includes instances in the Peregrine Falcon, Merlin, Sharp-shinned Hawk and Cooper's Hawk.

CHAPTER 4. NESTING SUCCESS

Figures for nesting success, usually expressed as young fledged per nest, will not be given, but some understanding of the dynamics of this subject will hopefully be gained by the following consideration of the major factors involved. As a brief introduction to a lengthy topic, the detrimental factors influencing nesting success are enumerated in Table 3. Nest parasitism of the young and nest-site

TABLE 3. DETRIMENTAL FACTORS INFLUENCING NESTING SUCCESS

Egg Loss

1. Weather
   - Unseasonable temperature
   - Severe rainstorms
2. Accidental nest destruction
   - Wind storms
   - Cliffs falling
3. Breakage and disappearance
   - Egg eating (intraspecific)
   - Egg eating (predation)
   - Accidental trampling
   - Egg collecting
4. Infertility
   - Addling

Death of Young

1. Weather
   - Unseasonable temperature
   - Severe rainstorms
2. Accidental nest destruction
   - Wind storms
   - Cliffs falling
3. Predation
4. Nest parasitism
5. Food supply
   - Starvation
6. Nest-mate interactions
   - Cannibalism
7. Disease

Parental Factors

1. Desertion
   - Human intervention
     - Shooting
     - Construction
     - Picnicking and hiking
   - Territorial effects
     - Intraspecific aspects
     - Interspecific aspects
2. Infertility
   - Old age
   - Sexual immaturity
   - Pesticide effects
3. Nest-site inadequacies
4. Death of a mate

preference will be covered under the topic "nests and nesting." Inter- and intraspecific conflict has been covered above.

Obviously, the absence of all detrimental factors should augment nesting success. Only two major factors which directly enhance nesting success are treated below, *i.e.*, renesting after egg loss and rapid acquisition of a new mate after death of the first.

NESTING SUCCESS–GENERALITIES

Nesting success may vary greatly from year to year. The cause of the variation can involve a breakdown at almost any stage of the breeding cycle or near total success under favorable conditions. Unsuccessful parental relations stemming from dozens of subtle factors not mentioned in Table 3 often result in parental insufficiency such as failure to produce fertile eggs or eggs at all. Viable eggs may not hatch for various reasons, but if they do, many pitfalls decrease the survival of hatched young considerably.

A quantitative study of nesting success in the Red-footed Falcon made by Hórvath (107) indicates a possible fate which could be expected for 100 potential nestlings in the wild. Infertility will cause failure to hatch in 24.8 of the eggs, 7.6 will be destroyed by predators either as unhatched eggs or nestlings, 21.9 will die as fledglings, while the remaining 45.7 will leave the nest. Thus, 67.6 per cent of the eggs will hatch (45.7 plus 21.9 out of 100) and, curiously, 67.6 per cent of the hatched young will fledge (45.7/67.6 times 100). Hórvath goes on to say:

> "Although this exact correspondence down to the last decimal is a coincidence, it is almost certain that the mortality rates of the eggs and fledglings are approximately identical. Examinations of the series shows further that the increase per nest of fledglings is only 1.6%. This means, for all of the nests, an annual increase of 80% of the whole Falcon population in the Ohat Forest" (107:587).

In support of Hórvath's findings, Ratcliffe (150) states that brood-size is slightly more than half of clutch size.

DETRIMENTAL FACTORS AFFECTING NESTING SUCCESS

Egg loss.

Weather. The effects of adverse weather conditions are easily understood. Unseasonable cold or heat can seriously affect the conditions of incubation. In hot climates incubation may actually function to keep the eggs cool. Brooding most certainly functions in

this manner in many species. Severe rainstorms can be particularly detrimental to ground nesters whereby flooding cools and kills the eggs. The effects of bad hail storms can be disastrous as well.

Accidents. Accidental nest destruction can occur in many ways. Locally, wind storms ruin countless bird nests each year. Trees are felled and nests are blown down by virtue of their wind resistance. Heavy rains, earthquakes and the increase in weight of the nestlings all cause many nest-sites to break away from cliffs.

Cade (39) includes accidental destruction and addling of eggs high on the list of spoiling factors of Peregrine eggs in arctic Alaska. Addling may occur as a result of parental neglect due to "the disturbing presence of large mammals such as man, wolves, caribou, moose, and bears. . ." (39:188) or by territorial conflict with individuals of the same or different species. Accidental destruction might also occur when incubating parents kick the eggs out of the eyrie.

Breakage. Broken, cracked and missing raptor eggs constitute one of the most puzzling aspects of egg loss. Considerable fact and speculation has been recently published. Emphasis previously placed on predation by crows, jays and small mammals is decreasing in the aftermath of a marked increase in the incidence of broken and disappearing eggs. Some now point the finger at the chlorinated hydrocarbon pesticides (49, 151).

Ratcliffe (148) sites 14 instances of broken or missing eggs in British Peregrine eyries with no evidence of outside interference. Broken eggs were found in over 20 per cent of the 59 eyries inspected in this 1951-1956 study. In 1961 and 1962 the causes of unsuccessful breeding of Peregrines in Britain centered around egg losses and defects (151). Eggs were eaten by adults, broken, simply disappeared or were infertile in 37 of 356 attempted nestings. Ratcliffe (149) found another dozen or more cases of broken eggs in the nests of the European Sparrow-hawk and Golden Eagle. In most, it is believed that the eggs were eaten or destroyed by the parent birds. Interspecific predation was considered unlikely.

In addition to breakage, eggs have been disappearing one-by-one from many nests in recent years. If clutches disappear all at once it is easier to suspect predation or human interference, but this is not the case (102). Ratcliffe (152) writes of a broken egg in a Merlin nest in Britain. Upon inspection he found three eggs still intact which later disappeared one-by-one. Pounds (145) discovered eggshell fragments under a European Sparrow-hawk's nest from which the eggs slowly disappeared.

In the above case the female was suspected of destroying the eggs. G. H. Hall (91) actually observed a female Peregrine Falcon eating one of her eggs in 1949. The eyrie was that of the famous Sun Life falcons nesting in downtown Montreal. The egg eaten was the first

laid (possibly the second, since egg shells had been found in the nest previously that same spring); four more were laid in nine days following the incident. Then, one at a time, these disappeared. On six other occasions over 17 years single eggs or pairs mysteriously disappeared from Sun Life Building eyries. Human disturbance and avian and mammalian predation were ruled out. Hall does not believe that poor food supply causes this curious activity, because pigeons and Starlings abounded in the area every year. Ratcliffe (148) speculates, after suggestion from Dr. J. D. Lockie, that a bird such as the Peregrine, in which asynchronous hatching is characteristic, may eat or destroy part of its clutch to adjust brood size to food supply. As another possibility, pesticides are becoming increasingly suspect as an inducer of this behavior.

Death of young. Most factors causing nestling mortality closely parallel those for egg loss or are treated elsewhere in this paper. F. L. Beebe (14) brought forth the novel idea that the area of the nest platform may influence brood size or nest success. His evidence is a single, very small eyrie platform that consistently fledged only one Peale's Falcon per year.

Cannibalism.

(A) *Eagles.* The only major factor affecting nesting success to be discussed is nest-mate interaction. Dominance of one nestling over the others is an often reported occurrence, but its manifestations are not clearly understood. Sibling cannibalism, however, is convincingly documented. E. L. Sumner (198) observed the phenomenon in action at a Golden Eagle eyrie in which the dominant nestling weighed almost twice as much as the smaller. Brown (33) mentions one confirmed case of cannibalism and several suspected cases in the African Hawk-eagle. Fratricide is believed always to be the case in the Crowned Eagle (7). Amadon (7) feels that Golden Eagles represent an intermediate between those species in which nest-mates always show cannibalistic tendencies and those which never do. Just as often as not an entire clutch of Golden Eagles will fledge. Cannibalism is also evident in the Wedge-tailed Eagle and Bald Eagle (198).

In the incident involving Golden Eagles observed by Sumner, the large nestling used force and energy out of proportion to its size, digging and pulling at its screaming victim. This illustrates one of the interesting features of cannibalism: it occurs far in advance of most of the young bird's other complex activities. The mode of action is almost mechanical as if depending upon pure reflex (198). Since it develops so early, cannibalism cannot be attributed to an extreme play instinct. Gordon (cited by Sumner, 198) states that the cannibalistic tendencies of young Golden Eagles disappear as the young learn to tear up prey for themselves.

(B) *Hawks*. Breckenridge (28) observed a female Marsh Hawk dismember and feed one of her nestlings which lay dead in the nest to the remainder of her brood. Allen (4) mentions cannibalism in the same species. In a nest with seven young four hatched on one day and the others over the next five days. The smallest chick was eventually eaten by the largest. The large nestlings so dominated the food that a second died of starvation, presumably, and the third late hatcher was also eaten by the four survivors. Sibling cannibalism is prevalent among young Marsh Harriers even when the female keeps the young well fed (47). It is more common, however, in nests where the female parent is lackadaisical about feeding the young, in which even food brought by the male elicits fierce competition. Salter writes about the Common Buzzard: "It appears to be quite the usual thing for the first-born to kill one if not both of his younger brothers" (165:102). This circumstance may be less pronounced in areas where food is abundant. Schnell (169) mentions a 40-day old Northern Goshawk which died in the nest and apparently was eaten by his nest-mates. Other hawks showing cannibalistic tendencies include the Red-shouldered Hawk and Broad-winged Hawk (198).

(C) *Falcons*. Cade (39) found little evidence for sibling cannibalism in arctic Peregrines, but did for Gyrfalcons. McCabe and McCabe (126) found the foot of a young falcon in a nest of Peale's Falcons and strongly speculated that cannibalism, either by the nestlings or the female, had occurred. Roest (159) found a leg-band of a nestling American Kestrel in a pellet below its eyrie. Since the nest was plagued by injurious flies, one can suspect that the bird died and was eaten by his nest-mates and/or parents. W. Beebe (15) indicated possible cannibalism in the Bat Falcon.

Disease. Sickness, apart from nest parasitism, is not often reported in nestling raptors. Hórvath (107) found an infectious eye disease in young Red-footed Falcons in Hungary which resulted in death. He states that young birds infected with the disease were often thrown out of the nest by the parents and, if a sick bird was returned to the nest, death of its brothers and sisters was imminent. Stensrude (189) reports the death of two Gray Hawk nestlings about a week old from the effects of frounce, a disease caused by the protozoan *Trichomonas gallinae*.

L. B. Bishop (16) describes rickets in young Red-shouldered Hawks. The birds grew in size and weight and the juvenile plumage began to show before complications set in. The symptoms were inability to raise themselves on their feet which were characteristically thrust forward, and apparent pain was suffered when being handled. Dissection revealed much subcutaneous fat, flabby, anemic muscles with lax ligaments, enlarged epiphysial cartilages and unusually soft, deformed long bones. The tibias were fractured as evidence of their attempts to stand.

Parental factors.

Desertion. Some observers believe there is a very critical time when, if a pair is disturbed, nest desertion is very likely. This time is just prior to laying when the female spends much time sitting on her empty nest (133).

Ratcliffe (150) considers desertion of a territory more of a psychological phenomenon than a physical inadequacy of the birds. He speaks of a variable threshold "level of acceptability," below which desertion occurs. Marginally occupied sites have a lower "level of acceptability" and are readily deserted, whereas it is more unusual for birds to desert an "ideal" site. This is in general agreement with Hickey's (102) classification of Peregrine nesting cliffs.

F. L. Beebe (14) implies that disturbance, be it human or otherwise, might not be as important a factor in nest desertion as the literature might indicate. The basis for this is the striking similarity of Peale's Falcon defense against eagles and man and the fact that the falcons are constantly disturbed and annoyed by the eagles.

Bond (23), on the other hand, found the most common causes of desertion of Peregrine eyries (11 examples) to be human disturbance in the form of shooting at or in the vicinity of the nesting birds, increased picnicking activity near the cliffs and road construction.

Infertility. Infertile eggs in raptor nests are not uncommon. Vaughan (213) found that the percentage of addled eggs in the Eleanora's Falcon varies from almost 10 to over 27 per cent in certain populations. Data presented by Hickey (102) indicate that about one egg in every clutch of Peregrine eggs fails to hatch. Hickey continues with a comment by H. A. Gilbert which states that in Britain infertile eggs are rare; at least 95 per cent hatch if not disturbed by falling rocks or man. Bond's (23) information for western North American Peregrines does not indicate an infertility level of any where near 25 per cent as indicated by Hickey. Cameron (40) found that 50 per cent of clutches of three in Swainson's Hawk in Montana contain an infertile egg.

Sterility manifested in failure to lay was observed by Hickey (102) at one Peregrine eyrie for a period of ten years and at two other sites for at least three years running. The females seemed generally unresponsive and courtship by the male lasted a month longer than normal. Speculation is that this condition may accompany old age.

In hawks, Hosking (108) comments that Marsh Harriers frequently lay full clutches of infertile eggs. He elaborates on an old hen which laid six infertile eggs, apparently after several previous unsuccessful seasons. Red-shouldered Hawk seem particularly prone to infertility. Stewart (191) reports an infertile egg in almost eight per cent of a series of 52 nests of this species. Dixon (57) found it rare to see a clutch of four Red-shouldered Hawk eggs without an

infertile one, even though in his experience four is the clutch size most often observed.

The nature of sterility is complex, but one factor of our modern civilization is certainly taking its toll. Ratcliffe (151) agrees with convincing evidence of other writers that sublethal doses of pesticides in adult birds cause first, a reduction in hatching success of the eggs; second, complete sterility of the parents; and finally, failure to attempt breeding at all. This pattern is accompanied by curious behavior such as egg eating and ultimately endangers the lives of the adult birds themselves. Indeed, this and other recent British articles clearly point the accusing finger at pesticides as a detrimental factor to nesting success.

The blame for recent raptor population declines as well is partly placed on the use of pesticides by comparing the time pesticides came into widespread use in Britain and the time of the onset of the decline. An area by area survey shows a close correspondence between the two (49). There seemed little doubt to Cramp (49) that birds of prey, like other species, are drastically affected by sub-lethal doses of poisons. The affects consist of decreased egg production, a decrease in the percentage of fertile eggs and a decrease in chick survival.

The Great Britain Peregrine survey in 1961 revealed the striking dimensions of the raptor decline there. That summer there was a large proportion of active nest-sites with infertile eggs or no eggs at all.

Although speculation is running high on circumstantial evidence, direct evidence is beginning to present itself in the form of organo-chloride residues in the eggs of some British raptors. Moore and Ratcliffe (132) first revealed residues to four to five parts per million in a Peregrine egg and pointed out that adult Peregrines may concentrate sub-lethal doses of poisons in their prey species to levels which, when passed on to the embryos, prove to be a block to development. More recent studies (152) indicate general contamination of British raptor populations of Common Buzzards, Merlins and Common Kestrels. Several eggs of each species were analyzed and the concentrations of each pesticide are included in tabular form.

In the final analysis, then, the British workers feel that hypotheses concerning some sort of pesticide-sterility-raptor decline relationship are reasonable. [Since this review was written, much more direct evidence of such a relationship has accumulated.]

FACTORS ENHANCING NESTING SUCCESS

Laying second clutches. Many raptors have the capability of completing a successful nesting even if their first clutch of eggs is

stolen. This was established by oologists who often collected a second set of eggs from a previously ravished nest. In fact, Bond (23) mentions two observers taking 12 fertile Peregrine eggs from the same eyrie in the same year (three clutches of four) and a fourth clutch of an undetermined number was laid.

Another fascinating occurrence of renesting followed an experiment by Wimsatt (227). He caught a female Peregrine at the nest and kept it in captivity for two weeks. The male evidently incubated the eggs for a few days, but abandoned them completely by the seventh day. At the end of two weeks the female was released after being marked. She homed to her original nest-site from 60 miles away and laid a clutch of four eggs ten feet from the first site, all within one week of release. Three of the second clutch of eggs were fertile.

Two details involved in laying second clutches depend on the general time factor inherent in any breeding cycle. Cameron (40) points out that if the eggs of the Swainson's Hawk are destroyed or collected they will nest again, but if deprived of nestlings they will not. Presumably the latter is a loss of too large an investment of time physiologically and seasonally for recycling to occur. The success of renesting may depend somewhat upon latitude, the birds in the north having a shorter season and more rigid timing demands which preclude second clutches.

Reindahl (154) found a clutch of eight Marsh Hawk eggs. These eggs subsequently proved to be infertile and the female renested and raised four young successfully. The interesting part is that the female abandoned the clutch of eight and immediately layed a successful second clutch. This would indicate a long-termed fertility on the part of the male.

Reports of the length of time required for recycling vary, but two to four weeks would seem average for most raptors except the eagles. Green (84) observed that if the first set of eggs of a pair of Peale's Falcons is collected or destroyed before incubation begins, a fresh set will be laid starting in about ten days. If incubation is underway, however, one may expect three weeks to pass before a second clutch is started. Walker and Walker (215) tell of renesting in the Marsh Hawk within two weeks after the first clutch was taken. Courtship flights were renewed, and a new nest was built during that time. This nest met with disaster and the pair attempted unsuccessfully to nest a third time only laying one egg which broke in the poorly constructed nest.

According to Tyler (211) a second clutch of Prairie Falcon eggs will usually be laid within 20 to 25 days after the collection of the first set. Red-shouldered Hawks may lay a new clutch within three to four weeks usually in a newly constructed nest not far from their first attempt (134). Bond mentions that "incubation of the second

set ordinarily began within 30 days of the time the first set was collected" (23:111) in Peregrines.

Table 4 includes most species which have been known to lay a second clutch as revealed by the literature reviewed. Certainly it occurs in other species as a general rule.

TABLE 4. SPECIES LAYING SECOND CLUTCHES

1. European Sparrow-hawk	(10)
2. Besra Sparrow-hawk	(10)
3. Red-shouldered Hawk	(134, 223)
4. Broad-winged Hawk	(36)
5. Swainson's Hawk	(40)
6. Marsh Hawk	(215)
7. Prairie Falcon	(211)
8. Peregrine Falcon	(23, 227)
9. Peale's Falcon	(84)
10. Shaheen	(10)
11. Oriental Hobby	(10)

Acquisition of a new mate. A second type of renesting behavior was revealed by bird collectors who often shot a second specimen of the same species and sex at a nest which had recently been deprived of one mate. If a nesting bird is killed or dies early in the breeding season, chances are good that its mate will find a new partner. Tragedy late in the cycle usually assures nesting failure and a single bird will be evident at the eyrie until the next spring. The timing here depends upon quick replacement of mates which is more likely early in the spring when migrating birds are still in passage. Replacement late in the breeding season probably involves single birds of adjacent nest-sites whose mates have died or have been destroyed (102).

Table 5 would indicate that among raptors, rapid acquisition of a new mate occurs in falcons almost exclusively. Presumably this conclusion is an artifact of the techniques of this reviewer, but it may reveal that the occurrence is far more common in falcons.

TABLE 5. RAPID ACQUISITION OF NEW MATE

1. Prairie Falcon	(217)
2. Peregrine Falcon	(34, 102. 133, 203)
3. Peale's Falcon	(84, 126)
4. American Kestrel	(45)
5. Common Kestrel	(80)

For example, McCabe and McCabe (126) observed a male Peale's Falcon caring for young in the presence of a new female at an eyrie from which the first female had been shot four days previously. Fayler (203) records an interesting incident concerning one female Peregrine incubating with another dead female only inches away. The first female had died on the nest from a gunshot or some other reason and the male immediately acquired a new mate which made her scrape on the same ledge. Hickey (102) writes of one example of double replacement of mates at a Canadian Peregrine eyrie. Apparently both birds of a pair which produced the eggs were killed a few days apart. The first acquired a new mate and was subsequently killed. The new mate acquired a new mate for itself and together they raised their brood of foster eyasses.

Nethersole-Thompson and Nethersole-Thompson (133) present a case observed by C. V. Stoney where a male Peregrine brought a new female to the eyrie of his original mate. The new female laid four eggs in the same scrape where the original female had also laid four. Bryden gives the following note on remating in the Peregrine after one bird has been killed:

> "The hawk will disappear from its eyrie for a few days, possibly even for a week; but it will inevitably come back with a new-found mate, discovered undoubtedly, in many instances, hundred of miles away" (34:491).

Time required for the new acquisition of a mate is often remarkably short. The record seems to be an account given by Frere (80) indicating that a female Common Kestrel found and returned to her nest-site with a male in immature plumage only two hours after her original mate was killed. Chubb (45) observed a similar case requiring only several hours in which the male American Kestrel sought a new mate. This case is extremely interesting in that the new female incubated, hatched and raised her predecessor's five eggs. The interruption came during the second week of incubation; the eggs hatched a little over two weeks after the new female took over. Evidence that a second female was involved includes: (1) anxious displays by the male around the nest and unsuccessful attempts by him to call the female off the nest; (2) deserted, cold eggs for nearly two days; (3) disappearance of the male for most of one morning; and (4) the appearance of a wild, hesitant female which did not know quite what was "expected of her even at feeding time" (45:625-626).

Nethersole-Thompson and Nethersole-Thompson (133) tell of a male Peregrine Falcon obtaining a second mate within 36 hours of the destruction of his first. Green (84) mentions the acquisitions of a new mate by a female Peale's Falcon in the Queen Charlotte Islands

within 40 hours of the death of her original mate.

Raising of young by a single parent. If a mate is lost late enough in the development period of the young, the remaining parent may continue to feed the nestlings until they leave the nest. This factor is not a major asset to general nesting success, but is documented in a few species. Decker and Bowles (53) observed instances in the Prairie Falcon and Red-tailed Hawk. Sutton and Parmelee (202) tell of two young Peregrines fledging five days after the male parent was shot. Reindahl (154) observed a nest of four young Marsh Hawks with no male present. Presumably the male had met with disaster and the female had taken over all domestic duties, including territorial defense which is usually left to the male. She defended so vigorously that the observer was struck several times on occasion.

CHAPTER 5. PREINCUBATION BEHAVIOR

Cade (39) lists the events of preincubation behavior of Peregrines as follows:

> "(1) the attraction of mates to each other, (2) mutual roosting on the cliff, (3) cooperative hunting excursions, (4) courtship flights, (5) 'familiarities' on the cliff, (6) courtship feeding, (7) copulation, and (8) nest-scraping" (39:189).

Following an introduction to this subject each of these factors will be taken up in order, although in reality some may begin simultaneously.

INTRODUCTION

In raptorial birds much courtship behavior appears to represent a reversion to nestling-like behavior. Billing, mutual preening, "playful" upside down head movements, nibbling of the feet, courtship feeding, crouching, wing fluttering and some display flights may all be seen at one stage or another in the growing family.

Courtship often involves a long pre-nesting association during which the pair bond is strengthened, territory established and defended with varying intensity and the sexes synchronized physiologically and psychologically for mating. In some species such as the American Kestrel this period may actually be characterized by an increase in intraspecific social tolerance unlike the conflict noted in the discussion of territory above (38). In fact, pairs of Kestrels may be more tolerant of other pairs during courtship than at any other time of the year as many observations of promiscuous behavior indicate.

Latitude has a profound effect on both the onset and duration of courtship; courtship begins earlier and lasts longer in more southern latitudes. In Florida, Red-shouldered Hawks' courtship flights begin early in December. Young hatch in late February or early March. Pre-incubation behavior is often evidenced in the African Little Sparrow-Hawk six weeks before a nest is started. The beginning of the cycle is characterized by an increase in dawn calling, followed in a few days by carriage of nest material in all directions by both parents (120). Courtship in the Prairie Falcon lasts about a month.

A clearer understanding of latitudinal effects can be gained from

consideration of a migratory species such as the Peregrine, the breeding range of which spans considerable latitude. Pre-incubation behavior of Peregrines in Massachusetts may last four times as long as that observed in central Alaska where Cade (39) found a pair producing their first egg of the season within seven days of their apparently simultaneous arrival at the eyrie. In the same paper it is mentioned that in California where Peregrines appear to occupy areas near their eyries the year round, courtship may last two and one-half to three months. Cade continues:

> "In view of this long period of courtship among peregrines breeding at lower latitudes, it would be interesting to find out whether or not the northern falcons have actually eclipsed this phase of the reproductive cycle, or whether courtship begins on the wintering grounds, continues during migration, and culminates on the cliff soon after arrival. The latter pattern is known for some species of migratory waterfowl, and would seem to be the most reasonable expectation for the far northern peregrines" (39:179)

One final point by way of introduction: Courtship display sometimes continues into incubation and nest-life of the young. Hosking (108) observed such display in a male Marsh Harrier with 30 day-old young. Cade (39) saw "characteristic" breeding behavior throughout the breeding season in Peregrines, even after the young had fledged. Fitch *et al.* (73) believe that courtship activity in the Red-tailed Hawk can be observed throughout the year.

PAIRING

General Information. Pairing in raptors, as with any species, requires a great deal of adjustment. There are many indications that this is not easy for birds in general, especially the pugnacious raptorial species. The pair bond is apparently strengthened to a great degree by all forms of courtship, territorial defense, nest building, etc.

Concerning female dominance in large falcons, Cade states:

> ". . .a reproductively successful pair bond can result only when the female falcon is clearly dominant to the male and when the male makes a biologically adequate adjustment to his subordinate role in the pairing situation" (39:244).

This dominance is believed asserted by the female by virtue of sexual

dimorphism characteristic of birds of prey. Cade's evidence for this dominance (not a widely held theory) includes: "(1) rights to food items, (2) rights to perching places, and (3) successful completion of coition" (39:194).

The role of the sexes in pairing is not clearly understood. Hickey (102) speculates that due to the relative values of eyries as ecological magnets, "pairing in the Peregrine Falcon is not based on sexual selection but rather on the selection of a nesting territory" (102:198). Cade (39) agrees that attraction of Peregrines to the same cliff is more important than mutual attraction between mates, but believes the two factors are both involved.

Data on spring arrival of the sexes may be important in analysis of this problem. Except where arrival is simultaneous (63, 121) the male usually arrives first (168, 217), an indication, perhaps, of his importance in territory establishment and, subsequently, in pairing. This line of reasoning is contradicted by Cade (39) who states that female Peregrines are just as likely to arrive on their arctic breeding grounds first as are the males.

In spite of contradictions, however, this reviewer believes that some thought should be given in captive situations to a procedure of placing males in a breeding pen first, several days or weeks before the female. This may lessen the possibility of the female reacting to and destroying the male as an intruder to her established territory and would also allow the effects of early arrival by the male to be expressed, if such exist.

Determination of the duration of the pair bond in raptorial birds is and will probably remain a difficult endeavor. Whether a pair breaks up each fall or every few years, or whether raptors "mate for life" has not been established. Regardless of the anthropomorphic appeal of the latter situation, a typical statement about "mating for life" usually takes the form of the following by Burns: "I believe this species [Broad-winged Hawk] frequently if not always mate for life, but unfortunately direct evidence is wanting" (36:242). Direct evidence is indeed lacking.

The only important statement concerning this matter comes from Cade (39) who suggests that pairs of Peregrines which remain together throughout the year represent the strong extreme of pair bond in this species. The weak extreme is expressed by pairs which do not maintain their association through one productive season.

At some active nest-sites pairing does not occur at all. Cade (39) mentions that other observers have noticed non-laying females in many Peregrine populations. Their numbers may vary from 15 per cent of the population to nearly 100 per cent in poor years. Ratcliffe (151) has observed similar situations and points out several possible causes. It could mean a higher mortality rate for males, a general excess of females or more complete desertion by males after being

disturbed or after unsuccessfully attempting to breed.

Polygamy. This is one very interesting aspect of the pair bond which will now be treated in some detail. The most common arrangement involves two females laying in two nests attended and defended by a single male (Peregrine Falcon, Montagu's Harrier, Marsh Hawk, Marsh Harrier). Next, two females may lay in a single nest with a single male (Peregrine Falcon, Montagu's Harrier, Common Kestrel, European Sparrow-hawk). Finally, one female may occupy a single nest attended by two males (Montagu's Harrier, European Hobby). All cases known to this reviewer will be elaborated on below.

European Sparrow-hawk. Hughes-Onslow (111) found two female European Sparrow-hawks using the same nest.

Marsh Hawk and Marsh Harrier. Most cases of polygamy in these species are of the first type mentioned—two females occupying separate nests. Yocom (234) observed such an arrangement with Marsh Hawk nests 2400 yards apart. When one female was shot, the male stopped defending her territory, but continued his defense of the other. Yocom considers this ample evidence for polygamy, since no other male Marsh Hawks were seen. Hosking (108) found a polygamous cock Marsh Harrier supplying food for two hens at separate nests. He believes that this was a case of forced polygamy due to the lack of a second male. Reindahl (154) confirms this type of polygamy with accounts of a male Marsh Hawk which vigorously defended two nests. His females laid clutches of eight and five eggs. Hecht (101) explained another instance in which two Marsh Hawk nests were slightly less than a half-mile apart. The male favored one nest, defending it more vigorously and bringing food to the young therein more often. There was a possibility that a third female was involved. Her nest was about one-third mile away from one of the other two; Hecht never observed a male at this nest, although he noticed the third female steal food from a male near one of the two defended nests.

Montagu's Harrier. Unlike with the Marsh Hawk, polygamous arrangements in the Montagu's Harrier are varied, with all three types recorded. Of the first type, Dent (56) observed one female in a territory joined by a complete pair. The hens fought some, the first winning. During the next week the pair produced a nest and eggs in the absence of the loser. The initial loser, or another female, then appeared and after decreasing conflicts between the two females, the second nested within 70 yards of the first. When the male brought food he would summon one or the other and give her the food. If the wrong one rose from the nest he would drive her back to her nest. After an exchange the male would settle near the nest of the female he had fed until she was through eating and back on her eggs. There

were four eggs in the first nest and five (two infertile) in the second. Greenwell, Greenwell and Bell (85) observed strange behavior of Montagu's Harriers; two females and a male were involved. All during the reproductive period prior to hatching the original pair of birds tolerated a second female on their nesting territory. Soon after the eggs hatched the second female became more dominant until she began taking food-passes from the male. She gradually replaced the initial female at the nest and successfully raised the young not rightfully hers. When she had gained strict possession of the young, the original female was expelled from the area both by the male and his new mate. In another case observed by Hosking (108) the two nests were 300 yards apart and both successful. Colling and Brown (47) found the less common arrangement of two males and one female at a single nest. One of the males was an "odd" bird and did not take part in nesting activities, although it was tolerated in and seemed to share the territory of the nesting pair.

Peregrine Falcon. Bond (23) mentions a suspect polygamous arrangement between two female Peregrines and one male. Two nests were found about 1000 feet apart and the male showed mild anxiety at either eyrie when disturbed. The females defended their respective sites vigorously from each other. Gough (83) tells of an instance in which a tiercel Peregrine deserted an incubating female for another. The tiercel was seen with the new female on several occasions. The first female subsequently disappeared after a vicious fight with her mate's new female. In Gough's rather anthropomorphic words:

> "The strange Falcon must have ultimately seduced the local tiercel from his allegiance to his mate, and the latter remained on the eggs forlorn until hunger compelled her to go foraging for herself. She must have been on one of these foraging expeditions when she chanced to fall in with her rival, and, as she was weakened by starvation and, worn out by her long period of incubation, her rival easily overcame and vanquished her" (83:435).

Spofford (187) found a Peregrine eyrie with three adults present. Unfortunately the paper was not available to this reviewer.

European Hobby. C. V. Stoney (cited by the Nethersole-Thompsons, 133) observed a female Hobby examining and sitting on several empty nests in the company of two males.

Common Kestrel. Two records of threesomes of Kestrels, two females and a male, using the same nest have been noted (123, 159).

Additional Comments. One other multiple mate situation should be discussed. Promiscuity is frequently observed in some falconiforms, the Common Kestrel being the strongest example, in spite of stong pair bond (39). Cade (39) found that if a male arrives

first at his established eyrie, he may indulge in promiscuous behavior with stray females before the established female arrives to chase her competition away. Copulation may occur between a male and two different females within a period of minutes (43, 67).

The cause of polygamy has been speculated to be a preponderance of females in raptor populations (101). The evidence is conflicting. Hickey (102) and F. L. Beebe (14) found little evidence in Peregrines for a marked difference in the numbers of each sex, but indicate a slight preponderance of females in eastern North American and British Columbian populations. A high female to male ratio is often upheld in nest censuses and migration studies. Five nests of European Sparrow-hawks reported by Mayr (125) held seven males and 20 females collectively. When shooting was more rampant in Pennsylvania, of 291 Northern Goshawks killed in 1936-37, 181 were females, 100 males. The latter evidence was considered less conclusive than actual nest counts, because female Northern Goshawks may be more migratory. Roest (159) did a small nest count in American Kestrels which indicated 65 per cent females.

Against the theory of a preponderance of females is curious agreement that roughly 65 per cent of the late summer to spring population of American Kestrels in the United States are males. Roest (159) found this in a count of 107 living birds, as well as in all banding returns prior to 1957. In addition, M. Broun mentions (*Hawks Aloft: The Story of Hawk Mountain*. New York, 1949.) that 65 per cent of observed migrating American Kestrels are males based on Hawk Mountain Sanctuary data. The wanton slaughter of hawks along the Pennsylvania ridges in the twenties and thirties revealed a preponderance of males in small accipiter populations. Of 113 Sharp-shinned Hawks collected, only 20 were females. Female Cooper's Hawks were noticeably less abundant (201). Speculation is that perhaps the females were flying higher and were not in gun range as often.

MUTUAL ROOSTING

Cade indicates that the earliest manifestation of pairing in arctic Peregrines is "the quiet perching of the members of the pair on the same cliff or other favorite perching place" (39:190). This behavior is much more widespread than this one reference indicates.

COOPERATIVE HUNTING

Concurrent with the beginning of mutual roosting, pairs of Peregrines begin hunting together if they have not been doing so throughout the year (39). Cooperative hunting begins by individual sorties in the nest vicinity without regard to the other bird of the

pair. Cade states that "this apparent disregard for the other's presence represents a conspicuous change in behavior, because prior to the beginning of courtship many peregrines hold to mutually exclusive food territories" (39:191). Subsequent to individual hunting sorties paired Peregrines actually team up during the hunts, usually within sight of the nest cliff. This behavior is more often seen before egg-laying and after the young no longer need extensive brooding.

COURTSHIP FLIGHTS

Good descriptions of courtship flights are hard to improve upon so this section will rely heavily on flights as related by the observers. Generalities and evaluations of observations are included therein.

Red-tailed Hawk. Fitch, *et al.* (73) found that courtship flights of this species last from five to ten minutes. The birds move in wide circles, often very close together, one immediately above and behind the other. One or both may extend their legs and dangle them loosely and scream every few seconds. Often, short, swooping, combat-like maneuvers occur before the flight is ended by a series of dives by one bird to a favorite territorial perch.

Red-shouldered Hawk. The courtship of the Red-shouldered Hawk was described by Dixon as quite a noisy affair, particularly early in the season.

> "From about nine o'clock in the morning until midafternoon they are busy nest building, loafing and indulging in queer aerial antics. . . .The usual program is for the bird leisurely to ascend in wide spirals to an elevation of 1500-2000 feet above the nest grove, where it will give a few preliminary flaps of its wings, the signal for the noise to begin, and squalling and diving it will descend to the same place from which it started or to the nest grove nearby, in a series of nose dives and side slips" (57:234).

Eagles. Brown (33) considers the soaring, sometimes undulating, flights of eagles during the breeding season genuine display. This solo display is most advanced in the Crowned Eagle, more often the male. It is more common to see eagles nesting in forested areas displaying in this manner than those living in open country. The flight is exemplified by a bird circling high above the nest-site rising and falling in a series of steep dives and swoops beating on the upswing and plunging down again. At the peak of each upswing the feathers

of the head may be erected and the head is thrown back. The whole time (up to 8 minutes in the Crowned Eagle) the bird is calling in its characteristic note. This display may be seen throughout the breeding season and even after the young have fledged. Display flights involving both parents are most often a means of mutual prenuptial stimulation, particularly when food and nesting material are brought to the nest-site. This dual display is manifested in high, soaring flights which position the male above the female in preparation for a dive toward her. She may simply avoid him or turn upon her back presenting her feet to his which are lowered. Brown has seen this process repeated 4 or 5 times before the female moves off with the male in pursuit. Often the flight terminates in the vicinity of the nest tree with the birds calling to each other. This type of display is well developed in the Crowned Eagle, Golden Eagle and the Bateleur, and has been observed completely or in part in many other species.

Marsh Hawk. This species has developed one of the most complex and beautiful courtship flights of all raptorial birds. Three excellent descriptions follow:

> "The hawk tumbled downward, twisting and turning this way and that. . . .It finally came out of its fall in an abrupt swoop that carried it abruptly upward. Its momentum spent, the bird looped over in a back somersault, then down in another dizzy spin—up and down, up and down, tireless, and with an almost monotonous regularity" (154:191).

> "The female sits in one of the cottonwood trees and watches the performance of her mate. . . .He first flies upward with much flapping of his wings till he reaches the fifty-foot height, then turns in the air with a curious motion that displays first the white rump and then the white of the wing-linings and underparts, and flaps down again to the fifteen-foot level. Then he turns and rises again, and continues thus, up and down, across the meadow for some time. As he rises upward he calls four or five short squeaky-sounding notes, . . .but when he flaps downward again, he is silent. The female. . .occasionally calls to him with a loud scream" (168:100).

> "Soon after the arrival of the Marsh Hawks in March, certain of these birds were often seen performing their spectacular courting dives. In doing this the bird, in a very evident state of excitement, dived from a height of perhaps

> a hundred feet at a very steep angle for about fifty feet, when it 'zoomed' up again to about its original height where it turned over *sidewise*, like the wings of a wingnut being turned onto a bolt. . .often incorrectly described as a somersault. In this inverted position the bird beat its wings two or three times, then righted itself by the same sidewise turn, and again dived into the great dip to repeat the performance again and again" (28:270).

Peregrine Falcon. Courtship flights in Peregrines, according to Cade (39), are only slight modifications of hunting and territorial or other defense tactics. This behavior may even alternate with periods of cooperative hunting. A typical flight might go as follows:

> "They consist of various spiraling flights to a high altitude (just like the ringing-up of a hunting falcon after quarry that is trying to escape by staying above its pursuer) followed by steep diagonal dives and sudden climbs out of such dives by one sex at the other, which again are similar to the stoop of a hunting falcon. The 'attacked' mate may flip up and present its talons to the 'attacker' in a position exactly like that used as defense against serious attack, . . .and grappling of the feet sometimes occurs" (39:191).

American Kestrels. Willoughby and Cade (225) describe a courtship display in Kestrels which they call the "dive display." It occurs more often during early courtship.

> "The display consists of a series of climbs and dives with continuous, powerful wing-beats and with a series of three to five Klee notes uttered near the peak of each ascent. The vertical depth of the dives is around 30 to 60 feet. The displaying bird usually starts by banking vertically and dropping at a steep angle of about 50 degrees to the horizon with powerful wing-beats which achieve great speed. At the low point the bird climbs steeply with wings still beating deeply. At the high point the Klee notes are given just as the bird banks and starts down again. Two to six such dives may be performed in succession, and a strong wind seems to stimulate this kind of activity. Sometimes the male swoops over the perched female at the bottom of his dive. The function of the Dive Display is probably analogous, at least in part, to that of the aerial displays of other open-country breeding birds—namely, territorial advertisement, attraction of a

mate, and repulsion of rivals (Armstrong, 1947)" (225:87-88).

FAMILIARITIES

The bodily movements of breeding behavior in Peregrines were discussed by Cade:

> "In California and Alaska I have noted that...vocalization is nearly always accompanied by characteristic movements which are somewhat variable but always include bowing or crouching of the whole body, turning of the head partially or completely in the curious upside-down position so often indulged in by tame hawks, drooping of one wing, spreading the tail, and turning in small circles or semicircles while the [rusty-hinge] call is being given....So far as I have been able to tell, this behavior is more typical of the male than of the female. That it has a sexual significance is obvious, but its exact function is by no means clear" (39:189).

Other familiarities at or near the Peregrine nest-site include mutual preening, billing, nibbling of the toes or beak of the other mate as if trying to take food and the so-called "aerial-kiss." Billing usually occurs while the pair is perched together on the cliff and is accompanied by turning the head upside down and engagement of the beaks in various positions (39).

COURTSHIP FEEDING

This behavior takes on several forms. The weakest form involves delivery of prey to the female by the male which simply drops it to her on the nest platform. Next, the male may deliver it directly to the female, either landing on the nest and dropping it at his mate's feet or else actually passing it from his beak to hers. Perhaps a higher form involves aerial passes of food and characteristic flight patterns described below. A more intimate form involves the male tearing pieces of meat from a carcass and offering them to the female. Finally, in connection with the last mentioned form, the female may lean down and eat from the meat in her mate's feet alternating bites of her own and bites offered to her. The latter two forms have not been frequently observed in the wild, but this reviewer found them very prevalent in captive American Kestrels.

There are two schools of thought concerning the function of courtship feeding. Many hold that it is epigamic behavior, *i.e.*, it leads to copulation. Others believe that it may not play a major part

in sexual relations at all, it being instead an early manifestation of the role of the male later on in the breeding cycle when he must supply the young, too, with food.

Cade (39) believes that courtship feeding is very probably epigamic or at least related to copulation. Both of these behaviors appear at virtually the same time in the breeding cycle of Peregrines and such feeding is often followed seconds or minutes later by copulation. It is argued, however, that courtship feeding is not actually epigamic behavior, since copulation is so frequent. There would "seem to be little need for a 'low-intensity' expression of the sex drive" (39:193) to stimulate copulation. Cade (39) also indicates that courtship feeding may be an indication of sexual readiness in falcons. Perhaps this may be of use to those attempting artificial insemination with respect to its timing.

All records of courtship feeding in the papers reviewed involve the male as the provider of the food. The argument by Cade (39) that courtship feeding might just be a "warming-up" period for when the male must provide food for a brood of nestlings revolves around the fact that courtship feeding does not cease at egg-laying, but copulation does for the most part. The male continues to feed his mate throughout incubation and into the growth period of the young in varying degrees depending upon the amount of brooding required by the young birds. Thus, in Peregrines a male may provide a large percentage, if not all, of the food for the family during a six to seven week period.

Cade's assessment of courtship feeding in Peregrines appears to comprise the first three forms listed above. His apt account of this behavior follows:

> "Typically, the male flies to the perched female, carrying a small bird in his talons. As he is alighting, the food item is transferred from his talons to his beak. He then bows slowly up and down before the female, often with his head turned partially or completely in the upside-down position, and he utters a chittering sound. He may advance toward her a little, still chittering; but usually she comes rather quickly to him and accepts the prey in her beak, after which she either turns away from him to pluck the prey or, more frequently, flies off to some other perch to eat" (39:192).

Cade continues with a description of a peculiar flight pattern associated with courtship feeding which he has observed in Peregrines, Prairie Falcons and American Kestrels:

> "In this flight the falcon holds her wings slightly arched

> below the plane of her horizontally oriented body and makes a flicking or fluttering that is especially conspicuous at the carpal joints; at the same time the tail in fanned out somewhat. . . .The fact that recently fledged young fly to their food-carrying parents in the same way confirms the interpretaiton that this behavior is an extension or derivation of the wing-quivering, food-begging response, which is performed by many nestling birds including young falcons" (39:192-193).

Other observations and speculations concerning courtship feeding include an observance of such behavior in the Marsh Harrier in conjunction with nest building (47). Food-begging by wing fluttering is not often observed during courtship feeding in Peregrines (39). Courtship feeding may play an important role in the nutritional needs of the female at this time. A final speculation, again by Cade (39), is that courtship feeding actually neutralizes aggressive behavior between mates, a necessity for proper integration of social relations.

COPULATION

General considerations. The onset of copulatory behavior often precedes nesting by over a month. It may continue for a short period after egg-laying occurs. Childs and Mossman (43) observed copulation of American Kestrels six weeks before eggs were laid. S. C. Bishop (17) witnessed almost daily copulations of a single pair of Kestrels from April 6 to May 4, about a month. Roest (159) mentions copulation in this species after eggs were laid. Copulation has been recorded in the Crowned Eagle as much as six weeks before egg deposition.

Since copulation occurs over a long period of time, Cade (39) believes that copulatory mounting itself may constitute epigamic display. The initial attempts may simply synchronize the sexes to assure insemination when the proper time arrives.

The frequency of the copulatory act varies with the stage of the breeding cycle. The frequency is low at first, gradually increasing prior to egg-laying which is followed by a sharp drop in frequency until cessation shortly after incubation begins (39, 120). As with female involvement in territorial conflict the sharp drop-off of copulation frequency is probably due to the unavailability of the incubating female (39).

Some maximum frequencies for copulation in American Kestrels were reported by S. C. Bishop (17) and Hartman (99). They are five times in twenty-five minutes and fourteen times in thirty-six minutes, respectively. The latter was a captive situation.

Pre-copulation behavior. Pre-copulation behavior gives some indication of the factors which sexually stimulate paired birds. Solicitation by the female is the most often reported occurrence, but does not always precede copulation at least in the Peregrine (39), Prairie Falcon (114) and Red-tailed Hawk (73). When copulation is preceded by female solicitation in the Red-tailed Hawk, she tilts forward and slightly opens her wings while perched near the male. Her body is almost horizontal and her wings are held loosely and flapped several times. Often the male will ignore her, while other times this behavior leads immediately to copulation. Other female solicitation in this species and others may involve the nibbling of the male's head and neck feathers. This is a reciprocal behavior, but the female is most active (73).

S. C. Bishop (17) believes that the female American Kestrel takes the initiative in mating by calling continuously for many minutes, fluttering her wings and persistently approaching the male.

Brown (33) observed female solicitation in Crowned Eagles. The female would bow her head and utter a call not unlike an older chick awaiting food. Similar behavior was noted in males, but association was with the female approaching with food or nesting material, not copulation.

Liversidge's observations of the African Little Sparrow-hawk would indicate male solicitation:

> "The female would be sitting on a branch and the male would take up a position in good view of the female where he would call repeatedly and excitedly, fluffing his feathers out, especially the rump, drooping the wings a little and lifting the tail. The head would be swayed from side to side, the whole body in a horizontal position. In this state he would approach the female which would assume an exaggerated food-begging stance with quivering wings. Copulation would then take place" (120:400).

Other observations of pre-copulation behavior include a series of aerial maneuvers in the Red-tailed Hawk (120). Seven out of eight occurrences of copulation in this species witnessed by Fitch *et al.* (120) involved a sitting female. Jaeger (114) saw copulation in Prairie Falcons. The female was perched on an enormous granite butte when the male flew directly to her; copulation took place without preliminary display unless the crouching of the female can be termed display. The copulatory act lasted ten seconds, ending as abruptly as it began with the male departing immediately after dismounting.

Post-copulation behavior. Patterns of post-copulation behavior involve either aerial displays or quiet perching in the Red-tailed

Hawk (64, 73) and American Kestrel (17). S. C. Bishop's accounts for the American Kestrel are illustrative:

> "After mating, the female sometimes continues to call and flutter her wings while the male rests near by with drooping wings and head drawn down on the shoulders. . . .[On other occasions] the male sometimes mounts high in the air and performs some remarkable evolutions—spirals, short dashes and a rapid drop ending on the back of the female" (17:268).

The copulatory act. Details of copulatory behavior for various hawks and falcons follow.

Red-tailed Hawk. Fitch *et al.* (120) indicate that copulation in this species lasts from five to twelve seconds, but may last twenty. The male may flap slowly while mounted and support himself with spread wings braced against nearby branches.

Gray Hawk. Stensrude (189) observed copulation in the Gray Hawk several times, but only in the morning hours and only lasting two or three seconds at a time.

Marsh Harrier. Hosking witnessed copulation of Marsh Harriers three times and describes it as follows:

> "During copulation the hen crouched very low, almost in a horizontal position, and the cock slowly flapped his wings" (108:4).

All three occurrences were with the hen perched on the same tree branch, a perch not frequently visited otherwise.

Peregrine Falcon. Cade describes copulation in the following manner for Peregrines:

> "The female will be perched on one ledge and the male on another 50 yards away. Suddenly the male flies toward the female. She squats, and he lands on her back, depressing his tail to one side of hers and maintaining his balance by fluttering his wings. During the act, which lasts 10 to 15 seconds, the male utters a constant chittering sound. I believe the female also chitters in a slightly lower pitch at this time. . .[This] is definitely true of female kestrels; . . ." (39:194).

Male falcons often attempt copulation with temporarily unreceptive females. Cade aptly depicts the refusal in female Peregrines:

> "When this occurs, she may simply throw-up her wings to ward him off or fly away to some other perch. If the male is persistent she 'cacks,' ruffs out her feathers, especially those on her nape and crown, and turns on him with her talons" (39:195).

Merlin. Stubbert gives the following account of copulatory behavior in British Merlins:

> "They landed on the branch of an oak tree and chased one another up and down the branch for about ten minutes, moving sideways with tails fanned and depressed. Sometimes they would jump up from the branch, fluttering together with wings partly raised like cocks fighting, then settle on a branch again and begin the hopping chase, first one chasing, then the other. After coition both birds sprang into the air and gave a magnificent aerial display lasting nearly an hour. They kept very close together, appearing almost touching and flew straight 500-600 feet, then making a rapid turn simultaneously, swooped down at tremendous speed, one above the other, the male usually, but not always, on the top. At tree top level they turned again and repeated the performance" (194:17).

American Kestrel. Willoughby and Cade (225) and Roest (159) have written on the copulation behavior of American Kestrels. Their details follow in order:

> "The female bows deeply with her legs extended beneath her so that her back slopes head down at an angle of 30 to 50 degrees to the horizontal and with her tail held in a line with her body or angled up slightly and compressed. The male squats on her back on his tarsi with his toes balled into fists, balances with his wings raised over his back and flapping, and brings his tail down vertically to one side of the female's so that the cloacae come in contact (see Figure 9). During copulation the male utters repeated loud Chitters; the female repeatedly gives either Chitters or Simple Whines. Copulation lasts 2 to 10 seconds, and repeated cloacal contacts are made during the longer episodes. The male mounts the female either by stepping up onto her back from the perch beside her or alighting on her back from the air. Often a flight by the male ends directly on the female's back with copulation following at once. In such instances the female seems to

anticipate the male's approach by standing in the copulatory position before he reaches her. Sometimes a female prevents an intended mounting by raising her wings or by hopping off the perch as the male is attempting to settle onto her back" (225:86).

"The female turned her back to the male and assumed a horizontal position, flipping her tail up and down a few times. The male flipped his tail also, and moved up until the two birds were side by side. Then he quickly mounted and copulation took place, with some gentle wing fluttering on the part of the male to maintain his balance. Copulation lasted twenty or thirty seconds, after which the male hopped over to another branch. . . .The female apparently initiated copulation by flipping her tail while in the horizontal position" (159:2-3).

NEST-SCRAPING

Many species of falcons are notorious for not lifting a twig toward building a nest, preferring instead simply to scrape in the sand or dirt of a ledge or to appropriate the previous year's site of another species. The occurrence of scraping is best known in the Peregrine. This behavior does not serve as "construction" of a functional nest, it being more symbolic and repeatedly carried out before incubation and to a lesser degree after the eggs have been laid (39).

Ferguson-Lees (cited by Ratcliffe, 150) implies that the inability to perform nest-scraping activity in Peregrines may result in failure to breed. Ratcliffe (150) disagrees, having never seen a cliff which lacked a site for nest-scraping. He creates further doubt by stating that scraping behavior varies in intensity, some making several scrapes before laying, others depositing eggs in the first scrape. Hickey states that there are "several instances where the falcon [Peregrine] is known to have laid a single egg in one scrape and then laid the remainder of her clutch in a different scrape on the same ledge or a different ledge of the same cliff" (102:187). Fowler (78) claims that a Prairie Falcon may lay one egg in a scrape, only to abandon it to raise a family 30 feet away. Still other large falcons usurp Ravens from their sites and lay directly on wool linings supplied by the conquered without apparent nest-scraping activity.

Ferguson-Lees' opinion that nest failure may result from insufficiency of the nest-site is substantiated somewhat by the studies of Willoughby and Cade (225) on captive American Kestrels. Their experiments indicate that ovulation is inhibited if no suitable nest-site is present. Whatever the case, nest-scraping "has become an integral part of courtship displays" (39:194) in Peregrines.

Interesting observations and theories concerning Peregrine nest-scraping were advanced by Nethersole-Thompson and Nethersole-Thompson (133). They write of a case where a female Peregrine paid little attention to the male's nest-site exploration until copulation had taken place several times. From that time on the female's interest in scrapes continued as the male's interest decreased steadily. Also, a scrape may be brooded for long periods of time on several days before egg laying.

CHAPTER 6. NESTS AND NESTING

This paper is not necessarily concerned with nest descriptions and types of nest-sites; rather it is more concerned with how the parents come to nest in a certain spot and how the parents and young behave toward the nest-site. Site choice, multiple nesting and the roles of the sexes in nest building are therefore discussed. Treatment of the nest building process will follow with extensive reference to the use of green material at the nest-site after actual nest construction. Sections on nest sanitation and nest parasites conclude this chapter.

SITE CHOICE

Site-selection tours. It is quite difficult to determine which sex selects the final nest-site or why a particular site is chosen. As will be seen below, much disagreement and unsubstantiated speculation exists concerning this matter.

Nethersole-Thompson and Nethersole-Thompson (133) speak of site-selection tours in several species of raptors, during which a number of potential nest-sites are inspected and copulation may occur. Willoughby and Cade (225) speculate that nest-site exploration might function as a sexual stimulus in American Kestrels.

These tours begin at varying lengths of time before egg-laying in different species. In the Common Kestrel, for example, both sexes begin inspecting possible sites a full three weeks prior to nesting (133). Willoughby and Cade (225) observed both sexes of American Kestrels participating in this activity.

European Hobbies often select a nest four or five weeks before egg-laying. About a week prior to laying, the female spends much time brooding an empty nest (133). Hórvath (107) found Red-footed Falcons occupying the nest-site, usually an unaltered Rook nest, two or three weeks before the first egg is laid. According to Davenport (51), long before the trees are covered with leaves, European Sparrow-hawks have chosen their nest-site, visiting it at dawn and dusk, soaring over the spot and screaming quite often. About six weeks later the eggs are laid.

Roles of the sexes. The roles of individual parents in choosing nest-sites was extensively treated by Nethersole-Thompson and Nethersole-Thompson (133). Some of their findings follow. The male Common Kestrel often takes the initiative during site-selection tours by coaxing the female with food and eventually chooses the final site

himself. The Merlin's choice of nest-site is apparently up to the female, but the male is present when the decision is made. The Montagu's Harrier male has been observed inspecting possible nest-sites before the arrival of the female, but once she arrives he watches from a distance while she tours and selects. This holds true even in bigamous pairs; both females choose their respective sites. The female Marsh Harrier chooses her nest-site. Both Golden Eagles participate in selecting the eyrie site, but the female seems to have the final say. After much display in the vicinity of several alternative sites, one or more sites are visited for long periods of time and eventually a choice is made.

One factor affecting nest-site selection is the length of time a pair has been mated (113). The Common Buzzard male may influence the choice of a new female, but not of a mate of several years. The Golden Eagle male with a new female has been observed at what was interpreted as acquainting the female with various alternative eyries. The influence of a male on the site-choice of a new female has also been observed in European Sparrow-hawks.

The Peregrine Falcon. The Peregrine, being the most extensively studied falcon, is the subject of much controversy concerning why a particular site is chosen. The importance of cliffs and altitude are the disputed factors. The kindling statement for the disagreement comes from Hickey, who writes about the cliff nest-site as an ecological magnet for this species. "Cliffs are the dominant features of the Peregrine's ecological niche over most of its present breeding range,..." He continues in a later paragraph: "...gaps in the population are filled according to each eyrie's value as an ecological magnet, and not according to latitude" (102:196, 198).

Bond (23) believes that Hickey's conclusions are an oversimplification when applied to western North American Peregrines. Bond cites several examples of top rated cliffs being unoccupied by Peregrines, while "less suitable" cliffs nearby were occupied. Cade (39) found Hickey's emphasis and evaluation of cliff types for Peregrines invalid in northern Alaska. The birds there seem to avoid very high cliffs as nest-sites. Cade feels that the concept of the cliff being an ecological magnet for nesting Peregrines "is misleading and directs attention away from other factors that are basically more determinative" (39:237). He feels that more emphasis should be placed on the characteristics and ecology of the falcons rather than the physical characteristics of the cliffs. Strangely, however, earlier in the same paper Cade points out that the cliff itself attracts the falcons, not the presence of another falcon.

Ratcliffe (150) adds to the controversy by advancing the following criteria for a "suitable nesting cliff" for inland British Peregrines:

"(a) An altitude of over 800 ft. above sea level but not greatly exceeding 2,000 ft.
(b) A total height of over 100 ft. in rugged country, or over 30 ft. in moorland country.
(c) At least one nest-site in not too easily accessible a place, and preferably a choice of nest-sites.
(d) A position at least half a mile from the nearest human habitation, unless the cliff is particularly high and precipitous" (150:25).

The altitudinal factor listed here is contradicted by Bond (23), who sets a much higher altitudinal limit for the nesting of Peregrines in western North America, some nests being found up to 10,000 feet. In general, there seems to be no evident explanation for a general altitudinal limitation on the nesting of birds of prey as long as food supply and climatic conditions are compatible with nesting.

In the heat of the above discussions it appears that little has been published concerning the role of the sexes in site-selection. There is room for new evidence on this matter not only for the Peregrine, but for all species.

MULTIPLE NESTING

Site choice may be influenced by the number of sites within a territory and success of broods of recent years at each site, as well as the above considerations. This leads us to the characteristic of multiple nesting, which is fairly widespread in the order Falconiforms.

By multiple nesting it is meant that a pair of birds may regularly nest at two or more sites in different years, or may build or repair two nests in the same year, finally choosing one or the other. For example, the African Hawk-eagle has one to three nest-sites used more or less alternately. Near six pairs of this species found by Brown (32), 11 nests were found. Ratcliffe (150) states that Peregrines often use two alternate nest-sites within a single established territory. One such territory had six suitable sites on a single cliff. In addition, more than one nest has been found in the territories of the following species: Northern Goshawk (12, 169), Common Buzzard (165), Red-shouldered Hawk (57), Ferruginous Hawk (41), Black Eagle (11), Peale's Falcon (14), Shaheen (10), Prairie Falcon (217) and Oriental Hobby (10). Surely there are many other examples, but this should suffice to illustrate the widespread nature of this practice.

In the preceding paragraphs too much emphasis has probably been placed on the alternating use of these sites. The choice of the nests to be used is much more complex than simple alternation. In

the Common Buzzard two nests may be repaired, even newly lined, but the actual nesting may occur in a third newly constructed nest (165). The Red-shouldered Hawk will use a second or third site if the first is disturbed (57). In the Black Eagle and Shaheen no hard-and-fast rule governs use of one site over another nearby. In Peregrine territories the alternate sites are not usually used in rotation, since in most cases, one site is preferred over all others (150). Baker (10) found a pair of Oriental Hobbies with two nests about 200 yards apart. Invariably after the first clutch of eggs was taken the pair laid a second clutch at the alternate nest-site, returning to the initial site the following year.

ROLES OF THE SEXES IN NEST BUILDING

There are two general divisions of labor during nest building in raptorial birds. First, the female may collect all the sticks and construct the entire nest alone. Second, the male may assist in varying degrees. Rarely does a male take the larger share of nest building, although Nethersole-Thompson and Nethersole-Thompson (133) mention an instance of an unmated male Hen Harrier selecting a nest-site and building a nest.

A few examples will help emphasize the importance of the female in nest building. Zirrer (cited by Schnell, 169) found that the female Northern Goshawk does the nest building. She gathers branches from fallen trees or collects them from the ground. Much time is spent choosing each limb and then arranging it at the nest. The African Little Sparrow-hawk female does most of the nest building, being recorded by Liversidge (120) to bring five times as many sticks as the male. Most of the sticks are carefully collected by the female, which pulls them off with her bill within 20 yards of the nest, then carries them to the site in her feet. There appeared to be no design to the placement of the sticks, each bird simply depositing larger sticks at first, then smaller ones until the platform was complete. Davenport (51) found somewhat different behavior, having repeatedly seen European Sparrow-hawks gathering materials below the nest-site, each sex taking its turn bringing a fresh stick or twig. Kendeigh (115) reports that generally in the genus *Accipiter*, females build the nest doing up to 90 per cent of the work in the European Sparrow-hawk.

Brandt (27) states that the Short-tailed Hawk male accompanies his mate when she brings a stick to the nest, but remains stationary in the breeze some distance above the nest. Both parent Verreaux's Eagles bring material for building or repairing the nest. Nest repairing may go on over a period of six or seven weeks (32). The Crowned Eagle may spend as much as four months adding to and repairing its nest. This may explain its enormous size as both sexes work together to add as much as six inches in some years (33).

NEST BUILDING

Nest-scraping in falcons was discussed under pre-incubation behavior. Concerning hawks, either this reviewer unconsciously rejected references to parental behavior during actual nest building, or it is not extensively documented in the articles reviewed. Nevertheless, a few points can be made.

Hawks may be very noisy during nest-site selection, but when nest building or repairing is begun in earnest, silence is the rule (36). The addition of nest material need not stop at egg-laying; Hosking (108) observed Marsh Harriers bringing new twigs and grass to the nest throughout incubation.

With regard to the physical treatment of nest material, Marsh Hawks carry large pieces of nesting material in their feet, but grass is usually carried in the bill (4). Allen (4) states that male Marsh Hawks often play with nesting material in the air, dropping it and then diving down to catch it before it hits the ground. Sometimes the male drops for the female, and she catches it.

Building nests in trees is not always an easy affair. Many of the newly placed sticks fall, particularly when a completely new site is chosen. Ray (153) found a complete ring of small twigs and branches under a Northern Goshawk nest, all apparently dropped by the birds during nest building.

References to the length of time required to build a nest are nearly lacking. Allen (4) states that Marsh Hawks spend a full week constructing their nest. Fitch *et al.* (73) indicate that nests of the Red-tailed Hawks, if new, are apparently built very rapidly, but they offer no definite length of time. Much more than that cannot be said.

The length of time nest construction is begun before eggs are laid varies, but in most hawks and eagles a few to several weeks are involved. Nest repairing in the Common Buzzard may begin as much as five weeks prior to laying. Red-shouldered Hawks in Florida often complete their nest, cup and all, a month or more before egg laying (134). Meiklejohn (127) found European Sparrow-hawks building nests six to seven weeks before deposition of the first egg, but only the outer rim was built at this time. About a week before laying commenced the bowl was added.

Martial Eagles begin nest repairing a month or more before egg-laying, with addition of much fresh green material and occasionally large masses of sticks (32). Wahlberg's Eagles begin repairing their chosen site two months before it is needed (32).

The large falcons again offer controversy over how an old nest is repaired. Ferguson-Lees (70) states that when a pair of Peregrine Falcons chooses an old Raven, Buzzard or gull nest, the original

lining is first removed. He does not elaborate further. Ratcliffe (1: disagrees with this claim, citing seven examples of Peregrine e deposited in recently robbed Raven nests, linings intact. Baker (1 found that Shaheens seem to discard a certain amount of the nesting material and replace it with more than a correspondi amount of new. Falcons in California often occupy old Raven's ne without changing the lining (211). Surely, all of these observatio are true within the experience of the observers; they simply poi out more inter- and intra-specific variation.

GREEN MATERIAL

Occurrence of the phenomenon. One of the most interesting a highly speculative aspects of falconiform reproduction is the curio behavior of adding green material to already completed structur There seems to be a strong desire or drive at work, which, accord to Burns (36), is strongest in the Broad-winged Hawk. Alm invariably green material can be found under and around the e and young of this species. Even blossoms sometimes adorn the n and if the leaves have not opened, twigs with leaf-buds may be us In an individual nest, however, only one type of leaf is used as a n

Table 6 gives the species known to display this behavior. It sho be noted that no falcon appears on the list. This may not be absolute exclusion, but certainly indicates that hawks, particula

TABLE 6. SPECIES WHICH ADD GREEN MATERIAL TO THEIR ALREADY COMPLETED NESTS

1.	Northern Goshawk	(36, 86, 16
2.	Sharp-shinned Hawk	(3
3.	African Little Sparrow-hawk	(12
4.	Cooper's Hawk	(19
5.	Red-tailed Hawk	(36, 73, 106, 139, 20
6.	Common Buzzard	(36, 16
7.	Red-shouldered Hawk	(36, 57, 17
8.	Broad-winged Hawk	(36, 10
9.	Swainson's Hawk	(36, 23
10.	Zone-tailed Hawk	(3
11.	Rough-legged Hawk	(9
12.	Ferruginous Hawk	(4
13.	Gray Hawk	(3
14.	Harris' Hawk	(3
15.	Short-tailed Hawk	(3
16.	Golden Eagle	(36, 19
17.	Marsh Hawk	(17

those which build their own nests, have a much stronger tendency to add green material.

Some believe that green material is accidentally brought to the nest. Fitch *et al.* found grass in Red-tailed Hawk nests throughout the nesting season, but dismiss this as material, "snatched up and carried incidentally, in the capturing of prey" (73:211). This is not true in some species. Schnell (169) emphasizes that green sprigs are not always brought to the nest one at a time by a female Northern Goshawk. This fact in addition to the following description of "sprig collecting" in the same Northern Goshawks virtually eliminates an interpretation that this behavior is anything but directed.

> "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 nestlings stage of the breeding cycle" (169:381).

There seems to be no particular stage of the nesting cycle when green material of some sort has not been found in nests. Fitch *et al.* (73) indicate that green material is brought to Red-tailed Hawk nests from early spring before the final site is chosen, until the young leave the nest. The early appearance of the behavior in this case may indicate a connection with courtship behavior.

Handley (94) and Peabody (139) observed leafy twigs beside incubated eggs in Rough-legged Hawks and Red-tailed Hawks, respectively. Sharp (176) found green material in Red-shouldered Hawk nests, particularly during incubation. The practice as observed by Sharp stops shortly after the young hatch and is not seen for the remainder of the reproductive cycle. Liversidge (120) in his paper on the African Little Sparrow-hawk states that all observed deposits of green leaves by this species occurred during nest relief. The first spray was brought the day the first egg was laid and during early incubation much additional green material was brought until the 12th day of incubation when the practice virtually stopped.

Dixon (57) found new green material in a Red-shouldered Hawk nest shortly after the eggs hatched and it was renewed as the nestlings developed. Similar observations during nestling growth are on record for the Common Buzzard (165), Red-tailed Hawk (106), Swainson's Hawk (233), Marsh Hawk (178) and Northern Goshawk (201). Brown (33) states that eagles bring green branches to their nest during most of the breeding cycle, particularly during the first half of the fledging period.

Functions. As may be expected speculation is rampant concerning the function of this behavior. No less than eight explanations for this behavior are given below beginning with the least likely and ending with more plausible ideas.

"The Broad-winged Hawk garnishes her eggs with a green leaf—symbol of the ancient law of instinct that is part of the poetry of nature" (103:137). Some believe that the use of green material is a manifestation of an artistic sense of ornamentation (36). Gromme writes that green twigs around the edge of a Northern Goshawk nest "lent an appearance of artistry and color" (86:17). Cameron (41) indicates that green alfalfa was carried to the Ferruginous Hawk's nest for "decorative purposes."

Brown (33) believes the main function of green branches brought to eagle nests is that of nest lining, probably to reduce damage to an egg or a small chick. Nest sanitation is a proposed function in Red-tailed Hawks (135) and Marsh Hawks (4). This may also be the case in some Northern Goshawks, but often, in most species, the small amount of material brought to the nest precludes such simple explanations.

Burns would combine several of the above functions and add heat regulation to the list. He writes:

> "It is more likely the lingering vestige of the instinct that led its reptilian ancestors to employ decaying vegetation to develop the embryo. No doubt the moist tender leaf imparts more or less heat to the eggs, and as the habit is not abandoned until after the brood is able to clamber to the side of the nest, it serves the treble purpose: first a soft and warm bed for the callow young, and as the decaying refuse accumulate and the large tree ants, wood lice and ticks multiply, the successive layers become a matter of sanitation and protection" (36:249).

Criddle (cited by Hogman, 106) believes that added twigs may act as a sunshade for the young and as a camouflage device to protect the young from enemies. Again, neither seems plausible since the amount of material brought is far too little.

Similar to Schnell's observations mentioned above, Dixon and Dixon (58) found a Northern Goshawk nest with two 23-day old young on a platform entirely covered with three inches of fresh pine boughs. None were placed in the nest cup during incubation, although a few were brought to the nest rim. Hard bark lined the cup before the eggs hatched. This may be a heat regulating mechanism. While incubating, little air is allowed to circulate under the eggs relative to the amount which could circulate under nestlings resting on spruce boughs.

The final idea is probably the most thought out, be it right or wrong. After observing that "sprig collecting activity" decreased as brooding of the young decreased, Schnell (169) speculated the following:

> "The female is obviously under the influence of estrogen while brooding and...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" (169:383).

As should be obvious, analysis of this matter is still open for research. It may well be that the above ideas are the closest one can approach the solution.

NEST SANITATION

Nest sanitation is important to the welfare of the young. It may have considerable survival value in that accumulations of excrement and prey remains below a nest or eyrie could attract various predators of eggs and young raptors, as well as nest parasites detrimental to the health of the new birds.

One of the striking features of this subject is the early, probably instinctive reaction of young raptors to discharge excrement over the edge of the nest. Since virtually no feces are found in the nests, this behavior must be present in the youngest nestlings (57). The birds stand erect facing the center of the nest and then back up until on the edge of the nest before defecating. This matter will be discussed further in Part 2 of this review which concerns growth and development of the young.

Parent birds of various species have been known to "clean house" occasionally by removing pellets, eggshells and prey remains from the nest. This has been observed often enough to indicate more widespread occurrence.

Colling and Brown (47) and Allen (4) have observed Marsh Hawks carrying pellets away from the nest. The African Little Sparrow-hawk (120), Marsh Hawk (226) and Red-footed Falcon (107) carry their eggshells from the nest. Horvath (107) even goes so far as to say that eggshells and excess food are carried farther from the nest during the early part of the fledging period by Red-footed Falcons than they are later on.

The removal of prey is more commonly reported, being observed in Gyrfalcons by Wayre and Jolly (216) and in Prairie Falcons by Fowler (77), for examples. Unused prey is discarded by parent Red-tailed Hawks within a day of its capture. This behavior disappears as the young begin feeding themselves and the nest usually

becomes quite littered (73). Schnell writes of actual "clean-up" actions by a female Northern Goshawk after a family meal.

> "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" (169:385).

This same observer saw this Northern Goshawk leave the nest carrying uneaten intestines temporarily laid aside during the course of feeding the nestlings.

Schnell also mentions a curious activity which may be a type of nest sanitation. He calls the activity "excavation" and describes it as follows:

> "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...on the surface of the nest platform....Excavation activities diminished as the season progressed" (169:386).

Whether this is to provide ventilation of the nest from below or a softer platform for the young by loosening the material in the cup or whether it is to provide a clean layer for the platform is interesting food for thought.

Despite the parents' attempts at cleanliness and the nestlings innate behavior, nests begin to deteriorate as the season progresses As young raptors gain weight and begin to move about, the somewhat cupped nest used for incubation becomes flattened into a platform. The harrier's nest is kept fairly clean as long as the nestlings are confined to it, but becomes quite littered with feces down and prey remains toward the end of nest-life. Being hatched on the ground, young Marsh Hawks wander from the nest, often defecating across it rather than shooting over the edge like elder tree nesting species. Shelley describes the nest of four 11-day-old Marsh Hawks as "trampled, filthy with excrement and over-run with carrion beetles" (178:287).

NEST PARASITES

Flies. Flies and their larvae are probably the most severe insect pest problem which confronts a raptor family. Both adults and young are bothered by them, the latter much more seriously. Schnell

observed a female Northern Goshawk catching flies which were pestering her and her brood.

> "She would watch intently when a gnat or fly landed nearby and then move slowly forward until within striking distance. A sudden stab with the beak secured the insect. On one occasion, an insect was swallowed" (169:381).

This same observer believes that young hawks have a reflex enabling them to dislodge or scare off insects even when asleep. He writes:

> "...The motion was not directed at any particular part of the body and was performed regardless of where the insect caused 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" (169:394).

The most often reported fly around raptor nests in North America is of the genus *Apaulina*, which is closely related to the Old World genus, *Protocalliphora*. The two will be treated below as one, the bird nest screw-worm fly.

The occurrence of these flies is fairly widespread, being found in the nests or young of Northern Goshawks, Cooper's Hawks, Red-tailed Hawks, Red-shouldered Hawks, Broad-winged Hawks, Golden Eagles and American Kestrels (104, 128, 167). Sargent (167) found that infestation of Red-tailed and Red-shouldered Hawk nests was nearly 100 per cent in his study area.

The flies more often occur in nests with a damply matted interior. New nests not having such an interior are less prone to infestation. Peregrine Falcons, because they nest on dry ledges where pupation of blowflies is impossible, normally escape the wrath of these insects (167).

Larvae of the bird nest screw-worm fly are blood-sucking parasites, obtaining their sustenance from the feet, eyelids, ear cavities and developing feather sheaths of the crown and nape. Sargent (167) reports one case, a female Red-tailed Hawk nestling, from which ten maggots were removed from her right ear and nine from her left; ten more were found on her crown and nape and her nest was crawling with them. When attacking the ear cavities, *Protocalliphora* larvae may stretch the ear openings to twice their normal size, completely plugging the external opening. When attacking feather sheaths the oozing blood and fecal waste of the maggots cause matting of the down in the infected area (167).

Hill and Work (104) found a brood of American Kestrels and another of Golden Eagles infested in the ears and nostrils with blood

sucking larvae. After removal of the Kestrels from the nest for observation a black crust developed around the ears. The origin of the crust was believed to be dark, blood pigment colored excreta of the larvae. When this crust was removed the ear canals were markedly swollen and filled with larvae, each containing a small amount of red blood on which they were feeding. The nostrils were deformed to the extent of the diameter of the larvae. The 22 larvae removed from two of the Kestrels measured from 2 to 8 millimeters in length. The *Protocalliphora* larvae from the two 13-day-old Golden Eagles appeared identical to those found in the brood of Kestrels. The black crust around the ears was present. Most of the larvae were removed and upon revisiting the nest a month later no larvae were found.

The effects of *Protocalliphora* larval attacks on the developing birds vary. Sargent (167) mentions several instances where the parasitism caused no apparent harm; the large hawks do not appear irritated, and there is no indication of deafness. Affected feather areas develop normally. In the American Kestrels observed by Hill and Work (104) the only physical effect on the young birds was restlessness and a larger appetite than two control birds.

Meng found the bird nest screw-worm fly in young Cooper's Hawks.

> "As soon as the hawk eggs start hatching, the adult flies, which look very much like bluebottle flies, deposit their eggs along the edges of the nests. Soon after being laid the fly eggs hatch, and the larvae find their way into the ear openings of the young hawks" (128:21).

A more complete life history is available in Dr. Meng's paper.

Other flies attack nestling raptors. Black flies identified as *Simulium canonicolum* were found at one nest of American Kestrels by Roest (159). The young showed excessive pigmentation of the cere, feet, etc., and swollen legs. Fitch *et al.* (73) report that seven of 26 Red-tailed Hawk nestlings observed in California died of the effects of the blood-sucking fly, *Eusimulium clarum*. Six of the seven deaths occurred in one season, usually before the nestling was nine days old. Young nestlings are particularly vulnerable to *Eusimulium* since the down is easily penetrated. This fly must play an important role in nest success since the survival of hatched young was reduced from 100 per cent one summer to 27 per cent the next, principally by the ill effects of this insect.

Ticks. In addition to flies, ticks are sometimes found on young raptors to the detriment of the birds. Webster (217) observed a marked difference in fledging success of hatched Prairie Falcons in different regions of Colorado. In the south up to 95 per cent of the

hatched young left the eyrie, whereas to the north only 35 per cent survived the nestling period. The speculative cause of this discrepancy involves a tick common to ground squirrels which infects the young falcons to an extent that the nares and ears harbor great numbers of the parasites. An apparent weakened condition prevents fledging and subsequently causes death.

Williams (222) found several larvae and nymphs of the tick *Ornithodoros aquilae* in several raptors in Colorado during the 1942 and 1943 nesting seasons. Species infested included the Prairie Falcon, Ferruginous Hawk, Golden Eagle and American Kestrel. The larval ticks were concentrated on the birds' heads, particularly in the eye region of older nestlings. Young nestlings had larvae on various parts of the body, presumably because the body plumage was not developed enough to prevent infestation.

CHAPTER 7. EGGS AND EGG-LAYING

EGGS–PHYSICAL CHARACTERISTICS

There is considerable controversy concerning whether or not size and pigmentation of eggs are directly related to their order of production. Hórvath (107) believes that the least colored, smallest egg is first laid and is followed by eggs of increasing size and coloring, at least in the Red-footed Falcon. He further states that smaller, less pigmented eggs are produced by younger parents.

In support of these statements, Burns (36) found that more often (four out of five times observed) the first egg laid is the smallest in the Broad-winged Hawk. In a large clutch of the Besra Sparrow-hawk Baker (10) found two quite small eggs, but the laying sequence was not determined. Davenport (51) often found one egg in European Sparrow-hawk nests marked considerably different from the others, but again, no mention of the order of laying was made.

Most evidence is in direct opposition to Horvath's findings. If weight is an indication of size, a clutch of American Kestrel eggs observed by Sherman (179) does not indicate either an increase or decrease in the size of consecutively laid eggs. The eggs weighed on the day of their laying, 212, 227, 220, 225, 228 and 204 grains in that order. Sherman also found the final egg laid to be finely speckled with chocolate brown instead of bearing large blotches. The fifth was also less heavily marked than the first four.

Other direct contradictions of Horvath's observations include the following: Dixon (57) writes that heavily marked Red-shouldered Hawk eggs are laid first and hatch first. Infertile eggs are always lightly marked or plain. Burns (36) speculates that a very small Broad-winged Hawk's egg found by J. H. Flanagan may have been produced either by an old bird or one that was unmated. Smith (183) found an unusually large clutch of Red-shouldered Hawk eggs, none of which was abnormal in size.

Eggshells of falconiform birds are extensively discussed in a paper by C. Tyler (210). Chemical structure and content, thickness, pore channels, pigmentation and various other topics are thoroughly treated.

Another consideration of the physical characteristics of eggs involves second clutches. Data on eleven second clutches of Peregrine eggs indicate that birds which lay unusually large clutches at first often lay fewer eggs the second time, but if the first laying consists of the normal three or four eggs, the same number will constitute a

second clutch (23). Burns (36) states that when a complete first clutch of Broad-winged Hawk eggs is collected, the second clutch usually consists of one less egg. Two clutches of six eggs were collected by Keyes (117) from a Peregrine eyrie during the same year. It is significant that the second clutch was as large as the first, and all 12 eggs were uniform in size and shape, but the second set was the lightest colored clutch Keyes had ever seen. Baker (11) found an exceptionally small egg of an Indian Black Eagle after the first clutch of one had been stolen.

DETERMINANT OR INDETERMINANT?

Whether falconiforms will continue to lay eggs as their clutches are taken one by one at the time of laying (indeterminant), or whether an individual species will lay only a fairly consistent clutch of a certain number (determinant) and then stop laying is an interesting, virtually untouched aspect of their reproductive cycle which may be of use to those attempting artificially to raise these birds by whatever method might be feasible. Only two contradictory observations shed light on this subject.

Against the desirable (to the captive breeder) characteristic of indeterminant laying such as that found in chickens is a statement by Ratcliffe that "Peregrines do not usually continue to lay if an incomplete set of eggs is taken,..." (148:26). More encouraging is an interesting experiment done by Davenport (51). From one European Sparrow-hawk nest he was able to collect as many as 16 eggs by removing each one soon after it was laid every day for a month. Thus, the European Sparrow-hawk and perhaps other species may well be indeterminant layers. This would enable a breeder to raise many more eyasses per year than is normally the case. The big "if" involves fertility which was not determined by Davenport.

TIMING OF EGG-LAYING

As with other events in the breeding cycle, egg-laying time varies from year to year depending on static and fluctuant environmental factors. It is widely held that weather affects the time of egg-laying, but most evidence collected by this reviewer does not substantiate this conclusion.

Peabody (140) believes that laying in Marsh Hawks does not depend on the spring weather. His evidence consists of observations of a dozen nests over four seasons in which the first eggs were invariably laid between May 10 and May 16. Burns (36) writes that the normal egg-laying period of a given species in a given locality consistently spans the same two-week period from year to year. Of course, extremely early nestings unexplainably occur on occasion,

and late clutches may be found when the first was interrupted for one reason or another. Dementiev (55) points out that temperature could hardly be a factor in Gyrfalcons which frequently lay with snow on the ground and winter weather persisting.

Age of the birds may have stronger effect on egg-laying than weather. Nicholson (134) indicates that very old pairs of Red-shouldered Hawks lay early in Florida regardless of the seasonal precipitation or temperature patterns, whereas young birds of the previous summer lay clutches some two to three months later.

SEQUENCE OF LAYING

It is a fairly widespread characteristic that falconiforms lay their eggs every 48 hours on the average. This has been reported for the Northern Goshawk (182), European Sparrow-hawk (10, 51), Red-shouldered Hawk (57), Broad-winged Hawk (36), Marsh Hawk (168) and American Kestrel (179). Certainly other species are involved.

Variation does exist, however. Burns (36) mentions that 72 to 96 hours may elapse between eggs on rare occasions in the Broad-winged Hawk. Baker (10) found that the Besra Sparrow-hawk lays eggs on alternate days as a rule, but it is not uncommon for 72 hours to pass between eggs. The same occurs in the Peregrine (39). The Swainson's Hawk has been known to lay a clutch of three eggs in as many days (40). Smith (183) mentions the first four eggs of a clutch of six Red-shouldered Hawk eggs being laid at intervals of 72 hours.

The Marsh Hawk seems to show the most variation. Hammond and Henry (93) found clutches of seven laid in twenty to twenty-one days, five laid in seven or eight days and six in ten days. There is some doubt whether the first clutch was produced by a single female. Allen (4) observed a Marsh Hawk nest very closely during the egg-laying period and found the sequence to be one egg per day for the first four days followed by three more on alternate days.

At least one researcher has proposed that the order of laying (or hatching) may determine the sex of the young. Shufeldt (180) found that in a brood of five American Kestrels, the largest (assumed to be the first hatched) was a male. The next largest was a female, the next a male and so on. There was an alternation of the sexes. This point is in need of definitive clarification or denial by more than common sense.

CLUTCH SIZE

One must be careful when studying clutch size in oological collections, since overeager collectors may well have stolen the eggs before the clutch was complete. It is just as risky to rely on field

counts since many nests are only visited once during a season, particularly in large studies, and again many incomplete clutches may be recorded. For this reason, and because usable figures are available in the literature, a species list of clutch sizes is not included in this review. It is more important to analyze the causes of variation such as food supply, intraspecific traits and latitude, and to form only brief generalities concerning clutch sizes of groups of species.

Variation. As evidence that clutch size does vary from year to year we need only to mention one good buteonine study. Mayo (124) averaged yearly clutch size data from 60 Common Buzzard nests for several years during the 1930's and found variation in these averages from three to five eggs. His average figures for eight consecutive years were 5, 3, 4, 3, 4, -, 3 and 5 indicating considerable fluctuation. Other evidence for year-to-year variation, to cite a few examples, can be found in papers by Cade (39), Dixon (57) and Hager (89).

The strongest causal factors proposed for yearly fluctuations in clutch size are food supply and weather. Weather factors have been sufficiently discussed in preceding sections of this review. In regard to food supply, Cade (39) believes that size of Alaskan Peregrine populations depends on the size of prey populations, the adeptness of prey at escaping capture by using the existing vegetation and the behavioral peculiarities of dominant prey species. Dementiev (cited by Cade, 39) states about the Gyrfalcon that the "number of eggs apparently fluctuates in dependence on the feeding conditions of the year (on the 'harvest' of lemmings and willow ptarmigan)" (39:207). Dixon (57) indicates that weather (rainfall) indirectly affects clutch size through its influence on the food supply, implying that weather is only a secondary factor relative to the availability of prey.

Other types of variation in clutch size are not periodic or fluctuant. Individual birds, age groups and geographically isolated populations may show intraspecific variation. H. W. Carriger (cited by Bond, 23), for example, puts forth the idea that clutch size depends somewhat on individual birds, particularly when larger than average clutches are involved. Carriger found that Peregrines which lay five eggs will do so year after year, but those laying three will often lay a different number, presumably four, the most often found clutch size in this species.

Age must certainly be a factor. Pring (147) found a clutch of one egg in the Common Buzzard from an old bird. Salter (165) made similar observations several years in a row in the same species. Wood (231) writes that younger female Northern Goshawks lay larger clutches and smaller eggs. For other reports of age affects on clutch size the reader is referred to the section on the breeding of immature raptors.

Another type of intraspecific variation involves the colonial nesting Eleonora's Falcon studied by Vaughan (213). He believes that larger clutches are laid by Eleonora's Falcons in the most dense nesting colonies. This is substantiated by the following data: First, birds of small colonies on islands near a large dense colony tend to lay fewer eggs on the average; second, smaller clutches are found in geographical regions where small colonies are characteristic.

Latitude effects on clutch size are best exemplified by data on the various races of *Falco peregrinus* in North America. In general, one can observe a decrease in the number of eggs laid from central North America northward (102). Bond's (23) data for Peregrine clutch size show a similar decrease from central North America southward to Mexico and Baja California. As Cade points out, specific northern and southern latitudes apparently "represent climatic extremes for the peregrine. It is possible that physiological stresses imposed by living under marginal climatic conditions might reduce reproductive capacity" (39:184-185).

The tendency for clutches to be smaller in more northern latitudes is certainly supported by Cade's (39) data from arctic Peregrines, where a mean of three eggs per clutch was found as opposed to a mean of 3.74 for clutches within the continental United States. The simple latitudinal relationship is complicated by the different subspecies, however, since Peale's Falcons of the Pacific Northwest regularly lay larger clutches than typical *anatum* Peregrines nesting farther south.

Hatching success in Peregrines supports a latitudinal variance in clutch size, the data being even more regular than for the number of eggs. Hickey (102) found 3.0 young per eyrie in the continental United States. F. L. Beebe (14) reports 2.7 per eyrie in the Queen Charlotte Islands. Hickey's (102) data shows 2.6 Peregrines per eyrie in southern Canada and Cade (39) found the lowest, 2.5 per eyrie, in northern Alaska.

The correlation between clutch size and latitude with fewer eggs in northern nests has also been noted in the Red-shouldered Hawk (191) and the Broad-winged Hawk (36).

While on the subject of clutch size it may be well to mention the size of second clutches laid after the first nest was robbed or disturbed. Evidence conflicts. Hickey (102) indicates that the most common size of a second clutch of Peregrine eggs is three, one less than a normal first clutch. This is the general trend for many species. J. G. Tyler (211), however, writes that second sets of Prairie Falcon eggs in his California study area almost invariably were the same size as the first sets.

Species considerations. As stated above, only generalities will be included in this section. If one wished to list the major raptorial

groups in a general descending order with respect to clutch size, the list would roughly be: (1) harriers, five to six; (2) falcons, three to five; (3) hawks, two to three; and (4) eagles, one to two. One can immediately cite exceptions. Smaller species of a general group often lay more eggs; all of the sources of variation listed above are factors. Nevertheless, from the literature reviewed, this writer places considerable merit on the general clutch sizes as listed.

CHAPTER 8. INCUBATION

TEMPERATURE REGULATION AND EGG WEIGHT LOSS

Incubation temperature. By inserting thermocouples into egg being incubated by wild birds, Huggins (110) found that durin attentive periods Marsh Hawk eggs were incubated at an averag temperature of 32.3°C (90.1°F). Egg temperatures varied from 35. to 28.3°C (95.7 to 82.9°F) over an extended period of observatior Thus it seems that in the natural state eggs can develop and hatch incubated within a certain temperature range. There is no specif incubation temperature. In the laboratory, however, Stanley ar Witschi (188) used a temperature of 96°F to incubate Red-tail Hawk and Cooper's Hawk eggs when older developmental stages we required for their embryological studies.

Brood patches are an important factor in successful incubation many avian species, some raptors included. These are areas of sk which become devoid of feathers and highly vascularized for bett heat transfer from the parent bird to the eggs. Tucker (208) stat that birds of prey develop a single median brood patch duri incubation. The feathers are apparently shed by a special local mou R. E. Bailey (cited by Willoughby and Cade, 225) agrees wi Tucker, but adds that only the females develop such patch Willoughby and Cade (225), on the other hand, found paire oval-shaped patches on either side of the breast in both sexes American Kestrels. Cade found brood patches "on the abdomen a near the breast" of three collected male Peregrines from the Colvi River area in northern Alaska (39:196).

A suitable nest-site does not seem to be a vital stimulus for bro patch formation, at least in American Kestrels. Willoughby and Ca (225) observed such patches in captive Kestrels in the absence suitable nest-holes.

Egg weight loss. It is quite normal for eggs to lose considerat weight throughout incubation. Sumner (196) confirms this poi with data from two Golden Eagle eggs weighing 144.8 and 145 grams one day, 138.1 and 138.4 grams, respectively, two weeks late Data collected by Sherman (179) on a clutch and brood of Americ Kestrels are more illustrative (weights in grains):

Weight fresh	227	225	228	204
Weight prior to hatching	—	186	192	174
First weight of nestling	154	157	166	139

This represents a 16 per cent loss of weight by the eggs during incubation. A newly hatched, dry nestling weighs roughly 68 to 73 per cent of the original egg weight.

CORRELATION BETWEEN EGG LAYING AND ONSET OF INCUBATION

There is a clear gradation of evidence on this matter from incubation of the first egg onward, to incubation beginning with the second or third egg, to incubation starting with the last egg laid. The evidence is presented below; the reader will necessarily have to draw his own conclusions.

Salter (165) believes that incubation in the Common Buzzard usually begins with the first egg laid, since the young hatch one to two days apart from eggs laid in a similar time sequence. Judging from four clutches of Cooper's Hawk eggs which showed different stages of development, Hoy (109) concluded that incubation began as soon as the female started laying. Reindahl (154) states that since young Marsh Hawks in the nest usually vary in size, incubation begins with the first egg laid. Early onset of incubation has also been indicated for arctic Peregrines (39), Red-shouldered Hawks (57) and African Little Sparrow-hawks (120).

Nearly as many papers mention incubation beginning with the second or third egg. Siewert (182) states that Northern Goshawks begin incubation after the second egg is laid and Hörvath (107) indicates the same for Red-footed Falcons, although the usual clutch is three to four in the latter species. In contrast to Reindahl's statements concerning the Marsh Hawk, Saunders (168), after observing three of a clutch of six Marsh Hawks hatch simultaneously, speculates that incubation starts with the third egg. Similarly, Allen (4) observed incubation in this species starting after four eggs were laid on consecutive days, although three more were laid on alternate days thereafter.

Hardy (97) found that incubation in the Red-tailed Hawk begins with the laying of the last egg. The first egg or eggs are left uncovered most of the time, although the adults remain nearby. F. L. Beebe (14) observed very little size difference in very young Peale's Falcons, indicating that incubation probably does not begin with the first egg. The same paper includes information from other observers which shows that incubation in British Peregrines begins with the

second-to-last or last egg laid.

The most convincing case for late onset of incubation was presented by Sherman (179) for the American Kestrel. She kept precise notes on the hatching of a clutch of five eggs of this species. The first fertile egg hatched 36 days after laying, the second was collected by the observer, the third hatched in 32 days, the fourth in 30 days and the fifth in 29. Clearly, incubation does not begin until most, if not all, of the clutch is deposited, this being more likely than a variation of six to seven days in the actual incubation period.

INCUBATION LENGTH

As with clutch size, lists of incubation lengths will not be given for individual species, but some generalities and significant data are worth mentioning. Oddly enough, a general list from the shortest to the longest incubation period follows the same order as that for the largest clutch size to the smallest. There is an inverse relationship between clutch size and length of incubation, with those birds laying the largest clutches having the shortest incubation periods. Certainly more precise calculations of incubation lengths are needed for almost every species, but general lengths are as follows: (1) harriers, 23 to 26 days; (2) falcons, 28 to 30 days; (3) hawks, 30 to 38 days; and (4) eagles, 35 to 47 days.

Again exceptions immediately come to mind, but some of the most significant papers support the above ordered list. For example, close observation by Wilhelm (221) of a clutch of six Marsh Hawk eggs revealed incubation periods in order of egg-laying of 23, 23, 23, 24, 23 and 24 days. Allen (4) indicates 26 days for each egg. Cade (39) writes that an incubation period of 28 to 30 days is apparently characteristic of the genus *Falco*. For hawks, the following examples will suffice: Red-tailed Hawk, 35 days (97); Cooper's Hawk, 30 days (170); European Sparrow-hawk, 35 to 38 days (51, 164); and African Little Sparrow-hawk, 31 to 32 days (120). The incubation period listed above for eagles is well substantiated by Brown's papers (32, 33) on the large raptors of Kenya and by many books treating these species.

ROLES OF THE SEXES IN INCUBATION

The sharing of incubation duties. Male birds of prey show two general patterns with respect to incubation. First, the male may never incubate the eggs and, second, he may take a definite share of incubation duties throughout its length. The second case is far more common, though in no raptorial species does the male do all of the incubating. It is interesting that in all falcons encountered in this review the sexes both incubate, while the hawks and eagles have

species which display both patterns. There is considerable controversy over the harriers although males have been reported incubating occasionally.

Saunders (168) believes that the male Marsh Hawk does little or no incubating, but is usually near the nest and defends it with more vigor than the female. Breckenridge (28) reached a similar conclusion, since in flushing Marsh Hawks from nests 75 times, not once did a male appear. During incubation the relationship between male and female Marsh Hawks seems to be a provider-incubator arrangement with the male catering to the incubating female, bringing her food and standing with her on the nest, but rarely or never incubating (4). Haverschmidt (100) writes that incubating female Marsh Harriers often call to their mates when hungry without leaving the nest. Haverschmidt has been able to locate several nests of this species by following the cries of the female. Peabody (140) offers some contradiction by stating that male Marsh Hawks probably do not feed the females during incubation, thus necessitating that the eggs be left uncovered while the female provides for herself or that the male incubates.

Brown (32, 33) indicates that in the eagles of Kenya which habitually lay only one egg, the female alone incubates. The male takes a larger share of incubation in species which normally lay two eggs. The female Wahlberg's Eagle does all of the incubating, spending about 85 per cent of the 24-hour day on her eggs. Periods away from the nest last up to two and one-half hours. The male functions only to bring prey to the female during incubation.

As mentioned above, more often both sexes incubate. The male Northern Goshawk may incubate for one to two hours in the early morning and early afternoon (182). Kendeigh (115) writes that the male Northern Goshawk may relieve the female up to four times per day for periods of an hour or more. In another *Accipiter*, the African Little Sparrow-hawk, Liversidge (120) found that at first the female incubates 80 per cent of the time, but this drops to 75 per cent as incubation progresses. The male covers the eggs for periods of one-fourth to three hours and the female for one to six and two-thirds hours at a time. The birds rarely shift position while incubating. While the opposite sex is on the nest, the second bird often spends much time on a single perch resting, preening or sleeping. The male spends a large part of this time hunting. The female usually leaves the nest for the first time in the morning at about 4:00 A.M. (June, England) and returns shortly giving a cry each time she flies onto the nest. Presumably she eats a bird killed the night before and stored.

In the Verreaux's Eagle both sexes incubate, the male less than the female and only during the daylight hours. During 18 hours of observation by Brown (33) the male covered the eggs for five hours.

one to two hours at a time. Since the female sat at night, she incubated about 80 per cent of the time. During the day the male sometimes stood on the nest with her for periods up to an hour.

Cade (39) found incubation by male Peregrines to be uncommon, while others have found males incubating for as much as one-quarter of the time. During incubation the male Peregrine does not roost near the scrape, but usually does so somewhere near the brink of the same cliff. Both sexes also incubate in the Red-footed Falcon (107), Red-tailed Hawk (135), Red-shouldered Hawk (57) and surely many others.

Male raptors rarely spend the night incubating, but occurrences of this behavior are on record. Roest (159) observed one instance in the American Kestrel, and Willoughby and Cade (225) write of a male Kestrel which invariably spent the night on the eggs at a nest in California. Liversidge (120) found a male African Little Sparrow-hawk on the nest one night out of eight nights checked.

Nest relief. Certainly, more extensive descriptions of this behavior could be found in ornithological books than were found by this reviewer in the periodical literature. The articles reviewed yielded the following information.

The male Northern Goshawk often calls from the edge of the nest area and is met there by the female. The male then proceeds to the nest to cover the eggs (182). The female African Little Sparrow-hawk, according to Liversidge (120), always surveys the nest contents before settling on the eggs. The male did so at first, but later settled on the eggs as soon as he arrived. The peak calling period for the female African Little Sparrow-hawk coincides with her midday incubation period. Presumably this encourages the male to hunt or to relieve his mate at the nest. Selous (172) believes that the male European Sparrow-hawk brings food to the hen which does all the incubating. Upon approaching the nest, the male gives a cry which draws the female immediately off of the nest if she is hungry. Much deposition of fresh green twigs occurred during nest relief.

Brown (33) indicates that both male and female Crowned Eagles often bring food to each other during nest relief. He elaborates on one exchange when the female brought prey from which she had eaten her fill, to a soliciting mate uttering a typical call.

Fowler (78) described nest relief of Prairie Falcons. The male flew silently to the ledge and uttered some low screams while looking straight down at his feet. He ran to the incubating female which stood up and left without a sound. The male took considerable time getting settled over the five eggs. The female's uneventful relief of the male was four hours in coming. The male was anxious to leave and did so quickly. The female was much more adept at covering the eggs.

As with the Crowned Eagle, nest relief is often accompanied by a food pass in other species, particularly the Kestrel. Roest (159) cites several instances of this behavior. Chubb describes nest relief of American Kestrels in the following manner:

> "...the male became even more attentive than ever [during incubation], but assumed no responsibility for the eggs except as a most faithful assistant. He would bring home a mouse or a snake,...Call the mate from her eggs, stand near a few minutes as if enjoying her pleasure, and then take his place in the nest. After an hour's exercise, following the meal, she would return calling and the male would relinquish his charges....These duties were carried out each day with systematic regularity" (45:624).

CHAPTER 9. HATCHING

GENERAL CONSIDERATIONS

Close observations of the mechanics of the hatching process are nearly wanting. This area offers a significant avenue for captive breeding research. The only pertinent statements in the articles reviewed were by Salter (165), who mentions that young raptors, as with most or all birds, can usually be heard peeping inside the shell before it has cracked open, and by Fitch *et al.* (73) who found that young Red-tailed Hawks require 24 to 48 hours to clear the shell after it has been pipped.

CLOSE SITTING

Often when eggs are about ready to hatch or are pipped, the female parent sits very close on the nest and will not leave unless vigorously disturbed. She flattens her body into the nest to avoid detection, and if finally scared off, she returns to the nest very soon after the source of disturbance is removed. In some cases, such as with the Martial Eagle, the observer may climb half-way up the tree before the female will flush, or with the Crowned Eagle which may allow an observer to climb to the level of the nest in a nearby tree (33). Of course these two instances are extremes, but they are indicative of the strong drive which keeps the female on the eggs at this critical time. Cade (39) also observed female arctic Peregrines sitting very close on pipped eggs.

SEQUENCE OF HATCHING

The sources of variation in hatching time of an entire clutch of eggs are numerous. The condition of staggered hatching depends on the attentiveness of the parents during the egg-laying period. Since clutches may take a week or more to lay, if incubation is started immediately with the first egg, one can expect much discrepancy in the size of the young. On the other hand, if incubation begins in earnest only after the last egg is laid, one can at least expect the young to hatch over a smaller period of time than required for the eggs to be laid. This is the principal problem with records of incubation length—eggs in the same nest do not get equal treatment from laying to hatching since there is a necessary lag between the laying of one egg and the next.

The best point to be made about hatching sequence concerns its relationship with egg-laying sequence. As already mentioned, one can generally expect a clutch to hatch in fewer days that it took to lay the eggs. Illustrative evidence can be found in papers by Hardy (97) on the Red-tailed Hawk and Sherman (179) on the American Kestrel. In the Red-tailed Hawk the second egg is usually laid two days after the first. The second young hatches one to two days after the first, indicating a slight decrease in hatching time relative to egg-laying time. In the clutch of six Kestrel eggs mentioned by Sherman, the first egg was infertile. The second and fourth eggs, laid four days apart, hatched on the same day, while the fifth and sixth eggs hatched in order on the next two days. The third egg laid was collected. If this reviewer's figures are correct, laying of the fertile eggs of this clutch occurred over a period of nine days, while the hatching period was compressed to a period of three days. Certainly this point needs further substantiation, but it is probably applicable to those species listed in the incubation section which begin incubation with the last egg laid.

The fact that variation in hatching time existed was taken for granted at the beginning of this section. The evidence for this is presented in the following paragraphs. Prentice (146) observed the hatching of three Swainson's Hawks in the same nest on the same day. A similar occurrence has been reported for the Harris' Hawk (220).

Hatching appears to be more spread out in the accipiters. Broods of four Cooper's Hawks often hatch over a period of three days (72, 170). Rust (163) writes of a clutch of five Sharp-shinned Hawks which hatched over a period of at least three days.

Marsh Hawks and other harriers again offer the most confusing story. Peabody (140) strongly believes that Marsh Hawk eggs hatch one day apart. Hosking (108) observed the hatching of five Marsh Harrier eggs over a period of 11 days. The intervals between hatching of the respective eggs were two, three, two and three days. Other observers (93) indicate that a brood of Marsh Hawks often takes at least eight days to hatch, while under other circumstances all may hatch in half that time. As final destruction of any hatching sequence pattern for harriers, Saunders (168) observed the first three of a clutch of six Marsh Hawks hatch simultaneously, but the others were not free of the shell until three and six days later.

Hórvath (107) mentions that Red-footed Falcons usually hatch 28 to 37 hours apart. In seven clutches of three Eleanora's Falcon eggs, the time required for each clutch to hatch varied from two to five days.

CHAPTER 10. SUMMARY

Falconiform birds unlike most avian groups frequently show development of a right ovary. This primitive condition is most pronounced in true hawks, intermediate in true falcons and least prevalent in vultures and buzzards. At least 14 species of raptors have been known to possess this unusual characteristic.

Sexual dimorphism with respect to size is strongly developed in nearly all falconiforms, the female being much larger in all but the vultures. A few species show color sexual dimorphism. American Kestrels and Marsh Hawks are illustrative examples with both types of sexual dimorphism.

During the nesting season raptorial birds may establish a mating, nesting and feeding territory, or a mating and nesting territory, or else a narrowly-restricted nesting territory. These types are characteristic of Golden Eagles, Peregrine Falcons and Eleonora's Falcons, respectively.

Territorial behavior is quite variable and depends on the stage of the breeding cycle, weather conditions, idiosyncrasies of the bird, the bird's sex, behavior of its mate, the magnitude of the threat and the prevailing ecological conditions.

Territorial function is speculative, but the several possibilities mentioned include sexual isolation, monopolization of the food supply, population dispersion, bringing the sexes together and strengthening the pair bond.

Inter- and intraspecific relationships affect the territory and breeding cycle of falconiform birds in numerous ways. Extensive treatment of the behavioral aspects of raptors as faunal entities is included.

All birds of prey raise a maximum of one brood per year. There is a rough correlation between the size of the species and the total length of the cycle; the larger birds have longer cycles.

Major factors affecting the general timing of the breeding cycle include photoperiodicity, climate, food supply, latitude and migratory status of the species involved.

Immature falconiforms are found at active nests, but the relationship between age and fertility has not been established to the satisfaction of most investigators.

Nesting success may vary greatly from year to year. There may be a breakdown at almost any stage of the breeding cycle. Egg loss, nestling mortality and the stability and fertility of the parents are the most significant factors.

Nest-mate cannibalism is characteristic of some raptorial species and is frequently found in many others. The development and occurrence of this phenomenon is not clearly understood.

At the onset of breeding, many birds of prey, if disturbed by loss of a mate or of a clutch of eggs, will acquire a new mate or lay a second clutch of eggs. Relaying may occur in ten days to four weeks, while acquisition of a new mate may take only hours or a very few days.

Many of the movements and mannerisms of courtship in raptorial birds may be observed at one stage or another in the developing young. There seems to be a reversion to nestling-like behavior.

The adjustments required for a successful pair bond in raptorial birds are difficult due to the pugnacious quality inherent in the predatory existence of this group.

Polygamy of several different forms is sometimes found in harriers and less commonly in a few other species. One causal factor may be a preponderance of females in wild raptor populations.

After pairing, the preincubation period is completed by mutual roosting, courtship flights, familiarities near the nest-site, courtship feeding, copulation and nest building or scraping.

Choice of the final nest-site often occurs after a site-selection tour. The sex which apparently chooses the actual site varies with the species.

Generally, the male and female build the nest together, but the female does the most work by far. As the eggs and/or young develop, fresh green material is often added to a nest, particularly by buteonine hawks. The functions of this phenomenon are highly speculative.

Nest sanitation has definite survival value for falconiforms, since prey remains attract predators and insects. Nests are usually free of excrement due to an early, probably instinctive reaction of young raptors to back up and discharge the feces over the edge of the nest. Many species have been observed carrying eggshells, pellets and prey remains away from their nests.

The most detrimental nest parasites are flies, particularly the bird nest screw-worm fly which has a blood sucking larval stage. Ticks may present a local problem.

The question of whether falconiforms are determinant or indeterminant egg layers is not answered in the periodical literature. Raptors usually lay their eggs 48 hours apart on the average.

There appears to be an inverse relationship between clutch size and incubation length. Those species laying large clutches often have the shortest incubation period. As with most generalities, there are exceptions.

Incubation temperature of a single clutch covers a wide range; there is no specific incubation temperature. The development of

brood patches is found in the order Falconiforms, but th distribution and dimensions are not well documented. In mc species both sexes incubate, but the female is usually more attentiv In some cases females do all the sitting.

It takes up to 48 hours or more for a raptorial chick to clear tl shell, once it is pipped. Hatching generally occurs over fewer da than laying, particularly in species which begin incubation with th last egg.

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