

The failure of Stevens' pair to attain fertility is more difficult to explain, especially as his falcon was producing eggs in April when the male should, presumably, have been as sexually advanced as the female. There is a suggestion here, when taken in context with the uniform failure of initial attempts by all pairs so far recorded, that prolonged association with an ovulating female may be a great stimulus toward sexual activity on the part of all males, and perhaps a necessity to some.

The uniformity with which such a very small number of experimental pairs has attempted to reproduce is indicative that a very high percentage of eyas pairs will make similar attempts if given the opportunity, and there now appears to be no reason why a good many of them should not be successful. All experiments to date indicate that Peregrines are extremely devoted both to incubation of the eggs and to care of the young.

Finally, it would now appear certain that the spatial requirements of Peregrines, and, by inference, of the other large falcons, differ in no significant way from those of other raptorial birds and many of the mammalian carnivores, being conditioned much more by an abundant food supply than any other single factor. Even the apparent minimal half-mile that normally separates the closest aeries may be much more a reflection of the average distance required by the male Peregrine to overtake prey from a starting point close to the aerie site without interference from the male of an adjacent pair, than to any inherent hostility toward other adult Peregrines. At any rate it is now definite that close confinement is no barrier to normal reproductive activity of either sex, and may be a stimulus to the female (see discussion in the Appendix of this paper).

The tendency of Peregrines to nest relatively close together in areas of high availability of food would further indicate that themuch closer proximity of other pairs breeding in confinement should also have no negative effect on reproduction. Enderson's Prairie Falcon studies (Auk 81:332-352, 1964) indicate that even the exchanging of mates of mature birds might be possible and at times advantageous.

#### Future Plans and Suggestions

A long term objective of the Raptor Research Foundation is the acquisition and distribution of potential breeding stock and the working out of practical techniques by which such stock can be retained in good health and with a minimum risk of loss for the two or three year interval prior to reaching reproductive age.

Some of the experiments to date indicate certain advantages to a course of training during this pre-adult period. In the first place, the regular handling then involved accustoms the birds to intimate contact with humans and the birds become reasonably tame. Equally important is the high degree of trust and tolerance between the sexes which can be effected if, beginning at an early age, they

are flown to the lure together. By flying them only to the lure and always in the same area, the risk of loss can be minimized while at the same time they can be kept in vigorous condition and excellent health.

Some of the current experiments by Raptor Research cooperators on the other hand are oriented toward eliminating the problems of time and skill inherent in any such training program. This would then only necessitate keeping a pair of birds taken as nestlings confined together for the length of time necessary for them to reach reproductive age. Inasmuch as this is essentially the procedure that has resulted in reproduction by many species of raptors in zoological parks, there is some reason to believe that such pairs might reproduce just as effectively as those that have been given outdoor flying during their pre-adult years. To my knowledge nothing of this kind has ever been given a fair trial with Peregrines. What is well known to falconers is that many Peregrines, and nearly all Gyrfalcons, if tied to a block and given no exercise at all, are extremely susceptible to aspergillosis. The degree to which the not inconsiderable exercise of flying about in a small room might make them less susceptible is not known. However, some Peregrines have been kept, as lone birds under these conditions, and have lived for many years.

The accumulation of the specialized knowledge prerequisite to the husbandry of any long-lived, slow-maturing species can not be hurried. The final objective must always be successful reproduction by a minimum of two, preferably unrelated, pairs that have themselves been produced in the artificial environment. With Peregrines this can not possibly be attained before 1971. Nevertheless, there are at least three pairs of adult Peregrines of known origin and background that have been provided with facilities under which reproduction could have occurred in 1967. Two of these were new pairs, and one of these has produced eggs. In addition, similar facilities have been made available to at least one pair of Prairie Falcons and one pair of Goshawks. Of these, the Prairie Falcons have produced two sets of eggs, the first set infertile.

By 1968 two more pairs of Peregrines could be added from immature birds that are already on hand, while by 1969 Raptor Research cooperators alone could have seven pairs of reproductive age plus a number of younger replacement birds or potential breeders, while the total number of adult pairs should number close to twelve. These pairs are widely spaced across the continent, both in Canada and in the United States, so that any losses to accident or disease in any one place can not be disastrous to the entire project. Some experiments with female Gyrfalcons relative to egg production are possible by 1967, but with mated pairs not before 1970. By 1971 the first nestings by domestic-bred Peregrines are possible, and this is a current target date. By the mid-1970's the domestication of the Peregrine should be an accomplished fact and from then on the demands of falconers on the wild population should level off and consequently decline, as an increasing number

of domestic birds come to reproductive age and as a more detailed knowledge of the husbandry of the species is accumulated.

(Editors' Note. Another important objective of the Raptor Research Foundation Breeding Projects is to provide a source of experimental birds for further investigations in raptor biology. In addition, the Foundation is very interested in developing techniques of re-introduction into areas where populations have been lost.)

#### Appendix\*

The exact set of conditions that leads to initial pair formation in free-living raptorial birds is extremely difficult to ascertain in the field and is impossible to duplicate in an experimental situation. Nevertheless, falconers working with a number of birds of both sexes do have opportunities to obtain an intimate insight into the nature of some of the pre-conditions to pair formation that are not available to most field naturalists. If my observations and experiments are at all meaningful, some of the conditioning experiences take place at a very early age.

First of all there is probably some kind of a visual influence on a nestling of the type of countryside in which the nest site is located as well as of the actual nest site itself. This information seems to be permanently retained throughout the life of the bird and tends to make it return on, or possibly before, reaching reproductive age, either to the vicinity of the home nest or to some place not far removed that closely resembles the home nest. This may well be the most important reason why eyas falcons will attempt to reproduce in an artificial situation while birds taken from the wild population later in life will not. Two other pre-conditioning experiences also take place quite early in the life of the wild birds. As soon as they fly well at all, the young take to intercepting the incoming, food-laden parent and, if there is more than one young in the brood, this behaviour quickly becomes highly competitive, the food being snatched from the feet of the adult while both birds are in flight. It is but a step from this pursuit of the adult to the pursuit and snatching of food from one another of the same brood. It is at this stage of development that the larger size of the females first becomes biologically important and from here on there then begins a series of experiences that recur often enough to be an important factor in the developmental patterns of both of the sexes. The larger females can consistently

\* Editors' Note: The material in this Appendix is a discussion of sexual dimorphism, pair formation, territoriality, food availability, populations, and survival in Peregrines. It is included here rather than in the main text of the paper because of its length, its intrinsic value, and its theoretical value as a basis for some of Beebe's procedures.

overtake the males and snatch food from them when they are laden. At the same time, and this is very noticeable both in Peregrines and the large accipiters, the males develop speed and flying skill considerably more rapidly than do the females and it is the young male rather than the female that is most likely to make the initial intercept of a food-carrying adult. Later, because of this same flying skill, the males begin successful hunting in advance of the females but only to have many of their catches snatched from them. This piracy of the males by the females is very much a part of the early experiences of both sexes in every brood where both sexes occur. Moreover, it must be a relatively commonplace experience throughout the life of every male Peregrine. It seems to me that the cumulative effect of this piracy would be both to eliminate (by starvation) any inefficient males and to make surviving males extremely efficient hunters. Surviving males would also learn to accept this piracy as a recurring norm by the time that reproductive age is reached, and probably much sooner.

Applying this concept of pair formation to experiment, and working with pairs of first-year birds of about the same age, the males can be conditioned in two to three weeks' time to a degree of indifference such that they will come down to feed, in company with a female, on a kill or lure that has been taken from them in the air by that female. That this commonly happens with immature birds in the natural situation is doubtful. More likely, the male simply has his prey snatched from him and must seek another quarry for himself. Nevertheless the pirating of the males is normal, and in my opinion a rather rigid pre-condition to initial pair formation that the male be situated in an area where prey is so abundant and regularly available that he need not leave despite the continuous presence of the piratical female. It is probably only under these conditions and with this pre-sexual relationship established very slowly over a period of one or more years during which no eggs are laid that new pairs are formed.

The experimental data certainly imply that the female must be maintained in very high condition and do little hunting before ovulation can occur. The production of eggs by unmated females in the natural situation is unknown, yet the holding of aerie sites by apparently unmated females in the natural environment does occur, and this even in areas where Peregrines are abundant and unmated males should presumably be available. Such lone females are often assumed to be individuals that have lost their mates, but the very rapid replacement of male birds at active aerie sites where the original male has been shot or trapped is well-recorded. Where these lone females occur in vigorous populations, it is possible that they represent a type of aberrant individual that could easily occur in a predatory bird, being simply a falcon so fierce as to be a threat to the life of any male or, and perhaps this is essentially the same thing, a falcon that for some reason persistently continues to do her own hunting. Either way or in combination, the sedentary state would not be attained and such birds presumably would not lay eggs. Similarly, in years of low food supply the necessity of continued activity on the part of the

female would reduce or inhibit reproductive capacity even in normally highly productive pairs.

The concept that the large falcons always mate for life has been questioned in recent studies. Nevertheless there are good records of the same pair occupying certain aeries for many years in succession (Herbert, R.A. and Herbert, M.G.S., Auk 82:62-94, 1965). This situation may be more characteristic of relict or weakened populations than of dynamic and healthy populations. Certainly the rapid replacement of the males in experimental situations with Peregrines, and the frequent change of mates indicated by Enderson (Auk 81:332-352, 1964) in his study of Wyoming and Colorado Prairie Falcons would indicate that most females, once mated, will accept any male during the reproductive season. That intruding males in a territory occupied by a pair are driven off by the resident male, and not by the female, is also indicative of this.

In areas where abundant nesting sites and seasonally abundant food coincide, Peregrine populations tend to take the form of extensive "colonies." These are generally linear or peripheral and while based somewhat on local topography, the primary relationship is to the food supply, the pairs being from under half a mile to one or more miles apart along a stream, or around a lake or island. The population densities encountered in these circumstances can be very misleading if the observer interprets the density of population in the colony as extending evenly outward in all directions, or even as extending lineally indefinitely, relative to nesting sites only, as along a river or a sea coast. The large population of Peregrines breeding on the Queen Charlotte Islands takes the form of six well-defined colonies which are based on a similar number of breeding concentrations of Ancient Murrelets, Cassin's Auklets, and Petrels. An equally well-defined colony on the Scott Islands off the northwest tip of Vancouver Island is based on a great breeding concentration of Cassin's Auklet. A colony of at least four pairs with aeries on the cliffs overlooking Campbell Lake south of Inuvik in the Mackenzie Territory of the Canadian Arctic appeared to be based primarily on the utilization of Arctic Terns which used this valley as a flyway. The populations of the Thelon and Mackenzie Rivers show similar concentrations, that of the Thelon being concentrated almost entirely in a lineal distance of some 25 miles according to E. Kuyt, Canadian Wildlife Service Biologist. The population of the lower Mackenzie River takes the same form, with two widely separated concentrations of Peregrine population, and Cade (Univ. Cal. Pub. Zool. 63:151-290, 1960) records similar colony-like densities on the Colville.

Some of the vanished populations seem to have had much the same distributional patterns. When first studied by R. A. Herbert, the Hudson River aeries still numbered nine or ten occupied sites (Herbert, R.A. and Herbert, M.G.S., Auk 82:62-94, 1965). This population was, at the time of the study, based primarily on the use of domestic pigeons supplemented by Yellow-shafted Flickers and Blue Jays. Inasmuch as the domestic pigeon is not a native

bird, it would appear likely that the primitive population of Peregrines along this river was based on the recorded use of the river valley as a flyway by the vast primitive population of passenger pigeons, under which circumstances it may well have been much larger than when first recorded. Similarly, the now-vanished Peregrine population of the Okanagan Valley of northern Washington and southern British Columbia, when first studied by Brooks in 1903, also consisted of groups of closely-spaced pairs. His early records list five pairs at roughly half-mile intervals on the cliffs overlooking Vaseaux Lake. There are no data on food species supporting this population, but the Peregrines here declined and vanished by 1927, coincident with the rapid development of irrigated agriculture in the valley which in turn could have caused the disappearance or the abrupt decline of some previously abundant species that could not tolerate the rapid change of habitat on the valley floor.

At any rate the tendency to form peripheral or lineal colonies around a food-supply or overlooking a flyway is natural to Peregrines and appears to be characteristic of healthy populations. Such colonies are almost certainly composed of closely related individuals that represent successful attempts by the offspring of a successful pioneering pair to return to, and themselves reproduce, as closely as possible to their own point of origin. In this situation Peregrines quite possibly change nest sites and mates as well rather frequently, as is indicated by Enderson (Auk 81:337-352, 1964) in his study of the biologically similar Prairie Falcon. Isolated pairs, where they occur, may fall into three categories. They may be (1) newly-mated, and presumably young, pioneer pairs attempting to utilize a new, or temporarily abundant food supply or they may be (2) old, long-established pairs persistently attempting to reproduce in a traditional situation of former abundance that is no longer adequate. Sometimes, however, isolated pairs are (3) holders of some minute fragment of habitat that is perfectly adequate and suitable for one pair but for no more than one pair. Long-established aeries on isolated seabird rocks, in narrow mountain passes or on isolated cliffs overlooking timbered country are the best examples of this third category. Here the topography is always such that it provides more than just the aerie site, tending always, in some way, to concentrate otherwise widely-dispersed prey species in the vicinity of the aerie. Reproductive success at such sites may be consistently high but the ultimate survival of young may well be low. It is studies of such isolated pairs rather than studies of healthy populations that has given wide acceptance to the concept of the Peregrine as being an intolerant species with very large territorial requirements.

Whatever the physiographic situation, the absolute requirement to successful reproduction in the wild is simply that the male be provided with frequent or regular opportunities to catch, in the air, some kind of small to medium-sized bird or birds at no great distance from the aerie site. The more abundant and the closer to the aerie site these can be obtained, the less are the territorial requirements for any one pair. In all of the experimental nestings

the male spent a considerable period of his time relieving the female of incubation duties. The more time, therefore, that the male must spend in hunting the less of his time is available for incubation. The greater the distance that food is captured from the aerie site, the smaller must be the quarry captured, but the smaller the quarry, the more frequently it must be hunted. A clear energy limitation to territory size is obvious, and this is not all, for the greater the distance the male must carry food toward the aerie site the greater is his exposure to piracy from other raptors, especially eagles and the larger buteos--unless he is in, or over, the territory of another pair of Peregrines.

During incubation, there is some reduction in the amount of food required due mostly to the very much reduced activity on the part of the female. Probably the more active natural male supporting a female would consume somewhat more, but this would again depend on the near availability, or otherwise, of the food taken.

The tendency observed in all of the experimental pairs to store food may also be of considerable significance. The practice was common to both sexes and to birds of both wild-caught and domestic-raised individuals. Uneaten kills are also commonly found near the aeries of wild pairs, so the behaviour must be normal and inherent in the species. In cool climates this storage of food may be of great importance during incubation and also during the early life of the young. Temperatures in the high thirties and low forties (Fahrenheit) are cool enough to suppress the activity of the flesh-flies and to slow decay considerably. In cool maritime climates, dead birds stored in the shade at ground level do not deteriorate significantly for several days, while in the arctic, even in mid-summer the permafrost with its constant 32° temperature is but a few inches below the surface lichens. Here, any small birds tucked into a hole in the ground-cover would keep even longer. The ability of Peregrines breeding in cool climates to store food may be an important factor in the greater success of this species in the higher latitudes.

One of the most significant behaviour patterns common to all of the experimental pairs that have produced eggs was their dedication to incubation. With the Raptor Research pair the longest observed time that the eggs were left uncovered was three minutes. The suggested implication is that falcon embryos are easily damaged or killed by any chilling of the egg. Most of what is known about temperature sensitivity of avian embryos relates to studies made of waterfowl or of gallinaceous birds where only the female incubates, and in these groups the eggs are left to cool for rather long periods without harm to the development of the embryos. It is very certainly known, however, that the newly-hatched young of the raptorial birds are extremely temperature sensitive and easily damaged by becoming chilled. If the developing embryo is as sensitive to damage or death by chilling as this combination infers, then one of the most lethal factors to successful reproduction would be any disturbance of sufficient intensity to keep both adults off the nest for any considerable time. The time required to do permanent

damage would of course vary with temperature and humidity, but there is an implication here that any attempt at intimate study of wild Peregrines during the incubation period, especially photographic or scientific studies of the eggs, could be disastrous to reproduction. Further, unless the individual attempting such a study were fully aware of the consequences of his own interference during this period, some very erroneous conclusions could be drawn as to the real cause of the resulting reproductive failure.

As long as the young birds are in the nest and probably for a period of from two to four weeks thereafter, the concept of each pair and its offspring living within a fairly well-defined territory has some validity. However, if there is any meaning at all in the work so far done with experimental pairs, it is that adult falcons are incapable of discerning their own young as distinct from the young of other pairs, and conversely, that young falcons are equally incapable of discerning their own parents as different or distinctive from other adults. It also appears that for a limited time, any adult Peregrine will attend and feed any immature-plumaged Peregrine that approaches it with the appropriate food-begging ritual. The random feeding of begging young of their own, and even of other species, by adults of many kinds of passerine birds is well known and recorded, but this behaviour seems to be unobserved in relation to the raptorial birds. Yet all of the experimental data clearly indicate that this can and does happen. Implied in this situation is the concept that the young of any one year may be rather less dependent on their true parents than they appear to be. Implied also is that flying young could have a considerably better chance of survival in areas where Peregrines have been able to build up colonies than in areas where the breeding pairs are widely separated. In the latter case, any inability to locate one of the only two adults in a vast area could prove fatal. In the former case this would be of less consequence as long as the young bird stayed within the very much larger area occupied by the colony.