EXPERIMENTS ON CAPTIVE BREEDING AND PHOTOPERIODISM IN PEREGRINES AND MERLINS

by
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Introduction

This paper was submitted to *Raptor Research* to complement R. W. Nelson's paper "On Photoperiod and Captive Breeding of Northern Peregrines" (this issue) which gives background material on photoperiodic principles. Little will be said concerning principles in this paper; the reader is referred to the preceding paper and to Willoughby and Cade (1964).

For reasons outlined in Nelson's paper, it seems possible that artificial manipulation of the photoperiod of captive taiga or tundra Peregrines will be necessary for successful breeding. Furthermore, it is likely that these manipulations will have to mimic the natural experience of the wild birds to at least some degree.

While it would be far better "science" to proceed in an orderly fashion towards the "full" explanation of photoperiodism in migratory falcons, as well as the behavioral, nutritional and other factors influencing breeding, I believe, as Nelson does, that our primary task lies in somehow achieving breeding. "Experimentation into the causes and internal mechanisms can come later" (Nelson, this issue). Unfortunately, it is obvious that we need information on physiological and behavioral mechanisms to achieve breeding. It was with this in mind that I began efforts both to achieve breeding and to conduct scientific experimentation simultaneously—an uneasy fusion of science and art and not a situation entirely compatible with either. The inadequacies of the work in sample size, lack of controls and experimental design will be obvious.

Methods and Rationale

In 1967 I began experiments with northern Merlins believing that attempts to breed the more difficult species, such as Peregrines, were appropriately preceded with knowledge gained from a species intermediate in some behavioral, evolutionary and morphological aspects between these large falcons and kestrels. The latter are almost routinely bred in captivity. These experiments have been continued to the present. In 1969 work began with northern Peregrines and is also continuing.

The experiments have been conducted with the following basic assumptions in mind:

1. Photoperiod is the key element in producing a physiological state in which

breeding will occur. In regions in which there is little difference in photoperiod between seasons, rainfall or other factors may be dominant; this is certainly not true of the birds used in these experiments.

2. The passage of *time* as such is not important; what is important is the completion of a series of physiological and behavioral events that lead to the state we desire (sexual maturity first, then breeding). This, of course, would include the "winding down" or termination of the breeding state before another series begins. It seemed possible, therefore, that as long as there existed "spare time" in the "physiological year" of the bird, that both sexual maturity and the number of breeding cycles per year might be accelerated. This presupposes that there is no fixed endogenous annual periodicity (see Immelmann, 1971, for summary material), a point of some insecurity with the birds in question. I have, therefore, carried on most of the experiments at a pace considerably accelerated from that normal to the species in the wild.

3. In most species of middle or high latitude birds a refractory period exists following breeding during which the bird will not respond to increased day length. There are no direct data on this point concerning Peregrines or Merlins, and I have assumed, largely from data on passerines, that an allowance of approximately three months for completion of a refractory period would be reasonable.

4. While it is possible that subtle environmental factors might conceivably be significant in breeding, I have chosen to keep the experiments as simple and well defined as possible and, with the exception of allowing the Peregrines to have a single, glassed window during the last breeding attempt, I have largely excluded visual and thermal components of the natural environment.

5. I have also assumed, apart from issues of pair compatibility, that behavioral issues are secondary in origin and significance to physiological ones and will take care of themselves once the physiological sequences have been set in train. Obviously, one can carry this sort of logic too far, but I have attempted to provide at least minimal room for the birds within the rather severe strictures imposed by living in Fairbanks, Alaska, and as experience is acquired, I am modifying those features of the experimental setup which seem to adversely influence behavior.

The Birds

Four Merlins were used. Two downy young, which ultimately turned out to be two females, were taken from a ground nest at 65 degrees 30 minutes N in 1967. This duo was used in the first series of experiments. A male and female were taken from an old magpie nest at 64 degrees 30 minutes N at about four and one-half weeks of age in 1969.

Three Peregrines were used. One female was taken in 1967 in the taiga zone at about 65 degrees N at four and one-half weeks of age and was flown in falconry during the summers of 1967 and 1968. This bird was maintained in a mews with windows on "natural" photoperiod until the fall of 1968 when all openings were closed and experimental photoperiods began. A male and female, approximately four weeks old, were given to me in 1969 and are of unknown origin. It is probable that their nest lay in the taiga between 65 degrees and 66 degrees N and that they are siblings. These birds were immediately placed in quarters from which they have never been moved and hence may have been together since they hatched. They have not been handled. The female is bold and behaves toward me in the manner often attributed to an "imprinted" bird. The male is shy in the presence of humans, but as a pair no signs of friction or undue dominance by one member has been seen.

Housing

Merlins have been housed in two different rooms, both in the basement of my house. Both rooms measure approximately ten by twelve feet with a nine-foot ceiling and are large enough for Merlins to fly in circles. The ceiling is covered with polyethelene to protect the flight feathers from abrasion. Walls are approximately half concrete block and half flattened logs. Nesting facilities have included opportunities to build scrapes in turf placed on the floor, in a roofed ledge and in nest boxes made from wooden crates. The latter are 9½ x 14½ x 19½ inches in inside dimensions. A round, five-inch hole was provided with a perch beneath the hole in these boxes. In all cases, the material provided for scrape-building was the local forest floor which is largely sphagnum moss.

The Peregrines were housed in a separate electrically heated building in rooms with the same floor dimensions as the Merlin rooms, but with a roof sloping upward from five and one-half feet to about nine feet. The interiors of the Peregrine rooms are insulated with white, rigid insulation. Nest ledges and open-ended boxes about two feet on a side and two and one-half feet in the longest dimension were provided and have been filled with forest floor or pea gravel.

All rooms were equipped in 1969 with boxes to house a television camera which is moved from place to place as needed. Signal propagation is by radio transmission although closed circuit is feasible. The usefulness of television is hard to overrate when you wish to keep close track of the birds. All rooms are also provided with an intercom sound monitor. Reception of both sound and television is normally arranged for in my living room where nearly constant monitoring is possible.

Incandescent bulbs were used in two ceiling fixtures in each room. Normally 150-watt bulbs were used when simulating long days; 60-watt bulbs were used for short days. Timers were used for all lights, but no dimmers were utilized. A seven-watt night light was always used with the Merlins, but not in all cases with the Peregrines. Most changes of photoperiod were made abruptly and in almost all cases increases were made equally at morning and evening so that noon, standard time, was the point of symmetry. All rooms were "mapped" with a light meter aimed toward the nearest light bulb and attention was paid to keeping light intensities close to the same for both Merlins and Peregrines. Details are not reported here, but at "long-day intensities" the perches commonly used ranged from 13 to 41 foot-candles in both species.

Feeding

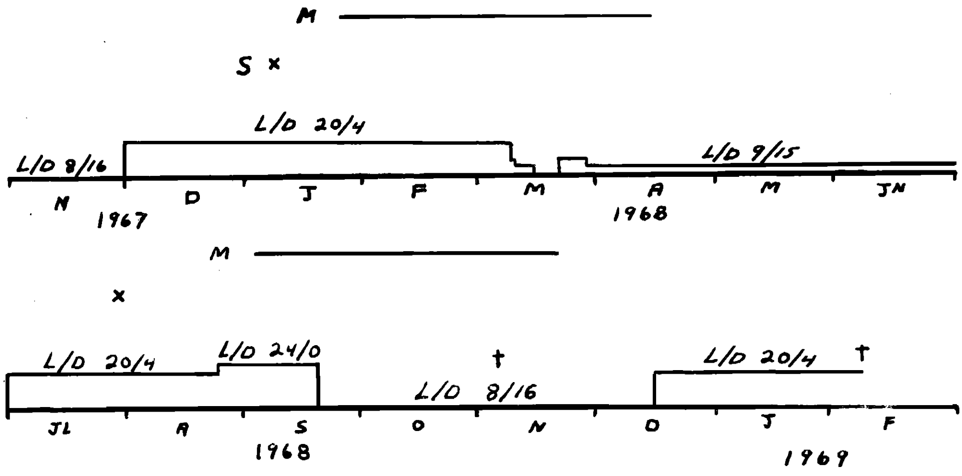
Over the years feeding has varied somewhat. The Merlins have always been fed twice a day and one feeding has always included a mouse. A laboratory mouse colony has been maintained and for the past two years the mice have commonly been fed carrots during the four days preceding killing and freezing. This treatment increases the carotenoid intake of the falcons and keeps the feet and cere yellow and, hopefully, provides for yellow egg yolks. These mice were also fed to the Peregrines at irregular intervals. During the last year large numbers of chickens were raised for the Peregrines. Heavy muscle and store bought chicken have been used, but all commercial food has been carefully trimmed of fat so as to provide for minimum intake of pesticides and PCB. While the outdoor Peregrine quarters are heated, winter temperatures in Fairbanks often cause temperatures inside the quarters to drop below freezing, sometimes to about 10 F. Feedings of the Peregrines are increased to twice a day at such times; at less severe temperatures only one meal is provided. Vitamin and mineral supplements are used at times, principally "Vionate." Special attention is paid to diet quality and quantity during long-day periods when breeding might be expected. Food to excess, often twice a day, is provided at such times.

Results and Discussion: Merlins

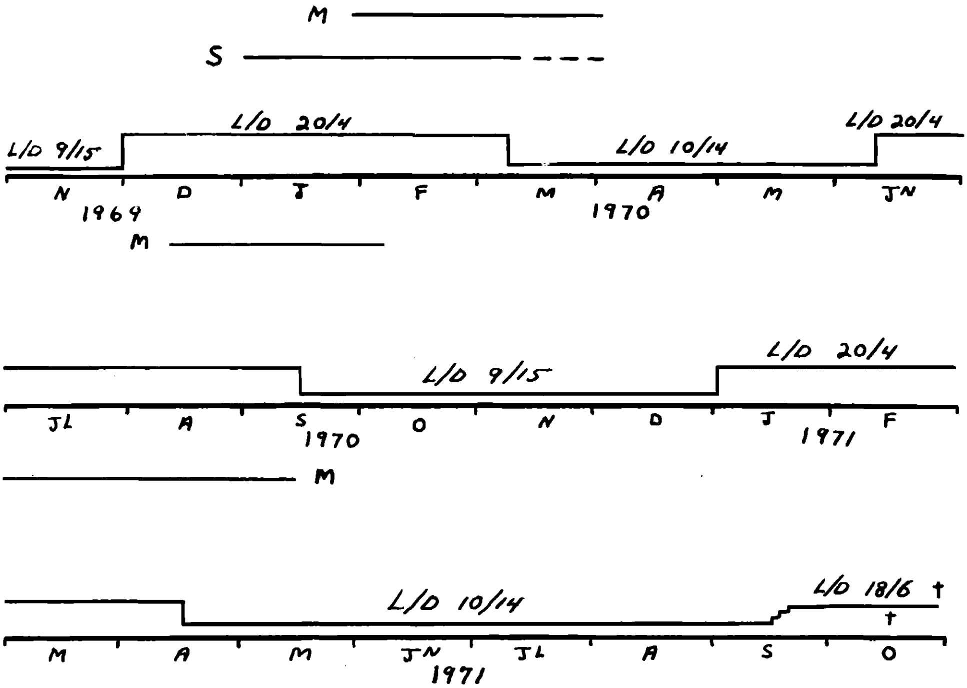
Basic data and experimental conditions are presented in Figure 1. Data are frequently ambiguous in endeavors of this sort and the figures record those events which can be clearly and definitely established, such as scrape-building and the beginning and end of a molt. Except in the first and last Merlin cycle, molted flight feathers were picked up and labeled with the date. Detailed data on sequence of feathers molted in all birds are available but are not presented here. Inception of new calls and other features of breeding behavior were noted but are not considered in detail in this paper.

Perhaps the single most striking feature of the Merlin data is the reproducibility from cycle to cycle with the same "pair" and from "pair to pair." Since light intensity has not been the same in all cycles, it is apparent that intensities

Additional notes on Figure 1. The lines marked with, for example, L D 8/16, represent the photoperiodic regime, and means eight hours of light/16 hours of dark. In the Merlin experiments, it was not always possible to determine whether or not a scrape had been built nor to determine the state of a scrape at all times without undue disturbance. The line or "x" marked S indicates the day, when known, when a scrape was begun and the duration of active maintenance, when known. In all cases a scrape was built as verified by inspection at the end of long days. The line marked M indicates the period of molt and does not distinguish between individuals but indicates the entire period when either bird was dropping primaries or tail feathers. The symbol † indicates death of an experimental bird.



TWO FEMALE MERLINS



MALE AND FEMALE MERLINS

Figure 1. Merlin experiments. Top: these represent the experiments with two females; Bottom: a pair. See additional notes on opposite page.

must be well above threshold levels during long days to be effective in inducing breeding behavior and molt.

It is also clear that some social factors which might be expected to affect timing do not do so. One "pair" consisted of two females and the lack of a male would seem likely to be very important if there are behavioral factors acting in concert with physiological factors to bring about such events as scrape-building and molt. At least in this single case there is a clear implication that behavioral considerations (apart from such survival issues as thoroughly incompatible pairs) may be a relatively minor consideration to the breeder, at least until the "hurdle" of the final burst of vitellogenesis in the female is reached. From here on it is likely that appropriate behavior on the part of the male is important for the female to enter the final phase of follicle growth, but again it seems likely that the appropriate behavior by the male is quite firmly determined by physiological factors, specifically by androgen levels.

The first duo of females produced some interesting behavioral data. Both size and personality of these females differed considerably. The smaller weighed about 200 g and was the more aggressive. She was the dominant bird except during one short period. The other varied between about 225 and 230 g and during her whole life had a slightly impaired function of her left wing. Under short day conditions the dominant, smaller bird always came down to the food first. When long days had persisted long enough to bring the birds close to the threshold of "courtship feeding," the dominant bird ordinarily allowed the other to go down first. On one occasion I observed the dominant bird allowing the other to pick tidbits from her beak in a session lasting several minutes. This may have been an abortive form of courtship feeding. During a later cycle the "submissive" female apparently reached a more advanced point in her hormonal development than she had in previous cycles, and conflict eventually developed over possession of the nest box.

During the course of the experiments with the pair, the length of the short day period was increased with each cycle in order to test the possible influence of a refractory period. At least for breeding behavior up to scrape-building and through molt, it appears that the refractory period is less than 81 days.

One of the initial assumptions–time as such is not important, but the completion of biochemical sequences is–implies that birds might be brought to sexual maturity at a point in real time earlier than normal for birds in the wild. Since successful reproduction was not obtained in these experiments, the issue remains undecided. It is a point to be kept in mind, however. The ease with which the Merlins were induced to complete about two cycles per year with respect to breeding behavior and molt raises some interesting questions. For example, with a number of species acceleration of "aging" may be possible. More than one "brood" might be brought off within a single year. It should be clearly noted, however, that such acceleration was less evident with the Peregrines. In the larger falcons, in which the issues of earlier maturity and more frequent breeding seem more urgent at the present time, acceleration may not be possible.

The failure of these experiments to produce actual breeding was something of a surprise to me and obviously one is obsessed by the question of why they did not breed. There are few facts to support any hypothesis, but there are suggestions in the data. In the case of the two female Merlins, I performed laparotomies 17 and 31 days after the inception of molt in their second 1968 cycle. (I was unable to determine the exact date of first feather drop individually on these birds.) The follicles in each case were minute. Possibly the minute follicles seen in the first of these laparotomies (see Risser 1972 for a technique for laparotomies similar to the one I used) imply that the ovarian follicles never approached the final stage of vitellogenesis. In the fourth and final cycle of the male and female there are some better indications. On the 29th day after day length was increased, the male was found dead. The condition of the bird was excellent and the apparent cause of death, judging from blood in the mouth and beneath the skin of the neck, was trauma possibly traceable to the female chasing him around the room. To this point breeding behavior had been essentially as it had been in previous cycles. The testes measured 5.0 x 4.0 mm (L) and 4.7 x 3.6 mm (R) and were clearly above minimal levels. On the 41st day the female died about 16 hours following an experimental injection of diethyl stilbestrol (5 mg), FSH (17 mg Armour Standard Porcine) and LH (8 mg Armour Standard Porcine) into the pectoral muscles for the purpose of promoting follicle maturation and ovulation. A glycerol repository was used (0.7 ml). Death may have been caused by poor needle placement resulting in direct entry of the injection into the blood stream. Examination disclosed a full clutch of five eggs "on the way" and the five largest follicles measured 14, 9.2, 4.9, 4.2 and 3.4 mm. The extended oviduct measured 28 cm in length and weighed 5.8 g. The epipubic bones were fully spread and the vent was relaxed and engorged. Two large but atretic follicles were present. These data present several interpretive dilemmas. There is no way of knowing whether or not she was actually going to lay in the absence of the male. It is possible that many failures to lay are accompanied by follicle growth such as that seen here, but atresia of all of them occurs and the investigator never knows. The earlier of the two laparotomies on the member of the female duo does not shed definitive light on the point, but it could be interpreted as implying that birds which do not lay do not typically go so far in follicle growth. This situation would be more consistent with what is known about passerines.

The atretic follicles pose a further problem. Is it normal for some follicles to become atretic, thereby playing a role in the regulation of clutch size? There were, in fact, five follicles in healthy condition and five is almost invariably the clutch size of Merlins in interior Alaska.

The male died twelve days before the measurements of the female's follicles were taken. This fact gives us some firm information. It is evident that the female was in the final phases of rapid vitellogenesis. It is also quite clear that if the male's behavior or mere presence with the female was the stimulus which, via the central nervous system, was the factor which caused her to enter this final phase, his role had already been played twelve days earlier. This would be at the 29th long day and, judging from the size of the follicles, about 17 days before the first egg was due to be laid. It is interesting and perhaps significant to note that he was frequently chased by the female. No courtship feeding or other evidence of a "good" sexual relationship with the female was observed before his death. He did, however, visit the nest box and show other behavioral evidence that he was feeling the impact of increased levels of reproductive hormones.

Although again it should be emphasized that one ought not make too much of such data, there were some experimental conditions present in this last, perhaps nearly successful, cycle that were not previously present. These conditions indicate something about procedures to be followed in the future. Previously, I had entered the room to change bath water and even when feeding I was often obvious to the birds when opening the door to toss in food. Just before long days were instituted in the last cycle I had prepared the room with a dark, cloth curtain perforated for a field of view for the television camera. This allowed me to complete all feeding and maintenance functions without being seen. No light bulbs burned out during this experiment so entrance to replace bulbs had not been necessary. Furthermore, this cycle had been preceded with a five-month short day period. It is possible that (1) I had been rushing the refractory period previously or (2) I was overly disturbing the birds previously, although there are no other data to suggest either of these.

Another factor which may have had something to do with the apparent near success of the last cycle was the fact that for the first time the long-day period was not instituted quite so abruptly as previously. Increases were staged as follows: day number 1, L/D 10/14 up to 12/12; day number 3, up to L/D 13/11; day number 4, up to L/D 14/10; day number 5, up to L/D 15/9; day number 6, up to L/D 16/8; day number 13, L/D 17/7 and day number 14 L/D 18/6. This was neither a smooth nor a "natural" increase, but it nonetheless resembled the normal wild condition more than the abrupt increases used previously. The final day length was also different from any previously used being, in fact, two hours shorter. This corresponds fairly closely with the natural day length experienced by the parents of these birds when they began their clutch in 1969.

While the implications that molt data may have on breeding condition are debatable, breeding and molt are at least related functionally and deserve consideration. Molts in my experience were rapid, in some cases so rapid as to leave the birds almost flightless. Extremely rapid molts were confined to the two females, although the pair molted more rapidly than do wild birds. In the case of the pair, female molts lasted (from first primary dropped to last primary dropped) 47, 53 and 56 days ($\bar{X}$ 52 days); molts of the males lasted 55, 50 and 69 days ($\bar{X}$ 58 days). All tail feathers were molted within this period; secondaries were molted slightly later, but are not considered in detail here. All molts were complete even though long days were terminated at different points in the cycle. On two occasions male and female molt began on the same day and on one occasion the male began three days later. Rapid molts may in some cases be related to abrupt shortening of day length. Cade (pers. comm.) feels that kestrel molts may have been speeded up in some of his work by sudden imposition of short days. Little evidence suggests that this is the case here. What rapid molts may imply here is that the photoperiodic regime was sufficiently abnormal to the birds that at least some of the endocrine machinery, possibly portions vital to breeding, was not operating normally. It seems possible that the rate of increase and decrease, the length of the light period, and possibly the intensity may all be involved. It is interesting to note, however, that Willoughby and Cade (1964) in their successful work with kestrels from more southern areas used similar conditions.

Detailed analysis of molt sequence and molt performance of the different sexes will not be made here. It is remarkable, however, how consistent molt was between different birds and different cycles. On four of the five molts occurring during the seven cycles reported here, the first feather was dropped (female) on the 58th day after long days were instituted. The single departure from this schedule could not be accurately determined but the first feather dropped on about the 65th day. The female duo later died, apparently from a prolonged carbon monoxide episode in the house. They were doubtless experiencing some intoxication during this cycle which may well have influenced the molt. This astonishing congruence of the start of molts strengthens the case that the results were indeed induced by photoperiodic manipulation.

Results and Discussion: Peregrines

Figures 2 and 3 present the Peregrine data. The Peregrine results are more difficult to deal with than are those from the Merlins. Not only do they suffer from the same problems of small sample size and lack of controls, but in extrapolating from Merlin data on speed of response I was led into an experimental schedule which may have been rushing the refractory period for Peregrines. It is also evident that Peregrines may be quite different from Merlins not only in speed of response but, perhaps, in a requirement for greater complexity in photoperiodic manipulation, as well. I have had, as yet, too little time to adjust my experimental procedures to my growing awareness of the problems. Unfortunately, the issue of sexual maturity is prominent in the Peregrine work. The only bird definitely old enough to be expected to breed was a female which has never had a male. The pair will not be three years old until the summer of 1972.

I will proceed, however, to discuss the results analytically, to some degree at least, because there are some interesting hints of important questions to be considered in future years.

The first experimental photoperiodic regime was imposed on all birds during the winter of 1969-70. This was the third winter for the lone female and the first for the young pair. Long days were begun on all of them on December 1, 1969, and 22 days later the lone female began a scrape which she enthusiastically maintained for about a week. During this same period, she molted 12 flight feathers which completed her previous molt. After this brief episode a relatively quiescent period of about 90 days followed and then a scrape was built which was maintained for almost five months, four months of which were after the lights had been shut down to L/D 10/14. The response of the young birds was similar, but out of phase by about a month and no scrape was built.

With the Merlins it was typical that all things happened with clarity and dis-

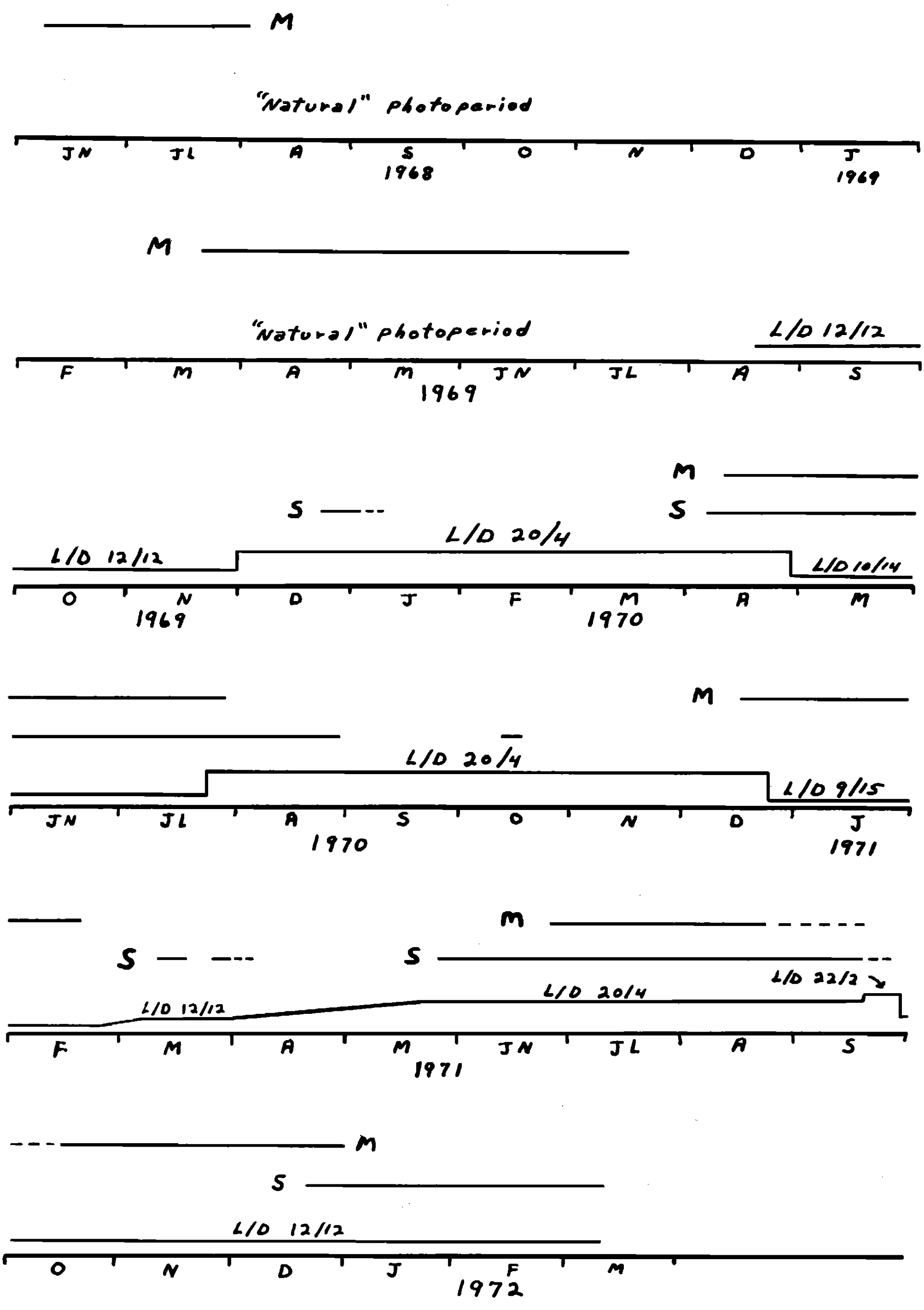


Figure 2. Lone female Peregrine. Symbols as in Figure 1.

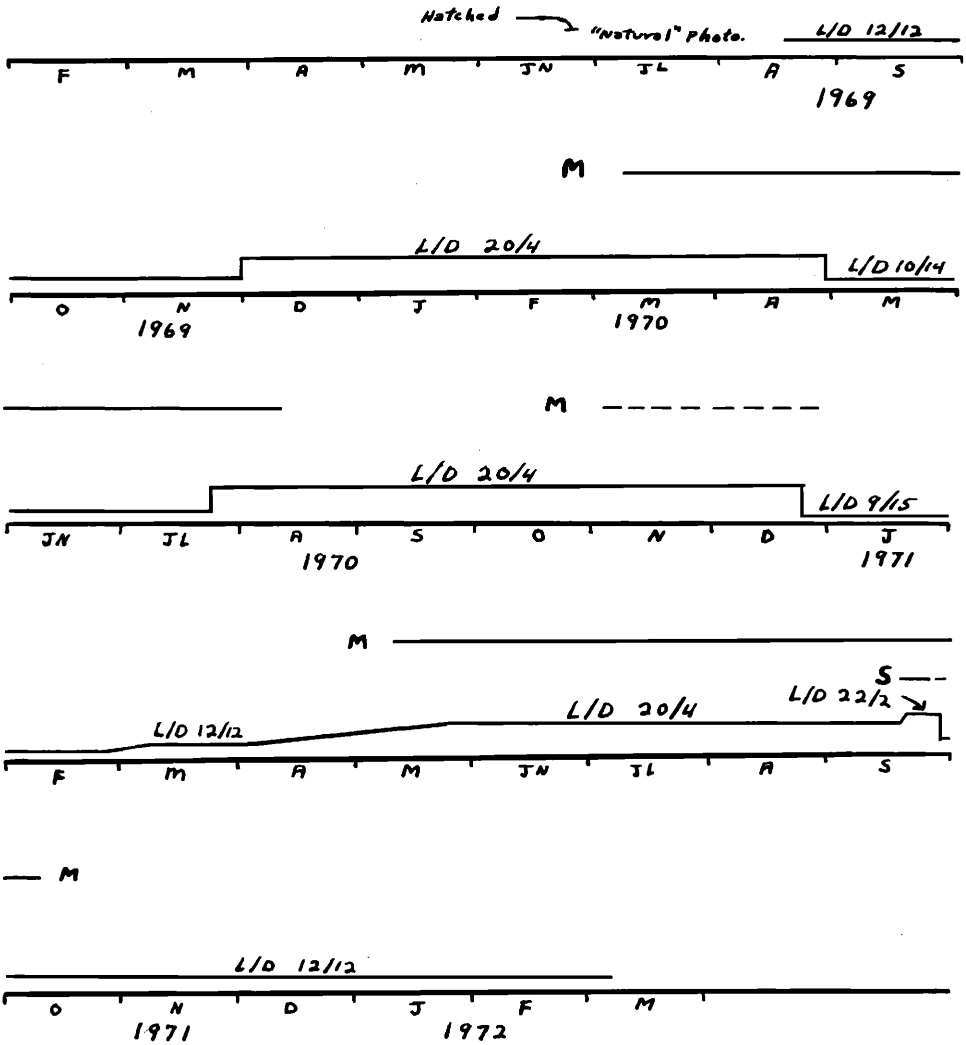


Figure 3. Male and Female Peregrines. Symbols as in Figure 1.

patch. Northern Peregrines seem more indolent in their response to photoperiod and there are several occurrences, particularly in the case of the lone female, which cannot be rationalized at this time. For example, although long days were instituted on December 1, 1969, "real" scrape building and molt did not occur until April in the case of the lone female. This is only about a month and one-half before she would have been expected to molt in the wild. She herself came from an egg laid on about May 21. Molt began in March in the case of the young birds, perhaps a bit over two months early. While this does argue for photoperiod having an effect, it suggests that I was unsuccessfully attempting to hurry a natural rhythm.

In the second experiment, I attempted to complete another cycle before the Fairbanks winter could exert too serious an effect, and began long days before molt was complete (although it was nearly so in the young birds) and before the older female had abandoned her scrape maintenance. After slightly over a month her scrape maintenance ceased. No further response was seen for an extended period and, when it did come, both scrape building in the lone female and molt in the young pair seemed somewhat tentative. Again, in the lone female, a brief period of scrape building occurred well after completion of activities of the previous cycle and well before she began scrape building in greater earnest. Her scrape building was not well developed during December, January and February, and at that time I attributed this lack of enthusiasm to the cold. More recent evidence suggests that this was probably not the inhibiting factor, since she has been very active and attentive with her scrape during the present December, January, February and March (1971 and 1972).

The final cycle reported here was an attempt to mimic their natural photoperiodic experience. It was also timed to come to fruition during the normal part of the year for the wild birds. Scrape building and molt in the lone female began approximately on time suggesting that the short day period begun in late December may have been a sufficient allowance for a refractory period. The young birds were closer to normal timing in the inception of molt than the lone female. In this case, perhaps suggesting that the young birds were simply not yet old enough until that point, a scrape was finally built in late September. For about a month, including the short period of scrape building, both young birds were "ee-chupping."

Recently, a number of people have commented on fall sexual activity in captive Peregrines, even to the point of egg-laying (Galicz *et al.* 1971). Nelson (this issue) has put this observation in perspective, pointing out that fall reproductive activity is quite common among birds. The hypotheses advanced to explain this widespread phenomenon on photoperiodic and endocrinological grounds are so far unsatisfying (see Farner 1959). My Peregrine data do nothing to explain the phenomenon but are, at least, interesting. The old, lone female has shown what might be taken to represent "fall" activity on at least three occasions. At the present time (March 10) she is enthusiastically maintaining and spending a great deal of time sitting on a scrape she began almost three months ago. She began this activity after more than two and one-half months on short days (L D 12/12) and she is still on short days. This is confusing, since it seems not to have the tentative character of previous, possible analogous, occasions of this sort. The young pair has shown an increase (the female, at least) in "ee-chupping" at feeding time during the past month (mid-February to mid-March), but otherwise they have shown no increased interest in reproduction. I do not know what these short bursts of activity imply; they do not even have the consistency of occurring on either long or short days. It does seem possible that L D 12/12 is sufficiently short to allow photorefractoriness to be dissipated, yet long enough to be photostimulating when the refractory period is past.

There are some hints that the birds may not really be responding to photoperiod with respect to this phenomenon and, in fact, an all-over look at the data might suggest that there is an implication of a yearly endogenous rhythm, a "circannian" rhythm (see Marshall 1961, and Immelmann 1971 for further discussion of this point).

There are many interesting attributes of the Peregrine data, but throughout one must realize that the data simply are too confused, fragmentary and lacking in both controls and sample size to support even the most enthusiastic speculator. I am, however, left with the distinct impression that for now we ought not depart too much from "natural" conditions with northern Peregrines. Further, there seems ample reason to assume as a working hypothesis that circannian rhythms (and diurnal rhythms) might be important, and to extend the hypothesis (perhaps beyond its stretching capacity) that one can "set" diurnal or annual "clocks" without intending to, by photoperiodic manipulations. There is at least some evidence that this might occur in the statements of a few falconers that eyass "tundra" birds taken to mid-latitudes at an early age molt in a manner consistent with "anatum" birds of the same latitude.

The question of why the Peregrines did not lay eggs may be gratuitous, since only the lone female was over two years old at the end of the work reported here. Unfortunately, we are quite in the dark about a crucial issue–the age required for sexual maturity in Peregrines. There are field observations of brown females attending eggs, although the original "layer" of such eggs is usually in doubt. The fact that typical adult plumage is normally attained before the bird is two years old is puzzling, if the bird is not to become a member of the breeding population. Nelson (1971) notes Peale's Peregrines which almost certainly bred at two years of age. In 1970 I found a molted brown primary (Right, number 8) beneath a Yukon River eyrie which fledged young. Obviously, the wild situation is different from the captive situation and although it seems probable that two year old birds *can* reproduce, we must wait for firm data.

In my own experiments the older female was certainly old enough to breed. The most obvious reason for her not laying eggs, if the experimental regime was otherwise satisfactory, may lie in the absence of a male. During the third cycle for the young birds it does seem possible that they were old enough, but I know of no northern Peregrines which have laid eggs in captivity at that age. The coming season will be interesting with regard to any "aging" effect due to photoperiodic cycles faster than normal, since they will still, by the clock, be rather young for egg-laying in captivity. Richard A. Graham (pers. comm.) has commented on the strong tendency for paired, captive female Peregrines of four years of age to lay eggs and for younger birds not to lay, although no taiga or tundra Peregrines are involved in this generality.

Comparisons and Generalities

While the experimental design for neither species provides for a rigorous test of photoperiodism, the data really allow no other interpretation. The case is particularly strong for Merlins, although the Peregrines also manifested evidence of response in both breeding behavior and molt outside of the normal wild breeding season.

Merlins respond rapidly and unambiguously. With the possible exception of the last cycle reported, there are hints that the experimental conditions have not been optimal for actual breeding. Molts, for example, were complete, apparently to the last body feather, but the rapidity suggests a fundamental abnormality, possibly reflecting unnaturally high levels of thyrotrophic hormone. Whether or not this hypothesized hyperactivity on the part of the anterior pituitary extends to the cells responsible for secretion of gonadotrophins is a moot point. If gonadotrophin secretion is too rapid or too high, it could certainly contribute to failure of breeding. While indulging in somewhat tortuous reasoning of this kind, it should also be pointed out that the results in some respects imply too *low* levels of gonadotrophins, but do not have anything to say on the issue of speed of secretion. Quite obviously we need detailed information on circulating levels of the hormones involved in reproduction to answer such questions.

There are many ambiguities in the Peregrine data which do not yet permit even hypotheses to be formed with much sense of security. It does seem clear that under comparable photoperiodic regimes Peregrines are slower to respond. Possibly these differences in the experimental response are correlated with differences in migration patterns. It is at least equally possible that the differences are due to experimental design. It is interesting that some molts in Peregrines have tended to be relatively close to normal wild molts in duration and in sequence. This may imply that experimental conditions were closer to those needed for breeding than were those used for the Merlins. In my opinion, the great behavioral responsiveness of the lone female Peregrine argues that she has been relatively close to egg-laying. In many ways she acts toward me as she should toward a male Peregrine, even to the extent of copulatory movements when I stroke her back or tickle her belly and cloaca. I have attempted to bring her along further by playing the part of the male without success.

One lesson seems clearly underlined by these studies, faulted as they are at this early stage: Even though examination of two species may suggest that they should respond similarly to photoperiod, judging from breeding locality, phylogenetic relationship, migration patterns and other generalities of the ecological setting of the species, we cannot assume that they actually do have the same photoperiodic requirements. Extrapolations and comparisons will be very valuable, but such must be made with caution.

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