ON PHOTOPERIOD AND CAPTIVE BREEDING OF NORTHERN PEREGRINES

by
R. Wayne Nelson
Department of Biology
The University of Calgary
Calgary, Alberta T2N 1N4, Canada

Introduction

With Peregrine Falcons (*Falco peregrinus*) of northern origin there has been a general lack of success to date in efforts at captive breeding. It seems apparent from the lack of egg-laying that northern birds will not come into full reproductive condition on natural daylengths of middle latitudes where a number of them have been held for some time. Some captive pairs have shown very good indications of incipient breeding condition. From these cases it is fairly obvious that northern birds in captivity require manipulation of the daylengths to which they are exposed to something much closer to the wild condition.

The RRF Captivity Breeding Conference provided a basic discussion of photoperiod (daylength) and photoperiodic responses in birds. The following discussion will not provide an in-depth analysis of the causes and effects of the photoperiodic response which many birds show, or the internal mechanisms involved. It will provide the following:

1. Some basic information on the timing and location of breeding, migrating and "wintering" northern Peregrines;
2. An outline of the daylengths which wild northern Peregrines experience through the year; and
3. A table of daylength changes which can be followed through the year in order to give captive birds photoperiods comparable to those to which the wild birds are exposed. Only in certain parts of this discussion will any effort be made to differentiate between *F. p. tundrius* and far north *F. p. anatum* birds; in general there is too little known concerning the dates and distances of migration of northern Peregrines.

Some Photoperiodic Experiments with Other Species

In order to provide a basis for discussion of the northern Peregrines and their photoperiods, I will attempt at the outset to outline some of the published experimental results of photoperiodic stimulation of other species, especially those experiments which seem to relate most directly to the northern migrant Peregrines.

By using long daylengths (with artificial lighting) to resemble summer days and short daylengths to resemble winter days, many people have caused a wide variety of bird species to come into breeding condition at various times of the year. Migratory species (at least) when placed on long daylengths put on weight —develop their fat deposits (Wolfson 1959)—presumably in preparation for migration. The length of time it takes for the birds to come into breeding condition depends on a number of factors (light intensity, species, etc.). While the testes of males will develop fully in response to long days, the ovaries of females will not develop fully solely due to photoperiodic stimulation. For full ovarian development females, apparently, also require "psychic" factors—nesting material and/or a nesting site and, perhaps, a photoactivated male also (Farner 1959).

Many species respond to the rather long days of a natural spring by breeding. However, before the longest day of summer is reached, their gonads have regressed and they have lost their ability to breed until the following year (see Schwab 1970: Fig. 1). The rather long spring days "turn on" the birds; the even longer days near June 21 appear to "turn them off." Various researchers have shown that by holding the birds at a certain daylength, they can be kept in breeding condition for many months. Male Starlings (*Sturnus vulgaris*) from California held on daylengths of 10½ or 11 hours remained in breeding condition "for at least 15 months" (Schwab 1970). With 12 hours of daylight they came into breeding condition and then passed through it in a couple of months, as in the wild. That is, the longer day apparently caused their breeding cycle to eventually end, whereas slightly shorter daylength caused the birds to remain in breeding condition for over a year (until the experiment was ended). The daylengths required for this response seem to vary with latitude (where the birds originated) and with species.

Some species, when held for many months on winter (short) daylengths, have eventually started to come into breeding condition. This response has led to the suggestion that birds summate or "store up" something from daylengths. Apparently, when they have "stored up" enough, they will come into breeding condition. This is the "summation hypothesis."

The period of *darkness* each day may be as important as the period of light. A number of experiments have shown that a long night (short day) which is broken by a period of light (even a short period of light) can affect the bird in the same way as a short night (long day).

When the birds have come into and passed out of breeding condition in early summer, keeping them on the long daylengths of mid-summer will prevent them from coming into breeding condition again, even a year later. After the gonads have begun to regress in early or mid-summer, the birds require a "rest period" of shorter days—a *photorefractory period*—before they can again come into breeding condition.

The refractory period has some peculiarities. If long days are introduced during the refractory period, in effect the refractory period starts all over again, i.e. the refractory period must be an *uninterrupted* period of short days (Wolfson 1959).

Farner (1959) has commented on autumnal sexual activities sometimes seen in birds, particularly in resident species. He suggests that the refractory period has ended relatively early (August—September) in these birds, while days are still long enough to cause appreciable stimulation of the birds. Sexual activities in the autumn apparently vary from year to year depending on weather conditions.

Farner (1954, cited by Engels 1959) suggests that for North American species which winter south of the equator, the refractory period may be rather long, ending sometime after the South American summer solstice (December 21). The birds could then be triggered to migrate northward by the still long (though shortening) days. Engels (1959) found that Bobolinks (*Dolichonyx oryzivorus*) (breeding 40-50 degrees N, "wintering" 15-25 degrees S) possess a photorefractory period. Birds held on short ("winter") days for eight weeks, then placed on 14-hour ("summer") days, came into breeding condition more quickly if the "winter" (refractory period) days were 10 hours instead of 12 hours long. Shorter "winter" days appear to hasten the end of the refractory period.

Most experiments with photoperiod appear to have been conducted with sudden changes from one daylength to another (e.g. from 10 hours suddenly to 14 hours). This has probably been done more as a matter of convenience than a result of experimental design. However, as will be pointed out below, it appears that from *gradual* changes in daylength more can be learned and some particular problems may be avoided. At the moment, in attempting to breed raptors, we must be primarily concerned with achieving successful reproduction. Experimentation into the causes and internal mechanisms can come later. Wild birds respond to *gradual* changes in photoperiod and it should be expected that they will also respond best to gradually changing photoperiod in captivity.

Annual Cycle of Northern Peregrines

For a northern Peregrine the year is broken into four distinct periods: migration south, "wintering," migration north, and breeding. It is with the breeding season that we are primarily concerned in captive breeding, but the other periods of the year are probably equally important in setting the stage for breeding.

In Figure 1 some of the available data on migration and "wintering" of northern Peregrines are summarized. Only the more important points will be considered here.

1. **Departure south.** White (1969) noted movements of Peregrines in Alaska during the first two weeks of September. Shor (1970) mentioned an adult Peregrine shot in Greenland on 4 September 1958 north of the Arctic Circle. From this it can be suggested that the birds might be beginning the flight south in the first or second week of September.

2. **Migration south.** In Wisconsin most migrating Peregrines are observed between 22 September and 5 October (D. Berger, cited by Enderson 1965). Berry's (1970) data suggest that the majority of falcons pass the Virginia coast in the period 28 September—12 October (or slightly later). On the Texas coast, from Enderson's (1965) and other data, the main portion of the migration appears to occur about 5-25 October. Enderson's data indicate that it takes about

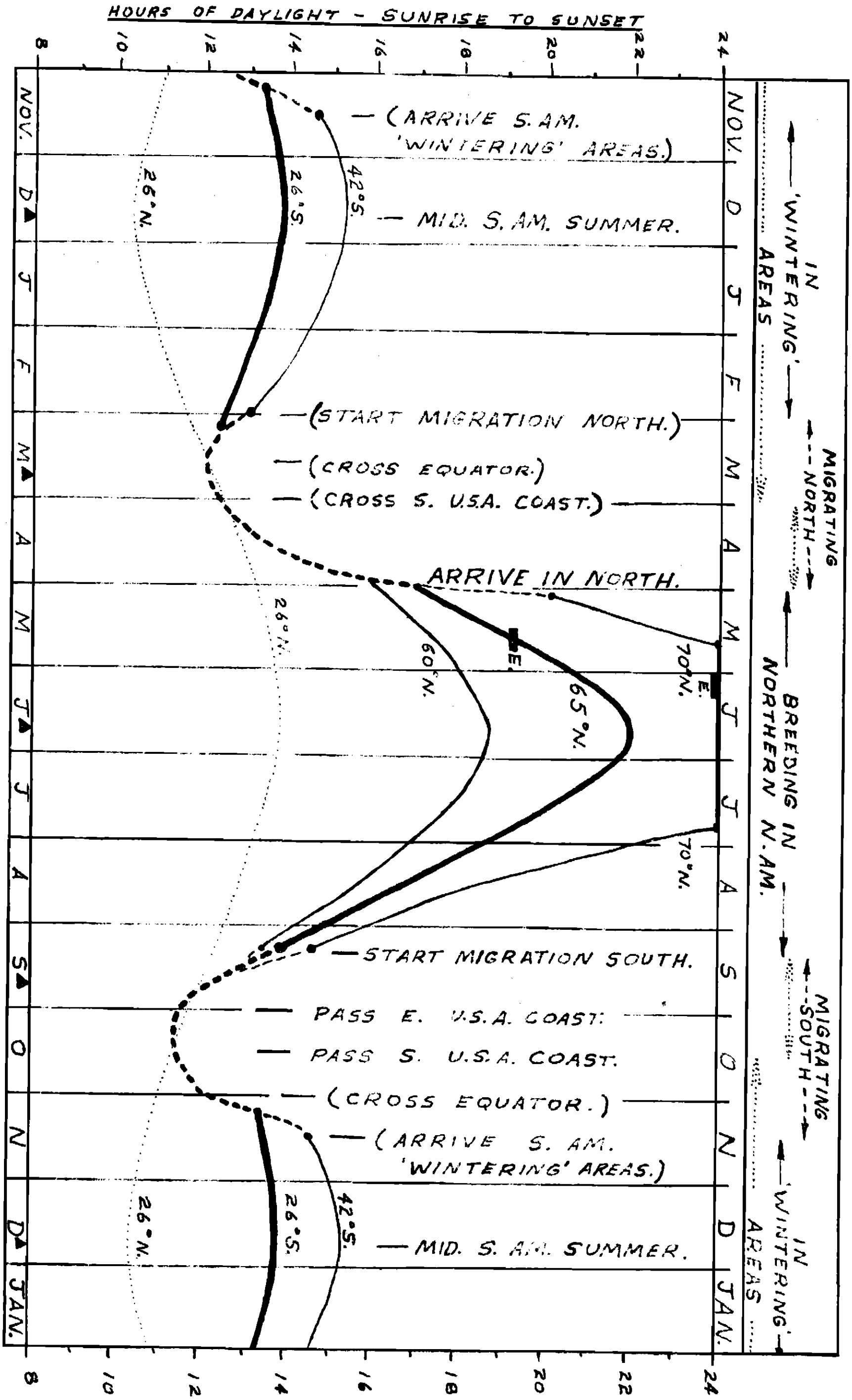

Figure 2. Approximate annual cycle of daylength (sunrise to sunset) to which a Peregrine breeding in northern North America is exposed. [Dashed lines indicate migration. Dotted line shows yearly photoperiod at Miami, Florida. Parentheses show uncertainties due to insufficient data. Solid triangles indicate solstices and equinoxes. E = egg-laying (from Cade 1960). Photoperiod data from Thomas (1953:181), Robbins *et al.* (1964:332), and U. S. Naval Observatory (1969:386-393).]

two weeks for a falcon to fly from Wisconsin to the Gulf Coast. By using this time and distance with Figure 1 we can roughly predict when the falcons will reach regions farther south. Birds wintering between the Tropic of Cancer and the equator probably migrate for just over one month. Falcons flying to south of the Tropic of Capricorn probably require just over two months.

3. **"Wintering" areas.** In Figure 1 band recoveries from migrant Peregrines taken in "winter" (November–February, the South American summer) are plotted from the data of Shor (1970) and Kuyt (1967). By specifying the period November–February I have eliminated a number of banding records which might have been from birds which were migrating (e.g. in October, March and April). Data from birds banded in Wisconsin (Enderson 1965) suggest less of a movement of that population to the southern parts of South America than do data from birds banded on the east coast.

Shor's (1970) data from east coast birds suggest that immatures and adults do "winter" in the same regions. There is a hint in his data that falcons which pass the Virginia coast earlier in the season migrate to "wintering" areas farther south. Birds banded before about 8 October are heading south of the equator, and those passing after about 8 October winter between the Gulf Coast and the equator.

White (1968) points out that Peregrines in North America exhibit "leapfrog" migration. Those breeding in the far north tend to winter farthest south. There is also a tendency for smaller birds to winter farther south. Kuyt's (1967) record of a banded nestling Peregrine (approximately 64 degrees N) being killed in Argentina supports this (Fig. 1). White (1968, citing Hunt 1966) further points out that falcons wintering near the Gulf Coast appear to be western or taiga birds, rather than pale *F. p. tundrius.* Darker taiga birds (see the tree-line indicated on Fig. 1) appear to "winter as far south as Central America and occasionally northern South America."

4. **Migration north.** Meredith (cited by Enderson 1965) observed wintering "arctic" Peregrines (presumably taiga birds) in south Texas until March. Other than this, there appears to be very little known about the northward migration of northern Peregrines. If we speculate that the flight north takes as long as the flight south, then birds in the southern part of the "winter" range would have to start north in late February or early March.

5. **Arrival north.** Cade (1960) and White (1969) indicate that Peregrines arrive in the Alaskan interior in very late April or early May, and on the Arctic Slope in the first or second week of May.

6. **Breeding season.** In the Alaskan interior, Cade (1960) noted one instance in which the first egg appeared about May 13. He estimated egg-laying to occur mostly during the third week of May in the interior (about 65 degrees N) and during the first week of June on the Colville River (Arctic Slope, about 69-70 degrees N). This would be about two to four weeks after arrival in the area. These falcons have only about four months–a rather short period–in which to carry out all their breeding activities.

Photoperiodic Changes in the Wild

The curves in Figure 2 are derived from the migration data in Figure 1 and from various sources of information of photoperiod. Latitude 42 degrees S appears to be at the southern extreme of the "wintering" range of North American Peregrines in South America.

The heavier line in the center of this figure illustrates the changes in photoperiod to which a Peregrine breeding at 65 degrees N is exposed through the summer. At this point, a difficulty arises: which birds winter where? There apparently is a difference between the migration patterns of *F. p. tundrius* (tundra) and northern *F. p. anatum* (taiga) (White 1968). A falcon from 65 degrees N could be of either subspecies.

1. If it is *F. p. tundrius* from 65 degrees N, then its annual photoperiodic cycle would most likely be matched by the heavier lines of Figure 2–26 degrees S in "winter" and 65 degrees N in summer. The nestling recovery shown in Figure 1 suggests this, also.

2. A taiga (*F. p. anatum*) falcon from 65 degrees N might winter as far south as the equator, and probably at, or south of, the Gulf Coast. In this region the annual photoperiodic changes are slight, and the "wintering" falcon would be experiencing days in which the sun is up for about 10½ to 12 hours, following, or slightly above the curve for 26 degrees N (Miami, Florida). Its period of migration north and south would likely be somewhat shorter than indicated by the dashed migration periods in Figure 2, since it would not have to fly to south of the equator. The "wintering" period would be slightly longer.

3. A falcon breeding on the Arctic Circle (66½ degrees N) would see the sun for the full 24 hours of the day only on June 21. Birds north of the Arctic Circle experience more days with 24-hour sunlight, depending on how far north of the Arctic Circle they are.

Since it appears that most northern falcons arrive in the breeding areas about the first week of May, a bird breeding north of the Arctic Circle would have spring and summer daylengths indicated by curves steeper than those shown for 65 degrees N and resembling more the curve shown for 70 degrees N. Birds breeding north of the Arctic Circle would arrive in the spring when days are 19 or more hours long, having flown north through a period of rapidly lengthening days. (The steepness of the curve indicates how rapidly daylength is changing).

Since falcons breeding farthest north can be expected to be "wintering" farthest south, the curve shown for 42 degrees S probably represents the "winter" photoperiod of birds from higher latitudes of the arctic (e.g. 70 degrees N).

As Figure 2 shows, once the bird has arrived in its northern breeding area, the rate of daylength increase slows somewhat from the rate during the migration north.

During the longest day of the South American summer (December 21), birds at 42 degrees S receive only 1½ hours more daylight than birds at 26 degrees S (about 15¼ and 13¾ hours of sunlight, respectively). By way of contrast, on December 21, falcons "wintering" at Miami, Florida, or Brownsville, Texas, would receive only 10 1/3 hours of sunlight, this being the *shortest* day of their

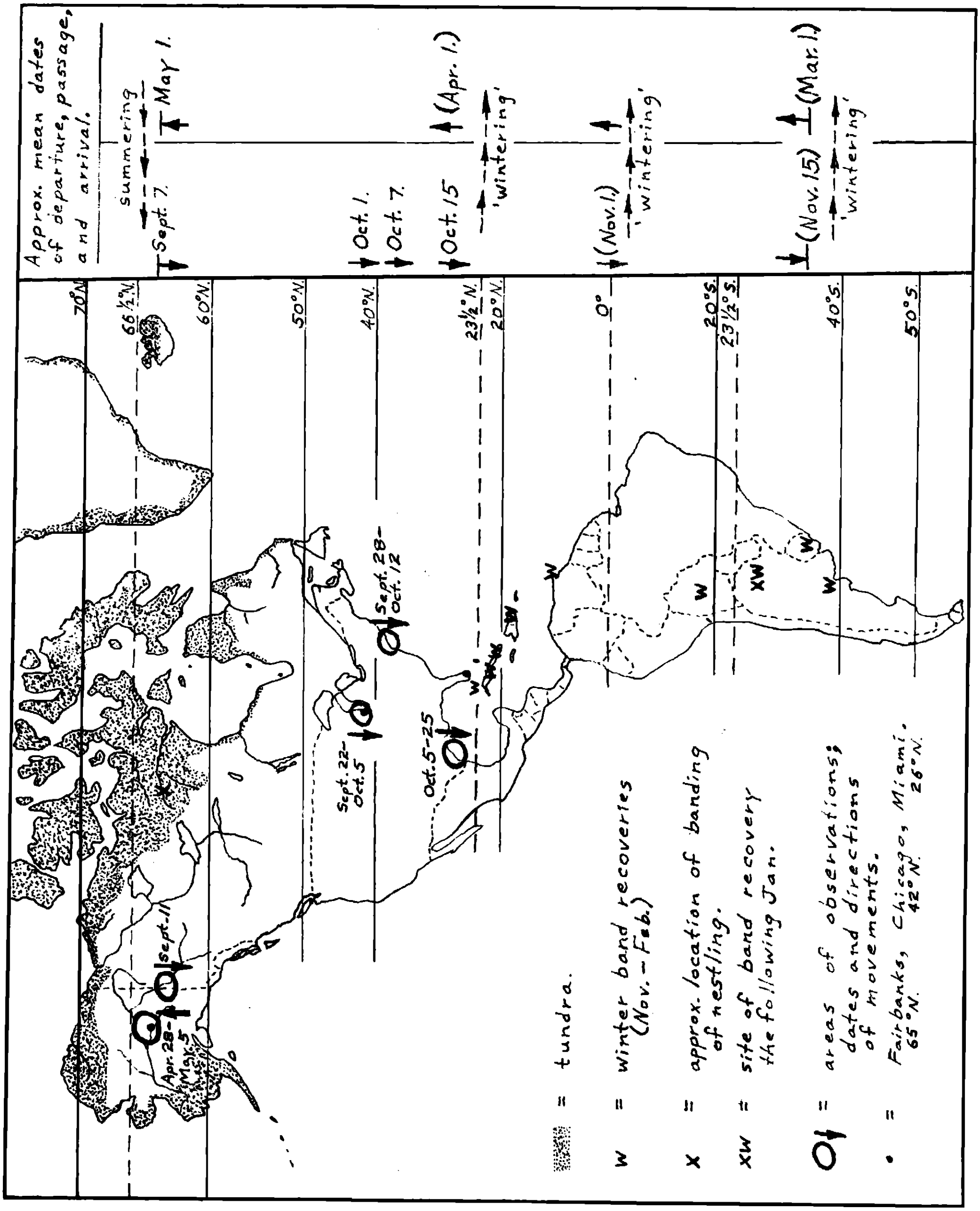

Figure 1. Winter band recoveries and migration dates of northern breeding Peregrines. [Banding data from Shor (1970) and Kuyt (1967). Migration schedules from (S to N) Enderson (1965), Berry (1971), Berger (cited in Enderson 1965), and White (1969).]

year.

Twilight must be considered, if only briefly. At 65 degrees N (Fairbanks, Alaska) the twilight extends through the night "so the city will not become even dark enough to require street lights or automobile headlights. This condition prevails each year from about May 15 to approximately July 27" (Nicholson 1963). The effect of this upon falcons (or any birds in which photoperiod has been studied) does not appear to be known.

Photoperiodic Cycles for Captive Northern Peregrines

Table 1 shows the approximate annual cycle of changes in daylength (sunrise to sunset) to which falcons from northern regions are exposed, based upon the data in Figure 1 and Figure 2. This table, if applied to northern Peregrines in captivity by means of artificial lighting (incandescent or fluorescent), should trigger these birds into breeding condition or, at least, bring them very much closer to it, especially if other factors are also conducive to breeding (i.e. the birds are undisturbed, food and water are plentiful, lighting is reasonably bright, adequate perches and ledges are provided, etc.).

At the outset, a decision must be made as to where the birds in captivity might have originated in the north. (Eyass-taken birds will not have this problem, although they may have imprinting problems.) On the basis of the migration data provided and the coloration of immature and adult plumages (see White 1968 for subspecies characteristics), it should be possible to make an informed guess as to the subspecies and latitude of origin. In cases of real difficulties or overlap, a means of solving the problem might be to follow the schedule of photoperiods for *F. p. tundrius* from 65 degrees N and, if required, gradually continuing beyond 22 hours of light towards 24 hours of light to discover when the birds come into prime breeding condition.

For reasons which will be pointed out below, in Table 1 the changes in daylength are *gradually* brought about with daily increases or decreases being provided, and the northward migration and northern spring periods for the captives are slightly lengthened. It will probably be possible to bring birds into breeding condition by first giving them two to three months on "winter" daylengths, then "migrating" them north with changing photoperiods; Table 1 begins with the "winter" photoperiods for this reason. It may not matter whether the daylength changes (additions or subtractions) are applied half at the beginning of the day and half at the end of the day, on alternate days at the beginning and end of the day, or consistently at either end of the day. There is some evidence, however, that the safest course is to make the changes equally at both ends of the day (see Meier *et al.* 1971 for some endocrinological evidence). By arranging the photoperiodic schedule ahead of time, it would be possible to have the beginnings of the changing days at convenient times for feeding and observing the birds.

The brightness of the quarters may have an effect upon the timing and schedule of breeding activities. Birds in the wild experience cloudy days, whereas captive birds under lights always have the "sun" present. It is possible that captive

Table 1. Photoperiod schedules proposed for use in captive breeding of northern Peregrines. [The columns indicate the number of weeks during which changes in photoperiod are brought about. The comparable situation in the wild is shown by the location of the wild birds and the approximate dates during which they experience similar photoperiods. (e.g. in Stage 2, start at 13½ hours of light per day; subtract one minute of light each day, to arrive at 12 1/3 hours of light in 10 weeks time. This is comparable to "wintering" at 26 degrees S, from December 22 to February 28.)]

Stage	Duration, in Weeks	Photoperiod Changes (add or subt. min./day)	In the Wild Location	In the Wild Month
tundrius breeding at 65°N, "wintering" at 26°S				
1.	6	13½ hrs. (no change)	26°S	15/11-21/12
2.	10	13½→12 1/3 hrs. (-1)	26°S	22/12-28/2
3.	2	12 1/3→12 hrs. (-1½)	Migr. N	1/3-14/3
4.	7	12→17 hrs. (+6)	Migr. N	15/3-30/4
5.	8½	17→22 hrs. (+5)	65°N	1/5-21/6
6.	13	22→11½ hrs. (-7)	65°N & Migr. S	22/6-30/9
7.	1½	11½ hrs. (no change)	Migr. S	1/10-14/10
8.	4	11½→13½ hrs. (+4)	Migr. S	15/10-14/11
Proceed to Stage 1.				
anatum breeding at 65°N, "wintering" at 26°N				
1-2.	10½	11 hrs. (no change)	26°N	15/10-28/2
3.	2	11→12 hrs. (+4)	26°N	1/3-14/3
4.	7	12→17 hrs. (+6)	Migr. N	15/3-30/4
5.	8½	17→22 hrs. (+5)	65°N	1/5-21/6
6.	13	22→11½ hrs. (-7)	65°N & Migr. S	22/6-30/9
7-8.	2	11½→11 hrs. (-2)	Migr. S	1/10-14/10
Proceed to Stage 1.				
tundrius breeding at 70°N, "wintering" at 42°S				
1.	6	14½ hrs. (no change)	42°S	15/11-21/12
2.	10	14½→13½ hrs. (-1)	42°S	22/12-28/2
3.	2	13½→12 hrs. (-6)	Migr. N	1/3-14/3
4.	7	12→20 hrs. (+10)	Migr. N	15/3-30/4
5a.	4	20→24 hrs. (+8)	70°N	1/5-21/5
5b.	9	24 hrs. (no change)	70°N	22/5-21/7
6.	8½	24→11½ hrs. (-12½)	70°N & Migr. S	22/7-30/9
7.	1½	11½ hrs. (no change)	Migr. S	1/10-14/10
8.	4	11½→14½ hrs. (+7)	Migr. S	15/10-14/11
Proceed to Stage 1.				

birds may respond slightly earlier on their schedule of lighting, *if* it is roughly equivalent to the light intensity outdoors. If indoor lighting is of low intensity, the birds will probably come into breeding condition somewhat late, and the male will probably be unsynchronized with the female (see Koehler 1969).

Some Captive Breeding Efforts with Northern Peregrines

1. In January 1967 Fyfe (BPIE 4) put a pair of eyass, intermewed, northern Peregrines into new quarters and onto artificial light (100-watt bulb). The birds were disturbed only at feeding time and were observed through a peephole. The lighting regime was as follows: Approximately three months on 12 hours of light, then increases of one hour of light per week until 24 hours of light was reached, then kept at 24 hours of light.

At about 15 to 16 hours of light per day the birds "become more noisy and aggressive, particularly the tiercel at the nest ledge" and they spent much time flying back and forth—"migrating." Both lost some weight. This activity slowed when they reached about 22 to 23 hours of light per day. While on 24 hours of light, the female spent much time on the nest ledge and was seen to sleep lying on her breast. Both birds became quieter and they molted normally.

There may be a number of reasons why this pair apparently just missed reproducing (e.g. intrusion into their territory at feeding time), but the consideration of the photoperiod provides some other good suggestions.

The "migration," noise, and aggression apparently began when the birds were on 15 to 16 hours of light. Compared to Figure 2, this photoperiod indicates the latter part of the natural migration phase. From this we might presume that (1) the pair, having the "migration" restlessness, tried to migrate or, at least, to "burn off energy" due to the changing photoperiod, and (2) being confined as a pair, with ample food and a nest ledge, they came into territorial behavior and incipient breeding condition somewhat earlier than might be expected in the wild.

The female of this pair originated at about 63 degrees N; the male was from somewhere in Alaska. The case of the female may be most important. At 63 degrees N the female would never see a 24-hour day; the longest day (June 21) might be about 21½ to 21¾ hours long from sunrise to sunset (with twilight through the night).

Just as photoperiod can act as a trigger to start breeding behavior and gonadal development, it appears (experiments discussed previously) that it also causes the birds to *stop* gonadal development and to stop production of eggs at a time when (even though the days are still getting longer) it would be impossible to rear young to independence before migration south must begin. From Figure 2 it can be seen that even birds at 70 degrees N lay eggs well before June 21. Most likely the birds are triggered to lay by the photoperiod a week or more *prior* to actual egg-laying.

In this instance with a nearly successful captive pair, is it possible that the photoperiod was increased *too quickly* (one hour per week) and *too far* (to 24 hours of light) so that the female was suddenly "turned off" by the very long days *before* she was sufficiently "turned on" (gradually) by the shorter days?

(In birds from southern regions, i.e. southern-*breeding* falcons, 24-hour light might provide stimulus for successful breeding. Such birds have a much longer summer and may not need a rapidly-acting "shut-off" mechanism like the birds in the north with a shorter breeding season.)

2. Berry (BPIE 18) described the behavior of his adult passage tundra Peregrines on Pennsylvania photoperiod: "Last fall, both birds very noisy, often facing one another with head down, tail elevated. Inspection of open air shelf disclosed a scrape . . ." Grainger Hunt (pers. comm.) has observed a 2½ year old passage tiercel come into courtship behavior in early December on Texas photoperiod. Why in the fall? There may be two (or more) possible explanations for this.

First, it was mentioned earlier that some birds (male juncos) start coming into breeding condition when held for a long time on short days. Tests with females on continuous winter daylengths do not appear to have been conducted in the same way to see if they would eventually come into breeding condition. In any case, it has been hypothesized that the triggering of migration and breeding condition may be the result of the *summation* of light striking a bird over a period of time, rather than the ratio of light to dark or the strict length of day. If this is the case, then northern falcons might be expected to come into some form of breeding condition at any time of the year, when they have "stored up" the appropriate amount of light stimulation.

Second, another possible explanation for the *fall* activity of some northern Peregrines held at middle latitudes concerns the triggering mechanism for the "spring" migration north. From Figure 2 it can be seen that Peregrines "wintering" south of the equator *begin the migration north in the autumn*—the South American autumn with its *shortening* days. Only when they near the equator will they come into spring and its lengthening days. It seems possible that these captive birds are reacting to the daylengths which trigger migration (shortening days) and, being confined with plentiful food and with ledges, the territorial and courtship behavior can immediately follow. Such birds will not reach full breeding condition due to lack of the triggering effect of rather long northern spring days. In these cases, "flying the birds north" with lengthening days (under lights) may be sufficient to stimulate them into full breeding condition; the shortening days will have started the process and lengthening days could complete it.

Other Considerations

1. **Cold winters and very short days.** By holding northern Peregrines overwinter in mid-latitude North America we are causing them to experience very short days, much shorter than they ever see in the wild. Judging by experiments on other species, shorter than natural daylengths appear to be of no major consequence to subsequent breeding seasons. However, keeping these birds overwinter in very cold weather might be pushing things a little too far. The northern birds, while they will tolerate prolonged exposure to zero or sub-zero weath-

er, certainly never experience such hardships in the wild. Their migration patterns indicate that they go to great lengths to avoid just such temperature extremes. By keeping them in *warmed* quarters they could be kept away from any inhibiting effect extreme cold might have on them. Under such conditions the 12-month cycle could be carried out at any time of the year, with birds breeding in December if one wished.

2. **Migration and wintering of the sexes.** While it is possible, it does not seem likely that a pair of falcons would migrate and "winter" together. There appear to be no migration records suggesting this. Until experiments are carried out with birds separated during the winter and re-introduced in the spring, versus birds dept together year-round, we will not know if there are any harmful or beneficial effects of either means of "wintering" the birds. It is possible that re-introduction of the pair in the spring (at the appropriate photoperiod) could be very stimulating to the birds.

3. **Twilight.** In the spring, at least, there might be some benefit derived from giving falcons a twilight period, particularly in the evenings. By allowing a small shaded (not glaring) bulb (e.g. 25-watt) to burn for a period of time in the evening, it would allow the birds access to their night perches without being struck suddenly with darkness. In the breeding season such a small light might be left on throughout the whole day to provide a nighttime twilight as in the wild.

4. **Gradual versus sudden changes in photoperiod.** Much of the experimental work with smaller birds, and some work with raptors (e.g. Willoughby and Cade 1964), has been done by suddenly giving the birds longer days (say, 18 hours of light) when breeding is desired. From the discussion above it appears possible to "turn off" breeding of northern birds by initiating a long daylength too quickly, especially if the daylength is much longer than that which birds from that particular birthplace would normally receive. Even if the birthplace of a pair of birds is known, we still do not know (yet) what the triggering photoperiod is for shutting off egg-laying. The photoperiod thresholds may be reached and the birds "turned on" or "turned off" *weeks* before we can see the effects.

Another reason for gradually taking the birds into the lengthening photoperiod of the northern spring (as is done in Table 1) is that we simply do not yet know where the trapped migrant falcons in captivity originated. By bringing the trapped migrants through a "winter" period of lighting (e.g. 26 degrees S if the birds appear to be *F. p. tundrius*), then taking them into the photoperiod changes associated with the "migration north" until they reach 16 hours of light per day (see Fig. 2), and then gradually "taking them north" by gradually lengthening the days, it should be possible to determine the exact photoperiod at which the birds come into maximum breeding behavior and then into egg-laying. Compared to a bird from 60 degrees N, one which originated at 70 degrees N would most likely require a considerably longer daylength in order to come into egg-laying. Gradually changing the daylengths may suggest where the falcons originated in the north.

Further, by *gradually* bringing the birds into the breeding photoperiod (by increases of about five to six minutes per day), and once having a clutch, it may be possible to obtain replacement clutches from the northern falcons simply by *keeping* them at the egg-laying photoperiod for a month or so before taking them back into the "natural" changes toward mid-summer daylengths and, later, the autumn. By holding them at the egg-laying photoperiod it should be possible to prevent them from reaching the "turn-off" photoperiod of a few weeks later in the "natural" summer. If the breeding season is extended in this way, then the "annual" regime could still be kept to 12 months by (1) eliminating Stage 7 in Table 1, (2) shortening the "winter" period slightly or (3) speeding up the period of the southward migration so that it takes less time to get to the "winter" photoperiod. Too much shortening of the "winter" may eliminate the required photorefractory period. Sudden increases in daylength pose the probability of over-shooting the triggering photoperiods and thereby preventing egg-laying. Much more could be learned from gradually increasing the daylength.

In a captive pair of falcons which was trapped on migration it is possible that the male and female originated from widely separated latitudes and that they would come into maximum reproductive condition at different photoperiods. If a problem such as this arises, three courses of action might be open: (1) keep the birds separated and on differing light regimes so that they would be synchronized for successful artificial insemination in the next breeding season, (2) attempt to synchronize them together by rather quickly increasing the photoperiod in the breeding season to the stimulating daylength of the slower (longer daylength) individual so that one might still be in breeding condition when the other just arrived in breeding condition, or (3) pair the birds with other birds which have responded to more comparable photoperiods to increase the likelihood that they were from similar latitudes.

5. **Observing and recording behavior and photoperiods.** This subject has been considered earlier (RRF Conference Behavior Panel Report), but with northern falcons there are some particularly crucial aspects.

From the preceding discussion it is obvious that responses of birds to "northward migration" and "spring" and "summer" photoperiods must be closely watched; otherwise it will be impossible to determine the causes of failures of pairs or to determine the photoperiods at which pairs did lay eggs. It cannot be emphasized too strongly that records (descriptions of behavior alongside the photoperiod of that date) must be taken so that (1) behavioral changes can be related to the photoperiods at which they occur, (2) the photoperiods and behavioral changes of unsuccessful pairs can be compared with those of successful pairs and (3) solutions to these problems may be arrived at as quickly as possible.

Conclusions and Summary

1. The lack of egg-laying by Peregrines of northern origin which are held in captive breeding situations suggests that these birds require photoperiodic manipulation in order to be induced to breed in captivity. The long daylength of the

northern spring is thought to be a necessity for egg-laying to occur.

2. The studies of Peregrine subspecies and of Peregrine migration (banding and censusing), fit together to suggest the photoperiodic changes that wild falcons experience through the year:

a. Northern *F. p. anatum* (taiga) falcons appear to "winter" north of the equator and presumably experience "winter" daylengths of 11 to 12 hours.

b. *F. p. tundrius* falcons appear to "winter" in South America, as far south as about 40 degrees S. They experience a second summer from November through January and begin migrating north during the South American autumn. Daylengths of the South American summer do not exceed about 15 hours within the migrant falcons' range. This is well below the suspected triggering daylengths for egg-laying.

3. The photoperiod which triggers egg-laying most likely varies depending on the latitude at which the birds originate; birds from farther north will require longer photoperiods in order to be stimulated sufficiently to breed.

4. Rather than giving the birds a sudden change from a short (winter) day to a long (summer) day, a gradual change over a number of weeks is recommended. A number of important advantages of gradual changes in photoperiod are pointed out.

5. When manipulating photoperiod, the light cycles must be followed very faithfully. Some precautions must be taken to ensure that the birds are stimulated by light only in the manner desired:

a. When birds are in the night period, their lights should *not* be turned on, not even for a matter of minutes. This could duplicate "long days" and destroy the photoperiodic schedule by advancing the birds ahead or prolonging their refractory period.

b. When in the refractory period of the year, birds must be subjected to *no long days*. Long days could cause the refractory period to start all over again.

c. Twenty-four hours of daylight may *inhibit* egg-laying in birds from below or near the Arctic Circle. If birds are known or suspected to be from this region, they should be taken rather slowly through shorter daylengths before being brought near to 24 hours of light as a last resort.

6. A table is provided which allows captive birds to be given rather close approximations of the photoperiods they would receive in the wild. Barring other interferences such photoperiodic manipulation should bring northern falcons into breeding condition in captivity.

7. By carefully observing and recording the behavior of the photostimulated falcons, it should be possible to determine the photoperiods at which they are stimulated to show breeding behavior and to lay eggs. By recording the behavior and photoperiod at which it occurs a number of captive breeding problems would appear solvable.

8. Separation of the sexes during "winter", and "wintering" birds in "nonbreeding rooms" may be helpful to the breeding of migrant birds. They could be re-united and/or allowed access to the breeding room at the appropriate photoperiod in the "spring." Both of these are conditions which apparently

occur in the wild about two to four weeks prior to egg-laying and both are likely to be very stimulating to the birds.

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