INTRODUCTION by R. Wayne Nelson

By considering the behavior of captive birds of prey prior to and during the time when eggs might be laid, it should be possible to learn much which could be applied toward the goal of achieving reliable production of captive-bred offspring. One of the major problems confronting captivity breeding is the acquisition of fertile eggs. In the many instances in which no eggs, or only infertile eggs have been laid, it could be presumed that at some point in the courtship behavior or sexual development one or both members of the captive pair had been blocked. Observations of the behavior of the captive birds should indicate where some of the problems lie.

This panel attempted to outline the courtship behavior of some wild and captive raptors, and discussed various methods whereby the captive birds might better be induced to take on the behavior and condition necessary for reproduction. The emphasis on the larger falcons reflects the urgency of the problem with those species; the information from other species provides very useful suggestions for captivity breeding of the larger falcons, due to similarities which appear within many of the species, and due to techniques which have been worked out with the other species.
Unfortunately, we must (literally or figuratively) leave the owls in the dark. There is a general lack of knowledge concerning much of the behavior of the owls prior to egg-laying.

The panel also attempted to indicate what some of the behavioral problems are, and how they might be avoided. The aim of the panel was to stimulate and encourage a better appreciation of what it takes to get birds of prey to behave appropriately in captivity, so that their behavior will bring them to reproduce successfully.

**THE NEED FOR A CHANGE IN DIRECTION—TOWARD THE SAME GOAL**

by Richard Olendorff

**Introduction.** Before getting started on the topic of behavior I would like to say that the other people on this panel, and certainly many of you in the audience, have spent more time contemplating the behavioral aspects of the captivity breeding of raptors than I. I suppose I am here because I wrote a lengthy review article on falconiform reproduction with emphasis on behavior, and carried out a very small captivity breeding project with one pair of American Kestrels during which rather detailed behavioral observations were made. Nevertheless, I consider my knowledge of falconiform behavior rather superficial and propose only to speak in generalities for the next several minutes to set the stage for the other panel members. In doing so, I would like to combine some aspects of the review article with some of the results of the kestrel breeding experiment.

**Importance of Behavior.** First of all let me point out that animal reproduction has often been researched with too little emphasis on ethology or behavior. Falconiform behavior must be important to us, but there is danger, too, in holding to stringent paradigms in the name of esthetics or ethology. So we must strike a balance which will result in production, a balance which may involve considerable artificialization (if I may coin a word) of the breeding sequence and conditions in general.

I used to think that habitat simulation and forced fulfillment of complete repertoires of reproductive behavior were the answers to all of our problems. I used habitat simulation with my kestrels with some success. As it turns out, though, this technique works very effectively for kestrels, but it is neither an effective nor an efficient method of rearing large falcons. This follows directly from the fact that copulation-producing behavior is an immensely complex sequence of events. Thus, we should glean only what is necessary from wild falcon behavior, and environment for that matter, emphasizing as we go those aspects which will increase the production of captive birds.

**Introducing the Birds to Their Mates.** Introduction of males and females has been discussed at great length. Although introduction is probably a problem in
itself, it is closely related to pairing in general. We have two types of pairing situations to consider: (1) the male with the female, and (2) the male and female with man in the artificial case. In raptors, as with any species of bird, pairing requires a great deal of adjustment, probably more than usual with the pugnacious raptorial species.

The worst failure is the situation in which the female will not tolerate a mate in the same room, the problem being introduction.

**Pair-bonding.** Assuming that the birds are successfully introduced, the next behavioral requirement is initiation and strengthening of the pair-bond. Of almost equal importance to the hormonal considerations discussed earlier at this conference are all forms of courtship such as mutual roosting, cooperative hunting, courtship flights, courtship feeding, and nest scraping (or building) to mention but a few. I think we can skip the matter of induction of physiological readiness, which has been substantially (albeit incompletely) discussed already, and move on to eliciting copulation.

**Toward Copulation.** Pairing and copulation-producing behavior have one very important thing in common; they involve sequentially presented stimuli which result in a sequence of responses. If the sequence is interrupted, reproduction may be inhibited through the neuroendocrine system. If the sequence develops adequately, reproductive processes will continue.

Let's consider the components of the sequence leading to copulation.

**Mutual Roosting.** Cade observed it in wild arctic Peregrines; Nelson has not observed it in wild Peale's Falcons. My kestrels engaged in it by the hours. In any case, this part of the behavioral sequence does not pose much of a problem. The opportunity for mutual roosting exists with the simulated habitat approach; it is probably unnecessary if artificial insemination is to be used.

**Courtship Feeding** should not be a problem provided that (1) the food is not tied to a stump or board, so that the male can take it to the female, and (2) the behavior is allowed to develop by the female. By the latter I mean that the female be kept adequately fed and/or be previously handled such as to prevent her from immediately stealing the food from the male. One such oversight could stop the sequence. Courtship feeding seemed very important with my kestrels, and I invite you to read about it in the article in Raptor Research News. Note particularly its relationship to the pair bond and its copulation-producing contributions.

Many other familiarities seen in the wild are also permitted and have been seen in captive situations; again, in the case of wholly artificial means they appear to be unnecessary. Billing, vocalizations, mutual preening, bowing, nibbling of the feet, and wing flapping do not present major blocks to the chain of behavior patterns leading to copulation, since they are readily allowed in confinement.

With cooperative hunting excursions and courtship display flights we run into
problems. They are virtually out of the question in the captive situations. Display flights are important. This can be seen from the facts that (1) courtship flights in many birds are so species- or genus-specific that they are being used in systematic studies of closely related bird groups, (2) birds of prey fall into this category, having quite distinctive courtship flights, and (3) in many cases, as with my kestrels, courtship flight behavior patterns are very stereotyped, a property which is shared by most instinctive behavior patterns. Courtship is instinctive in its basic pattern; and one instinctive behavior often acts as a stimulus for another instinctive behavior.

Assuming that your falcons paired reasonably well, it is possible that inhibition of courtship flights was the pitfall of your project. The external environment was the problem. Suffice it to say that the elicitation of instinctive, sequential behavior patterns will always be a problem, even at the outset of the wholly artificial paradigm.

In spite of the pitfalls and the failures, there have been some successes. In cases where birds have at least produced fertile eggs, they were able to abbreviate their courtship displays. They most certainly performed displays, nevertheless, but adequate courtship is not happening often enough with large falcons.

The Alternative to ‘Natural’ Captivity Breeding. The bright spot among the failures is the increased interest in artificial means. The disappointment of having a six year old falcon that will attack an old tiercel on sight certainly has led many to ponder the thought of bypassing pairing, and bypassing the territorial aspects of falconiform behavior. This leads directly to the question, “What behavior patterns, natural or aberrant, should be stressed if we forget about pairing bird to bird, and pair birds to man?”

The falconers among us realize the great extent to which falconiform behavior is plastic. We have seen the whole gamut from screamer to seasoned game hawk. As our discussion continues, we should reflect on how individual birds turned out, and how their behavior patterns might be used in captivity breeding. Realize, though, that behavior patterns which are undesirable in a bird used for falconry may be very desirable in a captivity breeding program.

As a young falconer I was taught that the only behavior patterns required of a game hawk which were not part of her natural repertoire were (1) for the bird to come down to you out of a tree or the sky, and (2) for her to let you approach her on a kill. Anything more was gravy, or simply unnecessary.

If we reduce captivity breeding to its simplest terms, the only unnatural behavior patterns required are (1) for the male to accept a man as a mate or at least as a sexual stimulus, and (2) for the female to lay eggs in a captive situation. As we have seen today, it’s not that easy, but there is reason for optimism in both of these situations. Couple (1) and (2) with artificial insemination, and possibly also with artificial incubation and hand- or foster-rearing, and we have a plan of some importance developing.

Summarizing. In summing up, and to emphasize the importance of artificial means, I would like to make the following points.
Simulation of natural nesting conditions in breeding lofts has until now occupied the efforts of many raptor aviculturists. This method has already proved too inefficient to keep pace with declines in wild populations and, as a result of the latter, in the numbers of birds available for captivity breeding and falconry. Unless some breakthrough occurs, we need an alternative to habitat simulation and forced breeding behavior.

Man has been augmenting the productivity of domestic birds for decades by bypassing the necessity of developing complex, copulation-producing behavior patterns. In light of recent successes with artificial insemination with raptors, and assuming that there are far more similarities between falcons and domestic birds than differences, we should place emphasis on behavior patterns which will increase the production of progeny by artificial means. It is irrelevant whether or not these behavior patterns are “typical” of falconiform birds. We should take advantage wherever practical of known behavior patterns of wild birds, but we should not be bound to them in the name of ethology or esthetics.

Contrary to some purists’ beliefs, two captive falcons will not a chicken make, either morphologically, physiologically, or psychologically. Such problems of the progeny will be solved when the time comes. Right now we need to produce—artificially, if we can, at least for the time being.

**TRIGGERS FOR EGG-LAYING**

by Frances Hamerstrom

Sean Morris, the brilliant young British biologist, recently told me of his work filming Blue Tits. As he spoke, one thing after another that I had noticed with raptors fell into place: for example, triggers that lead to egg-laying.

The Blue Tit must time its egg-laying so that caterpillars will be available to feed the young. There are early springs and late springs so she cannot use day-length as a guide. She prepares her nest early in the season and then loiters. When the male brings caterpillars to her in large enough quantities she starts laying—having started, she completes the clutch.

Balfour has stressed the close connection between the sex act and food in harriers. In my experience, harriers only breed well when mice are abundant, and furthermore it is my hunch that food is more important than aerial displays in harriers. Recently harriers have been breeding successfully without sky dancing in good vole years. There was one exception: many voles and almost no breeding. I suspect it was the year that they were carrying the highest pesticide residues.

For captive breeding, it appears we do not need all the triggers, but we do want to time them. Presentation of food is the easiest of all to time.

Falconers are accustomed to offering food once a day. I can think of few things less likely to trigger egg-laying. Notice I am not talking about availability of food, but of **presentation** of food. A number of species of raptors lay small clutches or fail to breed when food is scarce. When food is scarce it is less often
Essentially all falconers understand the advantages of tid-bitting in training. Holding half a Plymouth Rock hen on the glove gives at best one flight a day. I am coming back to that Blue Tit female—repulsive as it may be to some to learn from dickey-birders—the Blue Tit lays when caterpillars are presented often enough. Let’s give our breeding birds the idea that hunting is good when we want eggs. Tid-bit.

Furthermore, a trigger may lose its effectiveness if it is used constantly. I do not believe that my Golden Eagle, Chrys, would have laid six clutches in five years if she had not had frequent nest visits from me just before laying. She did not get this kind of attention until I figured egg-laying was near. Like the Blue Tit male, I spent several weeks in lack-a-daisical attention and then pulled out all the stops at once: frequent visits, nest building, neck stroking and using my voice. The most powerful response that she gave was to hay for nest lining. If hay was withheld and then dumped on her nest, she went straight into a copulatory reflex—possibly a releaser for ovulation.

Birds that have stick nests are fascinated by sticks. If you work with them with sticks and are getting along well with them with sticks, tease them—don’t always give them the sticks, hang onto the sticks, make it a little difficult for the birds.

As falcons and owls do not build their own nests, they are not apt to be “turned on” by hay or sticks. Old pigeon wings and such may stimulate sex play and ovulation in these groups.

Heinz Meng, when he mentioned how he crouched and ran along outside his falcons’ breeding room, immediately struck a bell as far as I was concerned—I think we need to vary things. Which of our breeding birds have a chance to defend their nest? We spare them this as hard as we can. We shy away the public, frighten away the dogs, and even hassle the children. Now, if you let the birds get scared sometimes, maybe it does them good as long as they don’t get too scared. Consider this possibility, because then they are defending a nest, which is the natural thing for them to do from time to time.

Many of us are inclined to keep trying everything that we can think of to produce eggs. Perhaps we need to learn to deny some of the stimuli for a time. They may work a week later.

It has become plain at this conference that raptors are not strongly determinate layers. To get more eggs—once you have some—two courses are open: keep taking away eggs (I’d leave one in the nest), or take the whole clutch and hope the bird will lay another.

References


(Fran’s book devotes almost half of its pages to her efforts toward captivity
breeding of her Golden Eagles. During the last several years, she and her eagles have come extremely close to producing captive-bred eaglets by the artificial insemination method. For a fascinating account of the ideas, methods, and techniques surrounding the courtship and artificial insemination of these birds of prey, I would strongly recommend that everyone interested in captivity breeding carefully read this book. And, by the way, it is in its third printing. R.W.N.)

BREEDING BEHAVIOR OF CAPTIVE AND WILD PRAIRIE AND PEREGRINE FALCONS
by Richard Fyfe

Introduction. One aspect of the raptor studies being carried out by the Toxic Chemicals Section of the Canadian Wildlife Service has been field studies of falcon behavior in relation to our pesticide investigations. These studies have been oriented toward documenting normal behavior patterns so that we would be in a position both to identify and interpret behavioral changes observed in the field. Detailed observations have been made on several pairs of Prairie Falcons (Falco mexicanus) which were known to be carrying very low residues of toxic chemicals and on one pair of anatum Peregrines (F. peregrinus anatum) in 1969 and 1970.

In addition to our field work I should indicate that for several years I have tried unsuccessfully to breed both tundra (F. p. tundrius) and Peale’s Peregrines (F. p. pealei) in captivity. The pair of pealei laid two clutches of infertile eggs in 1970 and again in 1971. Obviously, since the eggs were not fertilized, something was wrong, but what? Since we had observed that our presence altered the behavior of the birds we felt that it was not possible to observe normal behavior so long as the birds were aware of our presence. Therefore, in 1971 we built two observation blinds and were able to photograph and carry out detailed observations on the pair of pealei and on one pair of Prairie Falcons. Fortunately for us the latter pair were successful in producing four fertile eggs, hatching these and raising all four young to fledging.

For this report I have gone through our field notes and have tried to list the main behavior patterns for the Prairie Falcon in the wild, and have compared these with what we observed in the captive Prairies up to the time of egg-laying. I have done the same for the Peregrines, but since we did not have as much information on this species I have also relied on descriptions in “Der Wanderfalk” by Fischer (1968).

The behavior patterns described below and in Table 1 are listed in the order in which they were observed or described; however, each pattern does not necessarily follow in this exact sequence. In some instances several aspects may be ongoing at any one time with variation in intensity depending on the stage of the nesting cycle; for example, courtship feeding, nest display, mating, and male and female nest scraping may all be observed during the same day or series of days.
The observations described were made by Bob Gibbon, Keith Hodson, Tom Donald and myself, the majority of the observations of the captive birds being carried out by Tom Donald and of the wild Prairie Falcons by myself.

**Initial Indications of Breeding.** Initially, with both the captive Prairie Falcons and Peregrines, our first indication that something was going to happen was "cacking", or territorial behavior, by the male in the case of the Peregrines, by the female in the case of the Prairie Falcons. This occurred from a month and a half to two months before anything else and was the only early indication that something was happening. In the case of the Prairies, about one month later we heard our first "chupping" (February 26). (We do not describe it as "eechipping"; it is not the "eechip" of the Peregrine, but rather a "chup", an audibly different call.) By the middle of the next month everything had gone completely quiet with the Prairies, and as far as we could tell the birds were not paying any attention to one another. Then, very suddenly, we heard the chupping again (April 3), and we then saw what I describe as preliminary pair bond behavior.

**Table 1. Observed Courtship Behavior Patterns in Captive and Wild Prairie and Peregrine Falcons.**

<table>
<thead>
<tr>
<th></th>
<th>F. mexicanus</th>
<th>F. peregrinus</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>captive</td>
<td>wild</td>
</tr>
<tr>
<td>A. Attraction of mates</td>
<td></td>
<td></td>
</tr>
<tr>
<td>m. initially present on territory</td>
<td>na</td>
<td>X?</td>
</tr>
<tr>
<td>-prominent perching</td>
<td>na</td>
<td>X</td>
</tr>
<tr>
<td>-visiting potential nest sites</td>
<td>na</td>
<td>X</td>
</tr>
<tr>
<td>f. initially present on territory</td>
<td>na</td>
<td>X?</td>
</tr>
<tr>
<td>-prominent perching</td>
<td>na</td>
<td>X</td>
</tr>
<tr>
<td>-visiting potential nest sites</td>
<td>na</td>
<td>-</td>
</tr>
<tr>
<td>B. Establishing pair bond</td>
<td></td>
<td></td>
</tr>
<tr>
<td>pair remains on territory</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>aerial courtship</td>
<td>na</td>
<td>X</td>
</tr>
<tr>
<td>-mutual soaring</td>
<td>na</td>
<td>X</td>
</tr>
<tr>
<td>-courtship flight</td>
<td>na</td>
<td>X</td>
</tr>
<tr>
<td>-territorial delineation</td>
<td>na</td>
<td>X</td>
</tr>
<tr>
<td>cooperative hunting</td>
<td>na</td>
<td>-</td>
</tr>
<tr>
<td>mutual roosting</td>
<td></td>
<td></td>
</tr>
<tr>
<td>-in territory</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>-at nest ledge</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>m. visits potential nest sites</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>m. wailing</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>m. &amp; f. display at nest together (1)</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>m. tries to attract f. to nest by carrying food to nest ledge</td>
<td>X</td>
<td>X</td>
</tr>
</tbody>
</table>
F. *mexicanus*  
<table>
<thead>
<tr>
<th>captive</th>
<th>wild</th>
</tr>
</thead>
<tbody>
<tr>
<td>m. ledge display</td>
<td>X</td>
</tr>
<tr>
<td>f. remains on territory (2)</td>
<td>X</td>
</tr>
<tr>
<td>m. brings food to f. (courtship feeding)</td>
<td>X</td>
</tr>
<tr>
<td>m. &amp; f. feed on food together</td>
<td>X</td>
</tr>
<tr>
<td>familiarities (mutual preening, etc.)</td>
<td>X</td>
</tr>
</tbody>
</table>

**F. *peregrinus***  

<table>
<thead>
<tr>
<th>captive</th>
<th>wild</th>
</tr>
</thead>
</table>

<table>
<thead>
<tr>
<th>m.</th>
<th>f. remains on territory (2)</th>
<th>m. brings food to f. (courtship feeding)</th>
<th>m. &amp; f. feed on food together</th>
<th>familiarities (mutual preening, etc.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>X</td>
<td>X</td>
<td>X</td>
<td>-</td>
<td>X(F)</td>
</tr>
</tbody>
</table>

C. **Nesting preliminaries**

<table>
<thead>
<tr>
<th></th>
<th>F. <em>mexicanus</em></th>
<th>F. <em>peregrinus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>captive</td>
<td>wild</td>
</tr>
<tr>
<td>f. begging food with much wailing</td>
<td>?</td>
<td>X</td>
</tr>
<tr>
<td>m. begins making nest scrape</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>m. &amp; f. display at nest site (3)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>f. works on nest scrape</td>
<td>-</td>
<td>X</td>
</tr>
<tr>
<td>mating</td>
<td></td>
<td></td>
</tr>
<tr>
<td>- f. wails</td>
<td>X(faint)</td>
<td>X</td>
</tr>
<tr>
<td>- f. solicits by posturing</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>- following courtship feeding</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>- comes directly from ledge display</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>- following defense of territory</td>
<td>-</td>
<td>X</td>
</tr>
<tr>
<td>- no observed preliminaries</td>
<td>X</td>
<td>X</td>
</tr>
</tbody>
</table>

D. **Egg-laying**

<table>
<thead>
<tr>
<th></th>
<th>F. <em>mexicanus</em></th>
<th>F. <em>peregrinus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>captive</td>
<td>wild</td>
</tr>
<tr>
<td>f. dozing at length, appears sickly</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>first egg laid, f. shapes scrape</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>noticeably more aggressive</td>
<td>X</td>
<td>X</td>
</tr>
</tbody>
</table>

m. = male; f. = female
X = observed
- = not observed
na = not applicable
? = not clearly defined

(1) Preliminary pair bond behavior observed in Prairie Falcons.
(2) Female perching near nest site.
(3) Male and female ledge display in Peregrine Falcons.
(F) From Fischer’s “Der Wanderfalk.”

It is our hope that this table will serve as a rough guide to the behavior patterns which might be expected in Prairie and Peregrine Falcons. Without question, others will be able to add to the listed behavior patterns, and hopefully those with data on other species will also be able to compare their observations. It would seem useful for similar tables to be drawn up for other species, perhaps using the above as a base and merely adding or deleting behavior patterns where applicable.
PRAIRIE FALCONS

Preliminary Breeding Behavior. Preliminary behavior as described for the Prairie Falcon in the literature is listed as aerial courtship; however, other than limited mutual soaring, we have yet to see any aerial courtship in Prairie Falcons in the field. We have seen what we believe was described in the literature; however, it was not aerial courtship at all, but rather the interaction between two pairs fighting over a cliff site.

The preliminary breeding behavior that we did observe occurred early in the season as follows. A male and a female visited a series of nest ledges—the male going to the ledge first, then followed shortly by the female. At the ledge they would turn in a small circle, head down and side-by-side, both making the chupping sounds. It appeared that each was trying to force the other one off its feet by what appeared to be one trying to get its head underneath the other’s body to lift it up. This they repeated over and over again. In the wild I have seen this behavior only twice (Wayne Nelson has also observed something similar), and with our captive pair we observed this behavior on April 3rd and 4th and then it was all over. Its occurrence was early in the season, was very brief, and was something that could have been easily missed. I have not observed this behavior later in the breeding season and therefore describe it as preliminary pair bond behavior.

Male at the Ledge. The preliminary pair bond behavior seemed to initiate things and was followed by increased activity by the male at nest ledges. Initially males have been observed visiting two or more ledges, looking at them, making scrapes, apparently paying little or no attention to the female and seemingly satisfying himself with the ledges. We have observed this to some extent in our bird in captivity as well as in the wild.

Attracting the Female to the Ledge. Next, in general, the male tries to attract the female to the ledge of his choice by going to the ledge, displaying and calling to the female. This occurs very often in the early phases as over and over again the male goes to the ledge to display and he then comes out to look at the female, or simply stands, chups and then looks up at her. Very often he calls with his head actually face down.

Frequently, in the case of the Prairie Falcons, the males also apparently tried to attract the females to the nest by carrying food directly to the nest ledge, and this in turn signaled the onset of “courtship feeding.” The male would take the food to the ledge, get the female to come to him for food, and then take off, leaving her there. These two activities were observed in both captive and wild birds.

Food-transferring. In the wild the male Prairie brings food to his territory, following which the female runs or flies to him, wailing loudly and mantling as she comes. He then relinquishes the food to her when she grabs it, letting go with barely a struggle. However, in our captive pair the male at first would not
relinquish the food and for the most part hung onto it. Sometimes he would just stand there and eat, the female would approach, grab the food as well, and there would be a bit of a struggle. Usually they would end up eating it together, side by side.

Female at the Ledge. At this stage in the wild, occasionally the female would go to the nest ledge of her own accord. Although the male still tried to attract her there whenever she was elsewhere, as soon as she arrived he would take off and leave her, following which she would usually work on the scrape or perch beside the ledge.

In captivity we did not observe the female nest scraping in the early stages.

Wailing. I've mentioned how the female in the wild can be heard wailing. This is incessant, and if you were to visit an area where Prairies are courting you would be able to hear the wailing up to half a mile away whenever the female calls to the male for food or is wailing prior to copulation (copulation most often follows immediately after courtship feeding). In the captive situation we could hardly hear the female as her wailing, though continuous, was very, very faint. This may have been a result of the birds always being so close together in confinement.

Copulation. Mating begins several days to a month or more before egg-laying, and increases in frequency towards the laying of the eggs. (Captive Prairies first mating April 9, first egg April 15.) Usually mating took place in one of the following three sequences observed in both captive and wild situations.

1. Immediately after the male had fed the female and she had finished the meal, she would feak, put her head down and start to call (wailing) to him—he would then come directly to her.
2. The male would be at the nest ledge, the female sitting elsewhere. She would posture and call, and the male would come directly from the nest ledge.
3. Sometimes, with no preliminary that we could see other than the female bowing, the male would come directly to her and mate with her.

The most obvious behavior here was that the female literally postured (or so it appeared) any time the male flew towards or looked at her. I believe she initiated mating by the male in this way.

Often we saw the male simply look towards the female, and her head would go down, she would then posture, head down, wings out—and appeared to solicit the male to come. In the beginning he did not always come to mate, but as egg-laying approached, the mating increased in frequency. The most matings that we have observed in captivity was five times in a single day. In the wild the most that I have observed was three times in one hour. In Peregrines mating has been observed up to five times in one hour.

Lethargy near Egg-laying. Just before egg-laying there is a period when the females appear very sickly for several consecutive days at which time they just sit quietly with feathers puffed out. At this time the captive female was observ-
ed dozing on her perch, and whenever the male tried to attract her attention she appeared to ignore him as if past much of the sexual stimulus.

This was also very obvious in the wild and although I have not noticed the females ignoring the males, I have seen the females perch on cliffs for great periods of time, all the while looking very sickly. This is very obvious in both Prairie Falcons and Peregrines just prior to and during egg-laying.

Egg-laying and Aggression. It was apparent that after the first egg was laid, the captive birds became much more aggressive (Heinz Meng mentioned the increased aggression in his Peregrines before and during egg-laying, and it intensified after the eggs were laid). Our captive male Prairie previously was not aggressive, had always been shy, and was never very tame, therefore, in this case, the increased aggression was quite obvious. Usually aggression in the wild appears to intensify with egg-laying but is not as obvious or intense as observed in the captive birds.

Serious incubation did not start until the last egg, on April 21, with incubation following for 39 days (i.e. until the last egg hatched). We will discuss incubation periods in another panel, but I would suggest that you don't pay too much attention to some of the incubation periods that are listed in the literature for falcons or you could be in trouble.

Differences between Wild and Captive Birds. There were several things which we noticed were very different between the captive and wild birds in the last part of courtship, and in egg-laying. One activity that appeared to be normal to both captive and wild pairs was the male bringing food to the female, or bringing food to the ledge and the female coming for it. In the wild there seemed to be an obvious regularity to much of this behavior. The male would bring food within a set period of about an hour in the early morning, later in the morning, again in the afternoon, and so on. In the captive situation there seemed to be no regularity. Also in relation to incubation in the wild, male and female incubation periods appeared fairly well-regulated, but not in captivity, as our female Prairie simply didn't want to let the male have his turn at the nest for either incubation or brooding. Still another area of abnormal behavior appeared in courtship feeding, as mentioned, when the male was reluctant to give prey to the female. Later we observed the male feeding the female on the nest ledge, also the female feeding the male on the nest. I have seen nothing like this in the wild to date.

PEREGRINES

Early Activities. As mentioned, the first sign we had of behavioral change was "cacking" in our captive Peale's Peregrines—this was also the first indication that they were being territorial and that breeding behavior was beginning. This was followed by an extended period when the male would stand by the wire and wail (the "waaaik" call, which we have also heard very early in the season in the wild). For Peregrines, Fischer lists several preliminary courtship activities:
the attraction of a mate, mutual roosting, courtship flights, cooperative hunting, wailing, and the male moving from ledge to ledge. Some of these aspects we did see in preliminary courtship in our captive birds. We did not, however, observe mutual roosting at the ledge, and I personally have not yet observed this nor cooperative hunting in the wild.

**Attracting the Female to the Ledge.** Next in sequence is the activity of the male at the ledge, examining ledges and displaying, apparently trying to attract the female. Once again this seems to be very closely tied with courtship feeding. I have observed both captive and wild males carrying food to the nest ledge and the females coming to retrieve it from them. The male actually brings food to the ledge, apparently to attract the female there. Often, as with the Prairies, the male would go to the nest ledge and while bowed, call ("eechip") to the female, very obviously looking towards her, or alternately he would call, turn around, and then go out and apparently look to see if she was attracted. This seemed to be a very definite attempt to attract the female to the ledge and, again, was observed in both wild and captive situations.

**Nest-scraping.** In our captive *pealei* the male was the first of the pair observed to be making nest scrapes. In so doing he would go to the nest ledge, start bobbing, forming with his body, and foot scraping. (The same actions were used by the Prairies.) The female also made scrapes although generally a little later in the period when visiting the nest ledge.

**Copulation.** In the wild, we have observed copulation both following "courtship feeding" and following the male and female nest display on the nest ledge. In our captive birds we did not observe copulation, and this is apparently where the courtship broke down. Although lack of mating was perhaps partly the fault of the male, our observations suggest that it was primarily the fault of the female. In both captive and wild situations the male and female Peregrines shared in incubating and had regular changeovers. Also, both birds became aggressive at the onset of egg-laying.

**Pairing.** Our observations suggest that the preliminary courtship ritual with Prairies and Peregrines may occasionally be extremely short. At some sites we have had Prairie Falcons perching in pairs at cliffs throughout the winter and into the spring, at others lone males at the cliffs and at still others lone females. In the latter cases as soon as the mate arrives everything apparently is "go" suggesting that we have a situation in which we have long established pairs. (To some extent this has been confirmed by trapping and identifying the pairs several years in succession. Contrary to some of Jim Enderson's early findings in Colorado, we have found that our Prairies are staying with the same mates at the nest sites.)

To be more specific we have examples in which we have been watching an individual Prairie Falcon at a cliff for a week or more when suddenly a mate
arrives and the same day they have been observed copulating. There appears to be little or no preliminary activity in such cases.

Similarly with Peregrines, we watched a cliff for two weeks, on which the female was back first. Her mate from the previous year did not return, but a new male did, and, again, on the first day he was there they were observed mating. It is therefore not clear just how necessary some behavior patterns are, particularly the preliminary ones such as courtship flying.

Failure at Copulation. We feel there are several reasons why we did not get copulation in our captive Peregrines. One obvious observation was simply that our female Peregrine at no time solicited the male. On one occasion we did observe her bowing, but when the male came toward her there was no posturing. The male was observed on at least four occasions to attempt copulation, i.e. he tried to mate with the female; on only one occasion did we see her head go down, but that was all, and the male was not allowed to mate with her.

To further complicate matters the male apparently was afraid of the female (something that we found rather difficult to tell with certainty). Several times, for example, we observed that when the two were sitting close together, if the female turned toward the male he would immediately back off or fly. Also several times we observed him backing away from her when she approached. As a result of these and other observations we believe that the male was definitely afraid of the female. At no time did we observe familiarities (billing, preening, etc.) described by others for Peregrines and observed with our Prairies. All of which suggests our pair were not truly compatible.

These are some of the factors which we feel prevented copulation and prevented us from getting fertile eggs with the Peregrines, in contrast to the captive Prairies, which were compatible, mated, and from their first clutch raised four healthy young.

Blinds for Observing Behavior in Captivity. Initially it should be noted that with regard to our captive Peale's, because the female was laying eggs we believed that she was ready but the male was not. If we had not had the blind in no way we would have realized that the lack of fertilization may not have been the male's fault since we could not have assessed this without seeing what the birds were doing. The preliminary activities, vocalizing, and egg-laying apparently do not necessarily tell the whole story.

A blind allows you to see everything that is happening. With the Prairies we photographed and observed mating at about 12', and Tom actually watched the female laying the individual eggs. We therefore knew what was in the nest and what was happening at all times. Some of the activities occur so briefly that unless you can spend a considerable amount of time watching you may very well miss some of the important things. Nevertheless, with some record of sequence of behavior patterns it is possible to watch for and see the more important aspects.

If you establish a blind, don’t be too alarmed if at first you notice that your birds are a bit upset every time they hear you, because they probably will be, and may take a few days to adjust. However, after about a week they just seem
to forget about you. We found that we could talk and do almost whatever we wanted in the blind. However, watch cigarettes, lighted matches, cigarette lighters or flashlights in the blind because these bright lights can be seen through the mirrors. It is absolutely necessary to keep the inside of the blind at least twice as dark as the outside in order for the mirrors to function.

**Distractions.** In apparent contrast to the adjustments the birds make to sounds, we have noticed that the captive birds are easily distracted visually. With our Prairie Falcons, when they could see out of the building, any sudden movement would make them cease whatever they were doing. For this reason we covered one end of the building with fiberglass, and immediately activities proceeded without disturbance. Noises do not seem to bother the birds to the same extent, whereas we felt anything new visually was a very definite distraction to them.

**Disturbance, Desertion, and Damage to Eggs and Young through Visits and Gunshots.** My data from the field suggest that visits to eyries or the vicinity of eyries immediately prior to egg-laying or at about the time of the first or second egg may be very critical and the birds will readily desert. In contrast, once incubating, the falcons at least will take a considerable amount of human disturbance. (This appears to vary with individuals, and tolerance may be influenced by toxic chemical residues.)

Also in relation to disturbance, one aspect that we observed will be of importance to anyone working in the field. We noticed that if a person comes to an eyrie unobserved by the incubating bird, even while talking and making noise, the bird will remain tight on the scrape. This holds true most often with Peregrines, Prairies, and Golden Eagles, so that the incubating bird usually remains on the scrape until it actually sees the intruder. Even if one bird is flying around making a great racket, the other will usually sit tight, with the result that on sighting the intruder the incubating bird springs from the nest. Since in incubating eggs or brooding the small young, the adults work their feet under and between the eggs and/or chicks, when startled off, these may be thrown up to four feet from the scrape. We have observed and photographed the results, and actually have pictures of eggs and chicks three to four feet out in front of the scrape. We have also come to a cliff and have seen a chick go down to its death just because the brooding bird was startled, even though there was talking and noise from above to warn the adult. I suggest that anything which startles the bird on the nest with eggs or small downy young is actually endangering those eggs or chicks. As mentioned, the eggs and small chicks apparently are resting on top of the adult’s toes and tarsus, and may be flung out as the adult flushes. If the ledge is wide enough, and not of jagged material, this may not be too serious since the falcons can roll the egg back, or they will go as far as three and four feet and pick up even a day old chick and carry it back. Nevertheless the danger is a very real one, and I have recorded the results over and over again.

On the brighter side, we have also been able to observe the results when one approaches directly so that the birds can see you coming. First they sit up to
look at you, then raise, and finally stand. They, therefore, are able to leave the
nest when they want to, not when they have been startled.

For people doing surveys I suggest this is a very real concern. If you are firing
guns at cliffs, or if you are going to the tops of cliffs and looking over, when
there are eggs or small young, you are risking the possibility of cutting down
production by one or more, depending on how often it happens. We have re-
corded these results, and I mention them because it was a real shock when we
realized just how frequently this occurred.

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IMPRINTING, AND OTHER BEHAVIORAL CONSIDERATIONS
by Wayne Nelson

Introduction. The discussions of imprinting at this conference were, to this
observer, among the most important. Many of the egg-infertility problems may
be solvable by carefully considering that aspect of behavior. I will attempt to
throw some more light on imprinting and its problems at the end of this section.

This report is not a written account of my presentation to the conference;
rather, it is an attempt to synthesize and evaluate some of the discussions and
some of the questions which arose and which were concerned with the behavior
prior to and during egg-laying.

(An outline of courtship behavior in Peregrines (pealei) in the wild was pre-
sented to the conference, with 35 mm slides and 16 mm film. From this it is
hoped that the audience received a "feel" for the type of behavior patterns
which normally lead up to egg-laying in the coastal Peregrines.)

Based upon the courtship behavior seen in wild Peregrines, a discussion and
a number of suggestions for captivity breeding have been presented (Raptor Re-
search News, March-April 1971). That article considered a variety of factors
which appeared to be of importance to captivity breeding—e.g. spacious ledges
of a variety of types; one-way glass for viewing undisturbed behavior; avoidance
of disturbance; necessity of water at laying and hatching. Several further points
must be added to that article’s discussion.

Some Behavioral Considerations. 1. Aggression. Heinz Meng described at this
conference how he “encouraged” his tiercel Peregrine to “defend” the breeding
chamber. Dr. Meng would run, crouching, past the chamber, and the tiercel
would chase along the ledge inside the windows of the chamber. (This pair of
Peregrines was given food through the windows of their building.) This situation
is very similar to what sometimes occurs in the wild coastal Peregrines; prior to
egg-laying one or both adult falcons sometimes, for no apparent reason, sudden-
ly will fly up to a quarter mile from their cliff to harass viciously a perched Bald Eagle. It may well be, as Dr. Meng suggested, that stimulating aggression (NOT fear) may increase the pair-bonding of these birds—in captivity and in the wild.

2. Disturbance. There is a very definite difference between aggression and fear, between the response of a bird to a distant intruder and to an intruder which is at or in the eyrie. At the conference a number of interesting observations were reported.

(a) R. Fyfe described how captive Prairie Falcons (being watched from a blind) ceased their courtship activities when human beings or other animals were in view in the yard outside the breeding quarters; a translucent divider, obstructing the view of outside activities, allowed the birds sufficient privacy that their activities were not subsequently interrupted. These birds and others became very accustomed to sounds in the nearby area and from the blinds from which the birds were being watched.

(b) Maj. R. Graham told how a captive Peregrine laid a clutch (which was removed), then recycled. At the time when the second clutch was expected, the falcon’s abdomen distended somewhat, indicating that the first egg of the second clutch was soon to be forthcoming. He felt that his visits to the nest ledge, several times per day, prevented the falcon from laying that egg (and the second clutch), and that it had been absorbed.

(c) G. Galicz noted one instance in which his Peregrines’ breeding quarters was visited on one day—on the same or the following day an egg with no shell was laid. He suggested that the disturbance of the visit might have caused the production of the abnormal egg.

In view of these and other observations, it would seem wise to avoid entering the breeding quarters occupied by a defensive (territorial) pair, especially just prior to and during the laying of a clutch. Other means are available for checking on egg-laying.

3. Food-transferring and Diet. A plentiful supply of food appears necessary for egg production. In a variety of raptor species it has been observed that the males usually eat the heads of prey items before giving the food to the female or nestlings (Osprey—Ames 1966; Cooper’s Hawk—N. and H. Snyder, this conference; European Sparrowhawk—Herren 1970; Peregrines—Nelson 1971; and others). While the reason for this is not yet obvious, it appears to be of some importance—and it suggests that we might be wise to avoid giving our captive birds such unnatural diets as strictly or largely heads and necks. It is possible that extra-thick eggshells are resulting from diets heavily laden with calcium (bone), and that a few instances of nestlings dying upon hatching may be due to difficulties in breaking out of very strong eggshells.

4. Vocal Stimulation from Nearby Pairs. From the behavior and laying dates of wild Peregrines I have found no suggestion that the sounds (or other activities) of one pair either stimulates or inhibits the breeding of nearby pairs.
5. **Lighting.** There is some suggestion that clutches laid in the late spring or early summer may be due to relatively poor lighting within the breeding quarters. Some pairs which lay infertile first clutches (followed by fertile second clutches), and some pairs which refuse to come into any breeding condition, may be doing so because of various degrees of inadequate light stimulation (see Koehler 1969). Observations of the behavior of such late-laying or non-laying or infertile clutch pairs could indicate what their difficulties are—and observations made on them when brighter lighting is provided should give additional suggestions as to why these birds are behaving abnormally.

6. **Photoperiod.** Numerous writers in *Raptor Research News* and elsewhere have indicated the importance of long daylength and changing daylength upon captive raptors. The general lack of courtship behavior reported for tundra Peregrines (and Gyrfalcons) is obvious (see BPIE reports). One means of stimulating courtship (and egg-laying) in these birds, that apparently has not yet been attempted seriously, is that of giving the captive northern birds a photoperiod regime which follows as closely as possible the changes which the birds in the wild would receive—not simply giving them a long day-length only in the spring and summer, but giving them a changing photoperiod which judiciously duplicates that which the birds are seeing in the wild. This method must be tested, since all other methods appear to be failing with these northern birds. I hope to be able to expand on these thoughts at a later date.

7. **The Variety of Repertoires.** It seems fairly safe to say that no two pairs of birds will necessarily behave in an identical manner. Variations in behavior, leading to the same results, need not be considered as signs of gross abnormality. Fyfe (this conference) noted a number of similarities and differences between the behavior of wild and captive Prairie Falcons; in general the results were the same—e.g. in captivity the male may hang onto the food when he brings it to the female, but she gets food from it whether he gives it to her or whether they feed from it together; both male and female may incubate, side by side, but the eggs get incubated.

Also, it should be remembered that the birds may have to "learn" how to carry out some of the more intricate behavior patterns—e.g. they may have to "practice" a number of times before being able to complete copulation; the first feeding of the nestlings may be very clumsily carried out by the female. Don’t panic if the birds do not do something correctly or perfectly the first time you see it.

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**IMPRINTING AND CAPTIVITY BREEDING**

by Wayne Nelson

**Introduction.** To this writer, one of the most potentially useful concepts to fall into place at this conference concerned the imprinting of captive breeding stock. For the most part in the following discussion I will be considering the
larger falcons, but many of these observations and suggestions undoubtedly are applicable to other species. (I must thank Butch Olendorff for providing me with the initial stimulus which has brought the following thoughts and observations to the surface in my mind. While little of the following discussion is original information, the way it all fits together does fall into the category of—"How foolish of me not to have thought of that long ago." Because many captive breeders have not apparently seen the problem in this way, I am going to treat it in some depth.)

**Two Types of Captive Birds.** By observing the courtship behavior of the captive birds we should be able to recognize two types of birds:

1. those birds which are imprinted to their own species, and
2. those birds which are imprinted to human beings.

The former type, if given reasonable facilities, minimum disturbance, adequate lighting and photoperiod, etc., should be capable of breeding on their own. The latter type (imprinted to human beings) will possibly never "revert," never complete a courtship phase with a natural mate, and never produce a fertile clutch; they are probably good for only one thing—artificial insemination reproduction—and they should be very good for that. There may be some gradation between these two types, and there may be some reversibility of the imprinting in either direction. I would guess that the majority of the captive birds taken as eyasses fall into the latter category—imprinted to human beings.

From a hurried review of some animal behavior literature, it appears that little is known about imprinting in birds of prey. Konrad Lorenz (1937:263) noted:

"Heinroth failed to breed hand-reared Great Horned Owls, Ravens and other birds, for no other reason than that these tame individuals responded sexually to their keepers instead of to each other. In a very few cases known, the bird whose sexual reactions were thus directed toward man, finally accepted a fellow-member of the species which, however, was always regarded as a rather poor substitute for the beloved human and was instantly abandoned whenever the latter appeared."

Mendelssohn and Marder (1970), in discussing captivity breeding problems, pointed out:

"One of the reasons for lack of success may be that one or both partners may be imprinted on humans. Many birds of prey kept in captivity have been taken from the nest as young nestlings and been hand-reared. If they are reared without the company of conspecifics, they will, if young enough, develop imprinting on humans; the human companion will be accepted at first as a parent companion, later as a social companion and eventually as a sex companion (Lorenz, 1935). A bird may remain imprinted for many years or even for life. Young owls may become imprinted on humans until a relatively late age, since with these species identification of the companion seems to be visual, and visual
acuity develops in owls only after their intermediate plumage has grown.

Sometimes even rearing owls together with conspecifics does not prevent their becoming imprinted on the human foster parent (Heinroth and Heinroth, 1926)."

Age of Imprinting. Most readers are probably aware that at a very tender age (hours) ducklings, geese, chickens, etc., will fixate onto nearby moving objects (sometimes the appropriate sounds must be given, also) and exhibit the "following response" (a form of imprinting) in which the object—person, wagon, mother bird, etc.—is followed and treated as the mother bird. In birds which are not mobile soon after hatching, and which may even be blind for some days, the imprinting process does not occur until a later date in the nestling's life.

In the birds of prey it apparently is not yet clear exactly when the critical period occurs, when the young birds acquire the "image" of their species, their parent, and the features of their future sexual partner. There are some good hints as to when this occurs, however.

McElroy (1971, and various Hawk Chalk articles) has described behavioral differences between the "imprint" and the "brancher" in Cooper's Hawks trained for falconry. The "imprints", taken from the nest at about 18 days or less remained relatively tame, whereas branchers (fairly well feathered, quite mobile but not quite flying) never became very tame and were almost as difficult to train as wild-caught passage (migrant young) or adult Cooper's Hawks. In general terms, with some adjusting due to differences in the rates of development, this situation probably applies throughout the raptors.

In the Blond Ring Dove (Streptopelia risoria), Klinghammer and Hess (1964) conducted experiments to try to discover when the critical period for imprinting occurred. These doves first fly at about 14 days of age, and are fed by the parents until at least 21 days of age. They were tested when about 10 months old to see whether they would choose another dove or a person as a mate, after having been reared under a variety of conditions (naturally by the parents, hand-reared and isolated, etc.). The optimum imprinting (to people) was found to occur when the young doves were taken from the nest and reared by people at 7-9 days of age. If taken when somewhat younger, the doves were slightly less predictable in their choosing between a human and a dove for a mate. If taken when older than nine days, the doves usually chose another dove instead of a person. In isolated doves, which saw no other doves and saw only a man at feeding time and when pens were cleaned, the imprinting to people was more likely to occur. Some doves, even having been imprinted during infancy to their natural parents, did show some imprinting to people due to association (admittedly brief) through their life in isolation. This study of imprinting in doves may be the closest thing with which comparisons can be made with raptors. If the general situation of imprinting in doves sounds at all similar to some captive breeding attempts with raptors, I do not think it is coincidental. Indeed, it seems probable that many or most of the captive breeding stock, which we are trying to get to breed with a mate of their own species, are actually imprinted to human beings.
Some Successful Breeding Attempts. Following from the suggestions seen in the above information, does it seem entirely coincidental that:

1. Renz Waller's twice successful Peregrines (1942 and 1943) involved a female of unstated age and origin and a wild-caught adult male? (Waller, 1968.)

2. Philip Shultz's haggard pair of Prairies laid eggs in 1971 (one clutch of four, infertile however)? (Shultz, BPIE 35, Raptor Research 6:31-35.)

3. Richard Fyfe's successfully breeding Prairies (first clutch in 1971 hatched all four eggs) were taken from the wild as "five week old eyas" (male) and "four or five week old eyas" (female))? (Fyfe, BPIE 36, Raptor Research 6:35-36.)

4. Heinz Meng's successfully breeding Peregrines (pealei) (second clutch in 1971 hatched all four eggs) were taken from the wild when "they were almost branchers"? (Meng, BPIE 30, Raptor Research 6:25-28.) (Emphasis is mine.)

The ages of capture of Beebe's (1967) Peregrines (fertile eggs, 1967), Schramm's successful Peregrines (Peterson 1968), and Kendall's (1968) and Enderson's (1971) successful Prairies were not specifically stated in their reports.

Some Apparent Contradictions. In American Kestrels it has been shown in several instances that some hand-reared eyasses (even reared from eggs) eventually pair with their own species (Koehler 1969, Porter and Wiemeyer 1970). Porter and Wiemeyer (1970) mention some deaths of male kestrels which were caused by their female partners, but the histories (backgrounds) of those birds were not specifically stated.

The Captive Imprint. There are two situations in which "imprints" are found in captivity. The first situation involves imprinted birds which we do not realize are imprints because they are in a paired captive breeding effort. The second involves birds which in general are held singly, and which show signs (sometimes) of broodiness and probably courtship toward man, especially in spring. (Throughout these discussions I am using the terms "imprint" and "imprinting" rather loosely, mainly because I have been unable to find an adequate definition for these terms as they apply to altricial birds.)

1. The Imprint in a Pair. Probably most eyass-taken falcons (of the large species, at least) in captive breeding projects fall into this category. The two sexes probably show little interest in each other; the female probably dominates at feeding time. They both may become breedy, noisy, and very defensive in the spring, and infertile clutches (even after recycling once or twice) are the only result. They make good foster-parents as a rule.

Their apparent compatibility, their sharing of defense, incubation, and foster parent activities, and their disrespect toward human intruders in their room—all this does not tell you that they are paired, and it does not tell you that they are not imprinted to human beings. In fact, if the female does lay eggs, it tells you
that (a) your conditions are extremely close to producing fertile eggs, or, more likely, (b) your conditions are reasonably conducive to reproduction, but those birds are indeed imprinted to people and not to their own species.

**a. An apparent example of an imprint in a pair.** By watching the birds (see below for methods) during the courtship phase you should be able to determine if the pair has formed a pair-bond and is in fact *cooperating* in their activities.

Fyfe’s observations of the point of pair break-down in his Peregrines are very significant (Fyfe, BPIE 38, *Raptor Research* 6:38-39, and this panel report). This pair in 1971 showed most of the expected courtship activities. But, at the point several weeks prior to egg-laying when copulations should have begun, this pair failed; the female failed to respond to the approaching male. Had she responded to the stimulus “Approaching Male Peregrine,” she would have bent forward into the copulatory posture. The male would then have been able to alight on her back, and copulation could have been completed. This female laid eggs—obviously she was sufficiently stimulated by the other features of the captive environment, and she even recycled when the first clutch was removed. She was sufficiently stimulated for egg-laying to occur—but the male apparently was the *wrong* stimulus for the final and most essential behavior pattern—copulation.

**b. Possible solutions to the problem of imprints in pairs.** Assuming that the captive breeder desires progeny from his birds, and assuming that he has spent some time watching his birds and has seen no sign of copulation nor any sign that it might occur, what should he do?

(1) The arrival of the first egg is probably the first positive sign that we can react to. At that point, entering into the breeding room (perhaps at night), capturing the birds, and utilizing (rough) artificial insemination (A.I.) methods may be the only means of acquiring some fertile eggs in the first clutch. (In other words, one should have practiced A.I. beforehand to be prepared.) Handling of the female (with a partially-formed second egg within) would have to be carefully done. Candling of eggs at about 10 days of incubation should show whether or not fertility was achieved.

(2) The breeder could observe the behavior of the pair through the laying of the first clutch, and positively discover whether copulations were occurring, whether the male was just a few weeks slow (e.g. due to insufficient light stimulation), whether the female was not responding to his approaches, or whether he was not responding to her solicitations. Candling of the first clutch after about 10 days of incubation should confirm the infertility of the eggs, and removal of eggs should cause the birds to recycle.

This may be a very appropriate way of *synchronizing* the pair—causing them both to incubate for a spell, and develop the appropriate hormonal and behavioral responses, then stealing the eggs so that they both start from that point into the processes toward egg-laying and sperm production. Recycling could be expected to take about two weeks. (When recycling, one should be certain the female has an adequate diet and a supply of clean fresh water at all times.)

At about the 12th day after the first clutch was taken (this length of time appears to be fairly variable), if she is going to recycle, the female should again
enter into "egg-laying lethargy." Again, by observing over a number of hours
(read a book behind your one-way glass if things are not too active in the bird-
room), the person should attempt to confirm that the pair is indeed incompat-
ible, that copulation is not occurring. At this point, or immediately after the
first egg is laid, A.I. methods could be imposed upon the birds, to attempt to
obtain fertile eggs in the second clutch.

(3) A possible (but considered unlikely) long-term solution might involve at-
ttempting to leave the two imprinted birds entirely isolated from people for a
long period of time, feeding and wateriring them via trap doors, or in absolute
darkness. There is a possibility that, lacking any reinforcement of the imprint-
ing to people (that is, no person presenting food, etc.), the birds might "revert"
back, might successfully mate with the other bird in the enclosure. Aside from
a small number of instances with kestrels, there does not seem to be much sug-
gestion that such reversion will occur in other species.

2. The Imprint as a Companion = the Human Being as a Bird’s Mate. This
method appears to offer the best means whereby the imprints can be brought
into productivity. It takes some time, effort, and devotion to the cause—but
these are some of the usual characteristics of the people involved with captivity
breeding.

Apparently this method has not yet been seriously attempted with the fal-
cons. Olendorff’s comments on the Behavior Panel of this conference certainly
apply at this point.

This method has been very seriously attempted for several years, with some
Berry got fertile eggs from his Goshawk by this method. In 1971 Stan Temple
got fertile Red-tail eggs, and Bob Berry was completely successful with this
method, getting three full-grown youngsters from his Goshawk “pair.”

By pairing the imprint with a human being over a period of time (manning,
handling, etc.), and by manipulating photoperiod, nest or ledge materials, food
availability—the human mate should be quite capable of synchronizing the po-
tential breeders, which, of course, should be very definitely separated, lest they
kill each other fighting over possession of the shared human mate.

The A.I. involved actually has two possible techniques: (a) massage = rough
A.I. (also required for the imprints which are in pairs and are fairly wild), and
(b) cooperative technique—in which the bird attempts copulation with the hu-
man mate, and semen is cooperatively received from the male and shortly after-
wards transferred via syringe to the copulating female. Various degrees of grada-
tion between these two methods are possible and sometimes necessary (e.g. with
eagles)! We certainly look forward to detailed reports on the recent progress
with this most promising method.

Prolonging fertility for A.I. One behavioral aspect mentioned above merits
repeating in this slightly different context—this concerns the means of prolong-
ing semen production in the imprint male. To get the female to again produce
eggs we simply have to remove her clutch relatively early in incubation (if taken
late in incubation, the recycling period may be longer and less likely to occur).
The length of time the male bird of prey is actually producing semen is not known to this writer. It may be only a matter of several weeks or less. If the first (presumably fertile) A.I. clutch is to be removed to an artificial incubator in order to obtain a second clutch, by that time the male may have “dried up” as far as semen production is concerned. He may still be copulating with the human mate, but his semen production may have ceased (we definitely need some more information on this aspect of A.I. with raptors). And, in fact, the male may have been somewhat out of phase with the female (either ahead of, or behind her) for successful A.I. of the first clutch with his semen.

Synchronization of the separated pair might be brought about through causing the female to incubate her first clutch for 10-14 days—and getting the male also to incubate at this same time. The male might require some preliminary courtship and nestbuilding play activities with the human mate, but he should be motivated and prepared to incubate if he is provided with a nest and nest materials just prior to when the female begins laying. When she has begun laying the male could be provided with eggs for his nest (perhaps chicken eggs, tinted to roughly match his species’ egg color). Once the female is laying, the need for his semen diminishes. With eggs in his nest and perhaps with some help from the human mate, he should begin incubating those eggs, just as the female incubates the ones she has been laying. With both sexes incubating at the same time, presumably they will be rather closely synchronized, hormonally and behaviorally, even if they were out of phase prior to egg-laying. After both have been incubating 10-14 days (this would allow candling of the female’s clutch, and would allow both to become firm incubators), by taking away the eggs from the male and the female (perhaps from the male a day or two earlier), it might then be possible to have the pair perfectly synchronized in egg and semen production, so that in the second time around the human intermediary could ensure successful A.I. of the second clutch.

Another possibility exists for those birds which are held under artificial light. This method involves simply finding and keeping the birds at the photoperiod at which they produce eggs and semen. These methods are used to some extent with domestic poultry (I have not checked into the details with poultry). In Slate-colored Juncos (Junco hyemalis) trapped in Illinois on migration, Wolfson (1959) found that a day of 12 hours light—12 hours dark prolonged testis activity for about nine months. Schwab (1970), with European Starlings (Sturnus vulgaris) from California, prolonged sperm production in these birds for over 15 months by keeping them at either 10.5 hours light—13.5 hours dark or 11 light—13 dark. He found that 12 light—12 dark did not cause those starlings to continue sperm production for a long period of time. In natural conditions in California the starlings produce sperm for perhaps three months.

With raptors from various latitudes, of course the day-night ratio would have to be modified slightly to keep the birds producing semen and eggs. This method holds considerable promise for producing multiple successful A.I. broods per season. Until we know more about the effects on the birds of such prolonged stimulation, it might be very wise to give the birds some months each year in which they are not subjected to the demands of the breeding season.
The Captive "Non-imprint." When a pair of birds has been taken from their parents late in nestling life, beyond the major imprinting period, their chances for successful captivity breeding should appear to be very great—provided that (1) the pair is given appropriate and sufficient stimuli in their quarters, and (2) they are not imprinted to human beings through frequent or constant association such as at feeding times (remember that imprinting may not be confined solely to the "critical period" of nestling life, but may also occur by "association" through life). The same general situation may hold true for passage and haggard birds, in which cases the minimizing of disturbances may be extremely important.

Knowing the histories of the pair should give the person a good idea of whether the birds are imprints or not.

Candling of the first clutches of such birds (any breeding birds) for fertility is essential, unless successful copulations of the pair have been positively observed. If first clutches are infertile, the birds should be forced to recycle if at all possible, so that by the arrival of the second clutch (or third) the male might be sufficiently stimulated by the external environment that he might do his part. This allows the observer more time in one season in which to determine whether the behavior of his pair is appropriate, whether they are indeed "non-imprints."

Caution. Some care must be taken so that misinterpretations of the efforts of the breeding pair do not occur in the human mind. There is a definite likelihood that if the lighting is insufficient, the female will be farther advanced than the male, that copulations will not be seen until near the second or third (?) clutch—until the male becomes sufficiently stimulated or becomes synchronized with the female (see Koehler 1969). Some caution must be exerted here, so that the "case" is not incorrectly "diagnosed"—so that a case in which the male is insufficiently stimulated (e.g. by poor lighting) is not incorrectly diagnosed as being a case in which the male is imprinted to people. To avoid making such a mistake, and blundering into the breeding quarters during the laying of the first clutch to attempt A.I. at that point, it would seem wisest to watch closely the birds' behavior through the laying of the first clutch, and through the first 10 days or so of incubation, then steal the clutch and watch their behavior as the second clutch nears its time of laying—to learn positively whether the pair is in fact cooperating in their activities, to learn whether copulations are occurring or are being attempted.

Foster-parent Problems. Too little experimentation appears to have been done to date to be certain of the effects of foster-rearing on potential captive breeding birds. What good is a Prairie Falcon for captive breeding if the bird was reared by, and is imprinted to a Goshawk? It might be wise to use rough A.I. in such situations, but the problem would be less difficult if the Prairie had never imprinted to another bird species but had imprinted to man instead—or better yet, to Prairie Falcons. And think of the poor bird if it should ever be lost into the wild—trying to court a wild Goshawk! Foster-rearing by a different bird species may well create more problems by imprinting than it will solve. The scientific literature concerning imprinting in waterfowl illustrates some interesting
examples of similarly very confused birds.

Watching the Captive Birds. It is obvious from the foregoing that a number of problems in captivity breeding are solvable if the behavior of the birds is observed in the courtship phase. In the larger species at least, it is unlikely that the birds will be seen to do much of anything if the human observer is at all obvious (even through small peepholes) and within any reasonable distance. The courting birds seem to be rather shy.

How to watch. One-way glass (two-way mirror) is the obvious answer to this problem. While there was some criticism of one-way glass at the conference, it definitely has been shown by a number of people to be very useful (with wild and captive birds), as long as (1) the glass is aimed in such a way that the birds cannot see their reflections in it, and (2) the person is on the darker side (it should be almost twice as bright on the birds’ side—otherwise they may see you through the glass). Richard Fyfe has mentioned seeing a lighted match and a glowing cigarette through a “mirror” in a store. Presumably birds could be distracted temporarily by such activities behind the one-way glass.

At first the observations from behind the viewing port should not be very regular if there is any chance that the birds can hear the person there, or when arriving or leaving; the first visits should be irregular and of varying lengths so that the birds are unable to establish any regularity of sounds outside the enclosure. Ideally, they should be accustomed to sounds from the nearby area so that they pay no attention whatsoever to them. The quiet sounds of a radio, on and off during the day at various times during the year may condition the birds to expect any type of sound at any time from outside their breeding quarters. In this way, the sounds made by the watcher would in no way inhibit the birds from carrying out their normal daily activities and courtship activities.

What to look for in the pair. The various behavior patterns—or the lack of them—are the keys to solving the imprint—non-imprint problem. Of special interest should be those behavior patterns associated with the nest. Which bird does the building or nest-scraping? Which spends time perched at the nest? Do they perch close by one another? Which dominates at feeding? Does the male take food to the female? Do they attempt copulation?

In some species we now have at least an outline of what behavior patterns can be expected and in roughly what order they might be expected to occur. Among the outlines of courtship behavior which we have at present are those of the kestrel (e.g. Olendorff 1968), Prairie Falcon (Fyfe, this conference), Peregrine (e.g. Nelson 1971), Golden Eagle imprints (Hamerstrom 1970), Goshawk imprints (Berry 1968, 1970, this conference), and others. And certainly there are a great many clues and observations scattered through many of the BPIE reports and Raptor Research News articles for those who will reread them.

As our knowledge of raptor behavior increases, we will inevitably be able to shed light on more of the problems in captivity breeding. The assistance of all of the people involved with captivity breeding projects, in making a few notes a day on the undisturbed behavior of their birds, would undoubtedly be very helpful in the future in solving problems which we cannot yet see.
Summary and Conclusions—Imprinting. 1. Probably most eyass-taken raptors are imprinted to human beings; possibly some passage- and haggard-taken birds are also imprinted to people due to frequent association with man.

2. It seems to be very unlikely that an imprinted bird in a pair will ever breed with its feathered companion; the imprints consider human beings as "their species", and only human beings are likely to be considered as potential mates.

3. The age at which imprinting occurs in a nestling raptor is apparently not yet known; some evidence suggests that the critical period extends to ¾ of the fledging (flying) age; pealei fly at 41-43 days of age—imprinting might be expected to occur in this subspecies up to 30-34 days of age, the point when the nestlings are really beginning to feather out all over.

4. By observing the undisturbed behavior of a captive pair during the period of time prior to egg-laying, the behavior patterns should tell the observer whether the birds are imprinted to their own species (i.e. they are attempting to cooperate in their breeding efforts), or whether they are imprinted to man (i.e. they are ignoring each other, or refusing to complete the courtship and mating behavior with each other, and generally appear to be attempting to breed separately).

5. The behavior patterns which will provide the best clues for solving the imprint-or-non-imprint problem will be those concerned with the nest, food (sharing), and especially copulation.

6. Several possible solutions to the problem of imprints in pairs are discussed: (1) rough A.I. in the first laying; (2) (best short-term solution) rough A.I. just prior to, or during, laying of second clutch; (3) (least likely to succeed) leaving the pair together in total isolation for a long time (years), hoping that they might revert, or lose the imprinting to man, and mate with their feathered companion.

7. A.I. appears to be the only means whereby imprints will be brought to breed successfully. The cooperative A.I. technique with tame and manned birds appears to offer the best opportunities.

8. Some caution must be employed so that some non-imprints (which are insufficiently stimulated by a poor captive environment) are not incorrectly classified as imprints; behavioral clues are suggested.

9. Rearing birds with foster parents of another species may cause many difficulties due to the nestlings probably imprinting to the species of the foster parents, rather than to man or their own species.

10. It will be by watching the undisturbed behavior of the captive pairs that we will really begin to understand what their problems are, and why some of them are not breeding in captivity.

References


APPENDIX: USING CLOSED CIRCUIT TELEVISION FOR THE OBSERVATION OF RAPTORS IN CAPTIVITY BREEDING PROJECTS
by J. Gregory Thomas

The use of closed circuit television for observation purposes in a captivity breeding project can yield several substantial benefits to the researcher. First, the quality of the observation can frequently be enhanced. The silent video camera will not annoy or otherwise disturb the subjects of the observation. Hence, observed behavior should be more truly reflective of the raptors' reactions to each other and to their physical surroundings. Possibly, the researcher would then have the information needed to alter pairing of the raptors or to make a change in some physical parameter of the experiment that would lead to both breeding success and a better understanding of why or why not success was achieved. Second, with the addition of video tape recording equipment, the amount of observation the researcher could reasonably be expected to do can be greatly increased. In the terms of the statisticians, the "sample size" has been enlarged. This should help to improve the accuracy of conclusions drawn from the observations. Third, another important benefit comes with the use of video tape recorders. Observations can be saved and stored for later reflection and study. Also, the observations may be shared with other researchers. This would give a heretofor unknown depth to communication between researchers. It might also aid in preventing costly and time consuming "reinventing of the wheel." A more detailed discussion of the costs, techniques involved, and benefits to be derived follows this introduction. Systems and accessories both simple and complex will be included.

Preliminary Remarks. Most video equipment within a reasonable price range is of Japanese manufacture. Experience in selling and servicing such equipment has led the author to believe that it provides good to excellent results for a relatively small outlay of money. It is used extensively throughout educational institutions and in the business community. Therefore, it is sometimes possible to pick up good used equipment at only a fraction of the original cost. The key to getting a good buy in new or used equipment is to have access to a quality video dealer who can both advise on hardware selection and service it. Between five and ten percent of the initial investment on any video gear should be allowed for maintenance each year. Because of cost considerations, only black and white systems will be considered in this paper.

Briefly, other considerations that should not be overlooked include the following. Cable runs between cameras and display and/or recording gear shouldn't exceed one thousand feet. Longer distances often require the use of expensive line amplifiers. The general physical environment of the camera should be dry and have temperatures not below 32 degrees F or above 100 degrees F. Deviations from this will usually require the use of special environmental enclosures. Because of the high light levels used in most breeding chambers, light is rarely a problem. However, subjects should be frontlighted, and the camera can not look directly at very bright light sources without damage to itself. Theft preven-
tion should also be part of over-all system plans.

**Single Camera Systems.** The simplest system consists of one camera, wall or ceiling mounted, connected to one monitor. The least expensive setup of this kind involves using an existing TV receiver as the monitor. Most cameras have what is called an RF output signal as well as a pure video signal. The RF signal is adjustable for a range of channels usually running from Channel 2 through Channel 6. The coaxial cable from the camera is terminated with an impedance matching transformer which in turn is connected to the VHF antenna terminals of the TV set. The picture being transmitted by the camera will appear on the TV set when it is turned to the proper channel. This system can be had for $300 or less, if one already has a TV to use as the RF monitor. If it is not desirable or practical to use a home set in this manner, a separate video monitor should be purchased. The video monitor makes use of the video output of the camera, and it generally will have a sharper picture than the RF receiver. Complete systems that include a camera, monitor, cable, and in some cases even an intercom cost $400 and up. Caution should be exercised when considering the lowest priced systems. Picture quality and system reliability sometimes leave a lot to be desired. All in all such simple systems should greatly increase the ease and amount of observation the raptors receive.

**Multiple Camera Systems.** For more complete coverage of a breeding enclosure, or the observation of more than one enclosure, more than one camera may be needed. Each camera may have its own monitor, or a multiple-input-single-output switcher may be used to display the desired camera output on a single monitor. More details on switchers will be found in the section on camera accessories. The use of more than one camera per enclosure would likely involve using one camera with a wide angle lens for observation of general activity, and a second camera with a telephoto lens for detailed observation of the nesting site.

**Camera Accessories.** There are many camera accessories available that will greatly extend the usefulness of any video camera.

*Lenses.* Lenses come in a variety of forms. Wide angle lenses give a large field of view with little detail. Telephoto lenses give a close, detailed view of a small area. A zoom lens allows the user to adjust over the whole range, from wide angle to telephoto. Fixed focal length lenses usually cost less than $100. Manual zoom lenses start around $200, and remote controlled zoom lenses start at about $900. Special lenses for use in very low light levels run between $200 and $350. Lens choice is important since it plays a large part in what the observer will see.

*Scanners.* Scanners are devices that allow the camera to pan back and forth over the scene. They may be either automatic or remotely controlled to allow for stopping the camera on a particular part of the scene. Thus, a lens that is more telephoto than wide angle in nature may be used without losing the ability to see the whole scene. Automatic scanners run $125, and remote controlled
ones around $250.

*Pan and tilt devices.* Pan and tilt devices permit both horizontal and vertical positioning of the camera from a remote location. They cost between $700 and $1000. Coupled with a remote controlled zoom lens, this is the ultimate in control the researcher may have in choosing the scene to be observed.

*Environmental enclosures.* Temperature extremes or exposure to the elements requires placing the camera in an environmental enclosure, which costs around $200 with a heater and blower.

*Switchers.* Switchers for routing video signals to monitors or video tape recorders may be simple, inexpensive ($50 or less) push button devices, or sophisticated sequential electronic switchers costing $300 or more. The simple switcher will suffice in many cases, but the sequential switcher offers several special advantages. With the simple switcher, the camera output desired may be punched up for display on the monitor at will. With the sequential switcher, the monitor will sequentially display however many cameras are connected to it. The time between switching is adjustable, and if any one scene is desired for extensive observation, the sequencing can be stopped at that input. See the section on video tape recorders to see how this switcher may have further uses.

*Video tape recorders.* For cost reasons, compatibility, and availability, only video tape recorders (VTR) using half inch video tape will be considered. They are capable of making high quality recordings and are usually quite reliable. SONY, Panasonic, Javelin, and Hitachi are quality brands of both VTRs and cameras. The simplest VTRs record and play back a video signal and usually have a stop action feature. The next step up adds electronic editing and slow motion playback capability. The simple VTR costs between $695 and $800, while the more sophisticated models run $1000 to $1200. The maximum record time for these units is one hour with a conventional 2400 foot, seven inch roll of video tape. Special thin tapes may extend this time by 25%, but give decreased service life. A standard one hour roll lists for $40, but a dealer with any kind of volume usually makes them available for about $25. The tape may be erased, recorded on, or played 500 times or more before becoming unusable. The one hour time limit may be avoided by using a special time-lapse VTR. These record at a slower speed than a standard VTR, and therefore a one hour tape may be stretched to a seven, 12 or more hour tape. The author recommends that no greater than a 7:1 or 12:1 reduction be used if any degree of clarity is to be maintained for the picture. Besides being able to record extended periods of time, the time-lapse VTR can greatly aid analysis of the material recorded. The recorder is played back at standard speed until some unusual activity flashes by. Then it may be slowed down for detailed observation. Thus, a whole day’s activity may be recorded and reviewed in less than two hours time! Nothing is missed and researchers’ time is saved for other duties. If the output of a sequential switcher is connected to the time-lapse VTR, a sampling of a whole day’s activity for many cameras can be obtained. Time-lapse recorders cost between $1700 and $3000. The author personally feels the Javelin X-400 at $2000 offers the most in features and performance, especially slow playback. Its only drawback is that when service is required, only a Javelin dealer is likely
to have the tools to do the job. On all the VTRs discussed an audio input is available. With the use of microphones in the breeding quarters as well as cameras, nothing is missed.

**Summary.** From this discussion of closed circuit television, it can be seen that anything from a shoestring budget to a federal grant is needed for financing of a system, depending on the degree of sophistication required by the researcher. Closed circuit television can give the researcher the tools needed to do an in-depth analysis of the subject's behavior. From this should come better understanding of the complex processes involved in getting raptors to breed in captivity. Following this should be more successes and easier duplication of them.

[The author is in a position to offer new equipment at a 10-15% discount (plus shipping) to serious researchers. Also, the author will offer limited (time-wise, not ability) consulting services free to those seriously interested in the design and purchase of closed circuit television systems.]