

COURTSHIP BEHAVIOR OF LARGE FALCONS IN CAPTIVITY

by

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Abstract

The courtship behavior of captive Peregrine Falcons (*Falco peregrinus*), Gyrfalcons (*Falco rusticolus*), Prairie Falcons (*Falco mexicanus*), and Lanner Falcons (*Falco biarmicus*) is very similar in basic form and function. No subspecific differences in courtship behavior were apparent in Peregrines. Variations in the vocalizations of a species are common and function to communicate the intensity of motivation. The seasonal ontogeny of Peregrine reproductive behavior is similar in all experienced pairs. Gradual and consistent shifts in yearly development are evident during the first two years of breeding, but usually a pattern appears to stabilize by the third year.

Major interspecific differences were found in the frequency of aggressive and nonaggressive postures in both ritualized and nonritualized Displays and in their relative use by the male and female. Evidence from the behavior of captives supports the idea that females are dominant in the pair relationship. The influence of size dimorphism on the development and maintenance of female dominance is reflected both interspecifically and intraspecifically in the relative frequencies of agonistic behavior. We suggest that potentially severe injury resulting from aggressive fighting, combined with a pair relationship dependent on female dominance, has resulted in a repertoire of postures highly efficient in communicating fine changes in motivation and a vocal repertoire that varies continually with the intensity of motivation.

Introduction

We have been studying the courtship behavior of paired falcons in captivity as one part of an attempt to understand how behavioral and physiological mechanisms function in the reproduction of raptorial birds, and how these mechanisms are influenced by environmental factors. Pairing and reproduction may involve special problems for highly predatory birds—especially in confinement—because they are usually solitary and pugnacious much of the year and because they possess formidable beaks and feet, as well as a strong motivation, for killing other animals. These include, in the case of large falcons, birds similar in size and shape to themselves. Potentially, a falcon represents a hazard to its mate. Given these conditions, important social processes must be brought into play to counteract these strong aggressive tendencies (Willoughby and Cade 1964).

Thus, social adjustments that take place for effective pair-bonding and integration between male and female falcons are particularly rewarding subjects for testing current theories about pairing and sexual selection (Brown 1975), as well as for providing new hypotheses for further study. Such studies can also contribute much to the basic knowledge needed to propagate Peregrine Falcons and other threatened or endangered species in captivity on a practical scale.

The purpose of this paper is to describe thoroughly the courtship Displays and associated behavior of mated falcons, to assign tentative functions to them, and to propose some hypotheses about the role of sexual size dimorphism in the pairing of large falcons.

Materials and Methods

We have examined four species of the genus *Falco* for this study: the Peregrine (*Falco peregrinus*), Gyrfalcon (*Falco rusticolus*), Prairie Falcon (*Falco mexicanus*), and Lanner Falcon (*Falco biarmicus*). The former three species breed in North America. Lanner Falcons breed mainly in arid parts of Africa where their ecology closely parallels that of Prairie Falcons. Our emphasis is on comparisons between the behavior of Peregrines and Gyrfalcons. Observations were made regularly for four seasons on captive pairs of Peregrines and for two seasons on captive Gyrfalcons.

Three pairs of Peregrines were studied in detail, two from northern Alaska (*F. p. tundrius*) and one from the Queen Charlotte Islands (*F. p. pealei*). These pairs have bred successfully for at least three years. Additional observations were made on three pairs from the western United States (*F. p. anatum*), two pairs from northern Quebec, and one pair each from Alaska (*F. p. tundrius*), Spain (*F. p. brookei*), and the Queen Charlottes (*F. p. pealei*). All these pairs attempted mating, and the females laid eggs. Behavioral observations were made in 1972 and 1973 from April through mid-June and in 1974 and 1975 from late January through May.

Three pairs of Gyrfalcons from northern Quebec were studied for two years. Only one pair produced young in 1974 and 1975. Observations were made from early January through April. The Gyrfalcons and arctic Peregrines (*F. p. tundrius*) were placed on a schedule of advancing photoperiods, as described by Weaver and Cade (1974). This schedule is timed for Peregrines so that all subspecies are roughly synchronized to begin egg-laying at about the same date. We made incidental observations over a three-year period on four to five productive pairs of Prairie Falcons and on two pairs of Lanner Falcons, one of which has produced multiple broods for four consecutive years.

There was no fixed schedule of observation during 1972 and 1973. In 1974 pairs were observed regularly five days per week and periodically on the other days. Study was concentrated between dawn and 1100 hours, and, twice per week, for three to four hours prior to darkness. These are periods of greatest activity. Pairs with advanced photoperiod were observed from the time the lights went on until 1100 hours. Additional observations were scattered throughout the day. Observations in 1975 were made from "dawn" until 1100 hours every day. Additional observations were made at other times of day, with emphasis on the hours before darkness.

Throughout our studies, the falcons were housed in the Cornell Behavioral Ecology Building, Ithaca, New York. Pairs were kept together throughout the year. This facility was equipped for about 35 pairs of falcons and their young. Chamber dimensions and fixtures were described by Weaver and Cade (1974). Visual exposure of the falcons to humans was minimal, and none of the falcons was tame enough to allow a human to enter its room without becoming alarmed. Feeding was accomplished through chutes at two levels. Dead four-week-old chickens and adult Coturnix Quail (*Coturnix coturnix*) were provided as food. Rooms had to be entered occasionally to change water baths and, when necessary, to examine the health of a bird. Observation through one-way mirrors was possible from two levels in each breeding chamber. In addition to handwritten notes, still photography and video-tape recordings were used for the analysis of behavior. In both cases, pictures were

taken through the one-way mirrors without additional illumination. Vocalizations were recorded with a Nagra IIIB recorder and an Altec microphone and were analyzed on a Kay Electric Sonograph with a wide-band filter.

Results

Behavior during the first successful breeding season for a pair has been deemphasized in our analysis of results. During the first year, reproductive behavior is often contracted into a short and accelerated courtship period. Behavior patterns appear identical to those of experienced pairs, but their frequencies and seasonal ontogeny are different. Captive Peregrines show no subspecific differences either in the patterns of behavior or in its ontogeny; however, sample sizes are too small to be certain there are no average differences that might be revealed by statistically treatable samples.

Nearly all behavior patterns described herein are displays in that they are signals that have become specialized for communication (Brown 1975). The sequencing of displays into larger recognizable units, with their own specialized signal, is very common in animals. In this paper these units have been given descriptive names which are capitalized and called Displays. The terms *display* and *posture* are used interchangeably for behavior patterns that make up or occur independently of the more complex Display units. The names of vocalizations are also capitalized.

Descriptions and Definitions of Behavior in Peregrine Falcons. Among the many behavior patterns of captive Peregrine Falcons, 13 Displays and a few other behaviors are particularly useful in describing the pair relationship and the seasonal ontogeny of reproductive behavior. Many of these have been at least partly described (e.g., for wild Peregrines—Cade 1960, Fischer 1968, Nelson 1970; for captive Peregrines—Fyfe 1972, Nelson and Campbell 1973, 1974, Weaver and Cade 1974). In this section we provide a descriptive sketch of these Displays in captive Peregrines with some detail (1) on those not previously described or (2) in cases when the behavior of our pairs was significantly different from published descriptions.

1. *Head-Low Bow Display.* Four variations of this Display occur in contexts ranging from anti-aggressive through mildly aggressive. They are exhibited by either sex in response to movement or close proximity of the mate. The basic mode of this Display is nonaggressive, and the postures it includes are characteristic of many sequences preliminary to and during close mutual interactions. These characteristics include holding the head below the body plane, beak directed away from the mate and usually toward the substrate, and generally sleeked plumage.

There are horizontal and vertical forms of this Display. The Horizontal Head-Low Bow involves crouching in a horizontal body position, the head bent at almost 90° to the body plane and the beak often contacting the substrate. The Vertical Head-Low Bow is a less intense form, given with the body in a normal perching position, but with the head depressed. Body positions intermediate between vertical and horizontal are frequently observed, and there is complete intergradation in the amount the head is bowed (fig. 1a). Either form of this Display may involve vigorous bowing up and down from the head-low position to a normal posture with the head above the body plane (see Nelson and Campbell 1973). Often the Head-Low Bow is maintained without vigorous bowing, especially when in close proximity to the mate. Several vocalizations may be given during the Display, including the Eechip and Whine vocalizations (figs. 2a and 2b). It is also frequently unaccompanied by calling. Mueller (1971) has described similar displays in the American Kestrel (*Falco Sparverius*).

A third variation of this Display is the Extreme Head-Low Bow (fig. 1b). Its function is anti-aggressive, and it appears to be a very intense form of the Horizontal Head-Low Bow described above. During this Display the body is tipped far forward so that the tail is very high and in line with the body. Slight bowing may be included, and the Eechip vocalization is frequently given. This Display apparently involves a mixture of two motivational states—fear and copulation. It is given most often by the female during Mutual Ledge Displays (see below) and especially just before aborted attempts to copulate. The general form of this Display is, in fact, quite similar to the female's Copulation Solicitation Display (see below).

The Agonistic Head-Low Bow is a fourth variation of the more general Head-Low Bow Display. This Display includes the "deep forward bow" described by Nelson and Campbell (1973). It is given by either sex in agonistic situations, and by the male in precopulatory behavior. Feathers on the head, especially on the sides, may be flared out, and feathers on the shoulders are often raised. The head is held below the body plane, but the beak is frequently directed at the mate. Horizontal and vertical body postures are used, the latter especially by the male during precopulatory display (see Hitched-Wing Display). Eechip or Chitter vocalizations sometimes accompany this Display (figs. 2a and 2c).

2. *Individual Ledge Displays.* Individual ledge displays are given by the male or female (Male Ledge Display or Female Ledge Display, respectively) alone on a prospective nest-ledge. They are usually centered on a scrape (a shallow depression made in the substrate). Basic behavior patterns were identical in all subspecies studied. Major differences involved vocal peculiarities, which may represent individual variation more than subspecific difference.

a. *Male Ledge Display.* The scrape is approached in a horizontal head-low posture accompanied by a continual Eechip vocalization (figs. 1a and 2a). When sexual motivation is high, a "high step" or "tippy-toe" gait is used and produces a side-to-side swagger (also described by Nelson and Campbell 1973 in another context). The horizontal head-low posture is maintained during intense activity at the scrape, and a complete Eechip vocalization is given repeatedly. Pauses begin after five to ten seconds, during which the male looks toward the female. At any time, movement by the female is likely to elicit renewed intense display, and her reaction determines the duration of display. At low intensity the male may become relaxed, and the vocalization then is usually an incomplete variation of the Eechip.

b. *Female Ledge Display.* Female Display differs from male Display in several ways. In general it is less intense and is sometimes difficult to distinguish from nondisplay activity on the nest-ledge. The postures are less distinctive and more variable. Approach is usually entirely horizontal (i.e., head, body, and tail all in one plane) or with a slight lowering of the head. A complete Eechip vocalization is given. The female turns around in the scrape, mandibulates debris on the ledge, and scrapes frequently (see below). Pauses to look at the male are infrequent. Female Ledge Displays often change into apparent noncommunicative activity.

3. *Mutual Ledge Display.* Simultaneous activity by both sexes on the nest-ledge, usually centered on a scrape, characterizes this Display. The most intense portion occurs just as both birds arrive at the scrape, each in the horizontal head-low posture with beaks close to the substrate, vigorously Eechipping. Movements of each sex relative to the other and the characteristic pauses that occur during the Display have been described by Nelson and Campbell (1973, 1974).

Interactions with movements, postures, and vocalizations identical to those in Mutual Ledge Displays may occur infrequently on perches other than the nest-ledge.

4. *Billing.* Billing is often seen during the longer Mutual Ledge Displays, and occasionally when the pair is perching very close together. Billing involves twisting the head sideways,

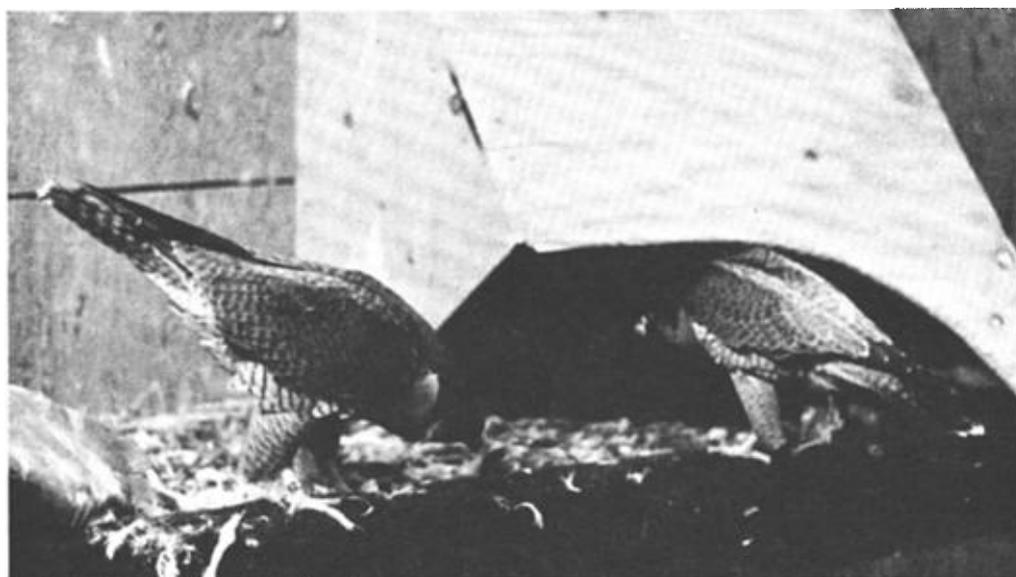
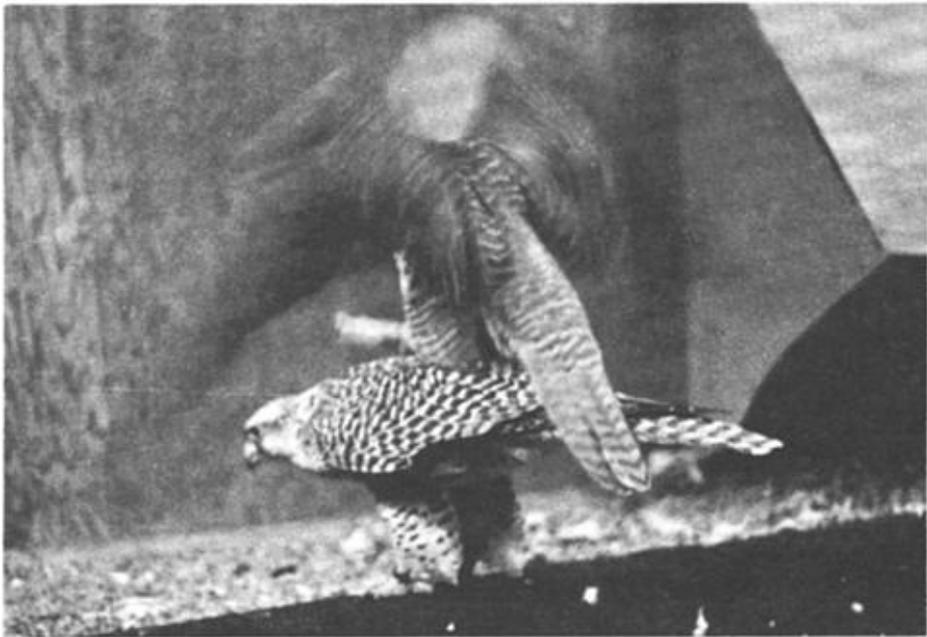
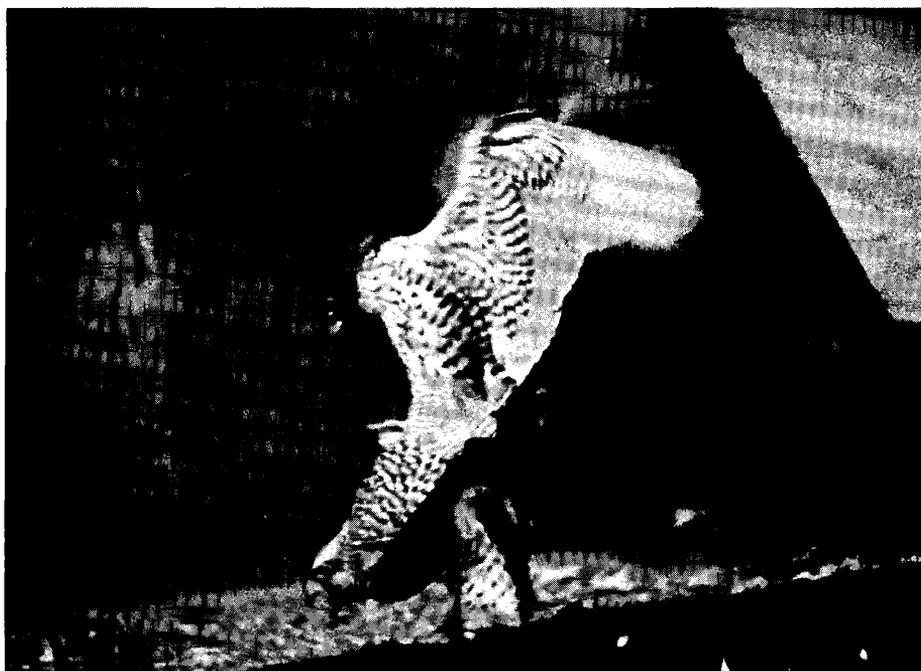


Figure 1. Courtship postures common to four species of large falcons. (a) Male Peregrine approaching the scrape in a Horizontal Head-Low Bow. (b) Peregrines during a partly aggressive interaction; female on left in Extreme Head-Low Bow; male in a transitional posture showing some aspects of the Hitched-Wing Display.



(e) Gyrfalcons as the male flies to mount; female in Copulation Solicitation posture.
(f) Gyrfalcon copulation; male in Curve-Neck posture.



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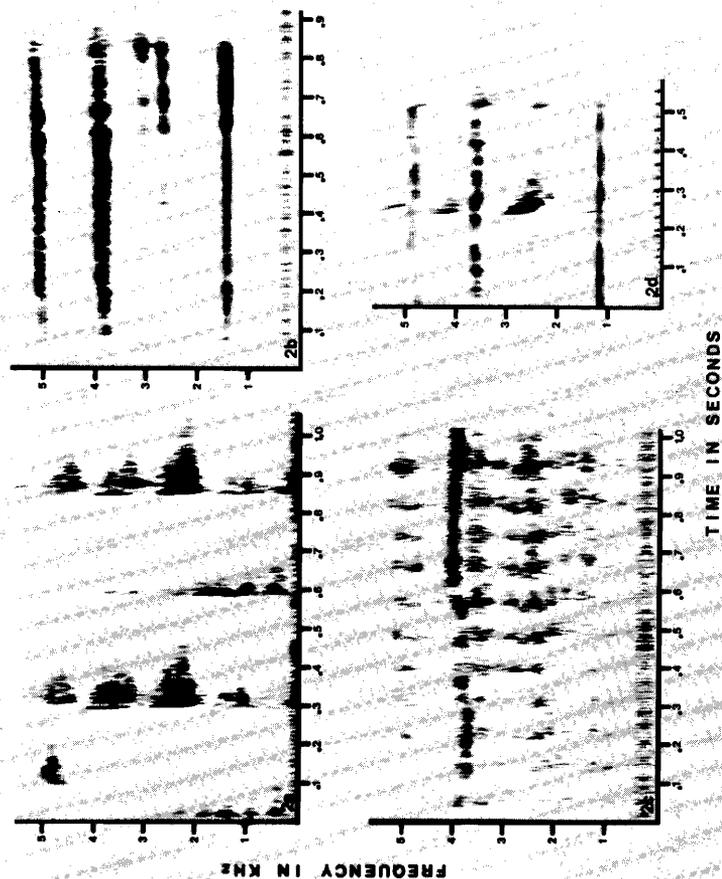


Figure 2. Peregrine Falcon vocalizations. (a) Eechip (two units) given by either sex during Ledge Displays, Food-Transferring, contact vocalizing, aggressive interactions, by male during copulation (phonetics in figure: ku ee chip, ku chip). (b) Wail (one unit) given by either sex when motivated to change the social context. (c) Chitter (segment only) given by either sex, especially by the male during aggressive interactions, precopulatory behavior, and during copulation (horizontal band at 3.9-4.0 KHz is a female Whine used here to solicit copulation). (d) Copulation Wail (segment only) given by the female during copulation (burst at 0.25 sec. is part of male vocalization).

especially by the female, and nibbling between beaks. The female's head is usually very low with her beak directed upward, while the male faces downward. If billing occurs during a Mutual Ledge Display, the normally loud Eechip vocalization tends to diminish toward Peeping and quiet female Chupping—incomplete variations of the Eechip sound unit.

5. *Scraping*. Scraping is exhibited by either sex during solitary activity on a ledge or as part of an Individual Ledge Display. There is some question as to whether the behavior should be considered a component of Display. During scraping the body is canted forward, weight on the breast, beak frequently in the substrate, the tail relaxed and sloping toward the ledge. A shallow depression, the scrape, is made by vigorous backward pushing with the feet. This behavior often occurs in a series with a shift in position between bouts of scraping. No vocalization accompanies this behavior. With the exception of females from about five days before laying, no "rocking" movement is made before settling on the breast. The rocking behavior always occurs as a falcon settles onto eggs for incubation and has been described in detail by Nelson (1970) for wild falcons. The behavior in captive birds is identical.

6. *Food-Transfer Display*. A common courtship Display involves the transfer of food from one mate to the other, usually male to female. Either sex may initiate a transfer. The female uses a Wail vocalization or rarely a Whine, combined with a vertical head-low posture to solicit transfers when the male does not have food. If the male has food, the Wail and Eechip vocalizations are used about equally by the female, often accompanied by the Vertical Head-Low Bow Display.

Male solicitation, which elicits the female's approach, always occurs when he has food, either spontaneously or initiated by female intention movements to engage in transfer. This solicitation by the male is characterized by a very sharp and clear Eechip vocalization. The male alternates between a relaxed posture, with the head up, and a posture with his head down while he manipulates or contacts the prey item. This posture, with the head low, does not appear to be the nonaggressive Head-Low Bow Display. Transfer from the female to the male is not obviously solicited.

Prior to actual transfer, the male picks the prey item up in his beak and stands vertically, head up. The female maintains head-low postures, often horizontal, and both sexes give complete Eechip vocalizations. Nelson and Campbell (1974) have described variations on the actual transfer sequence and behavior associated with incomplete Displays.

7. *Hitched-Wing Display*. Engaged in by both sexes, this Display is especially characteristic of the male throughout the reproductive cycle, developing as sexual motivation reaches its peak (Weaver and Cade 1974). It is consistently given in flight to and from copulation and during male precopulatory behavior. This Display can be divided into two forms, flying and standing (figs. 1c and 1d). The latter is probably the same behavior as the Slow Landing Display described by Nelson and Campbell (1973, 1974).

During Hitched-Wing flight the wings are held high, with short wing-beats mostly from the wrist. The legs are well forward, and the tail is depressed resulting in a slow-motion, bouncing flight. Frequently the flight path involves low approach to the perch with a last-minute bound above and then straight down onto the perch. No bounce occurs when the male flies to mount for copulation.

Standing Hitched-Wing Displays occur briefly to moderately long (2 seconds) after the male lands on a perch, frequently in the context of Mutual Ledge Displays. It is always expressed prior to copulation. Most often the body posture is vertical to semihorizontal, high on stiff legs. The head is low, and the wings are hitched up high against the body to form a deep, V-shaped depression along the back. Another variation includes a horizontal head-low position, legs stiff and wings hitched.

The male precopulatory posture is especially interesting in its combination of the sexually motivated Hitched-Wing Display and components of the Agonistic Head-Low Bow. The body is vertical, wings hitched and legs stiff. The head is lower than the shoulders with beak directed at the female, which is usually soliciting copulation (see below). Vigorous bowing, frequently with a side-to-side swing, is part of this Display. The Chitter is a frequent male vocalization during precopulatory behavior.

8. *Copulation Solicitation Display*. The female's motivation to copulate is communicated by a series of postures and vocalizations, partially described by Nelson and Campbell (1973). Solicitation may begin with the Whine vocalization, concurrent with or just preceding a Vertical Head-Low Bow. This is usually given when the male is at some distance. Primary solicitation will follow if the male shows reaction. During primary solicitation, either following the vertical solicitation just described or independently, the female assumes a horizontal head-low posture. Again the Whine vocalization is given, the tail is close to horizontal, panel feathers are raised, and her orientation is usually perpendicular to the male. This phase of the Copulation Solicitation Display may continue for up to 30 seconds. Just as the male shows intention to mount, the female sleeks her panel feathers, crouches and leans forward slightly, and sometimes begins to move her tail up and to the side in preparation for copulation.

9. *Copulation*. During copulation the female is pitched forward, making an angle of about 45° with respect to the perch. The Copulation Wail is given throughout (fig. 2d). As the male mounts, the female spreads her wings out at the elbow about one-fourth open. The tail, up and to the side, may be partly spread.

The male flaps his wings throughout copulation, maintaining an upright posture with the neck extended and bent in a curve (fig. 1f). Usually the male gives one or two bursts of the Chitter vocalization just before, during, and/or just after mounting, and then Eechips sporadically. Some individuals give bursts of Chitter throughout. Toward the end of copulation the male stops his tail movements, pressing his cloaca against the female's. Rapid wing-beats accompany this tail-press. The female may spread her tail partly at this time, and the male departs with a Hitched-Wing Display directly afterwards.

10. *Threat Behavior*. The two major Displays have been described by Nelson and Campbell (1973). The characteristic posture for Horizontal Threat is with tail, body, and head all in a horizontal plane. The beak is directed at the mate, wings slightly extended, head and body feathers erect. In Upright Threat, the body is vertical with most feathers erect. The tail and wings may be spread to varying degrees; the beak is usually open.

Comparison of Peregrine and Gyrfalcon Courtship Behavior

We present here details of only those aspects of Gyrfalcon behavior that differ from the Peregrine behavior already described. Most of the courtship Displays and behavior patterns of these two species are very similar and can be designated by the same names. Unless otherwise stated, components of the various behavior patterns in both species are typified by the description for Peregrine Falcons in the previous section.

1. *Head-Low Postures*. Head-Low postures are exhibited by both species in quite similar contexts. Gyrfalcons show Horizontal and Vertical Head-Low Bow Displays, and use head-low postures during all Ledge Displays and Food-Transferring. As in the case of Peregrines, the accompanying vocalizations are somewhat variable; most often a Whine or brief Chitter is given for the Bow Displays, and Chugging occurs during Ledge Displays and Food-Transferring (fig. 3).

The frequency with which these Displays and postures are exhibited is the major difference between the two species. In Gyrfalcons there is very little intermediate variation be-

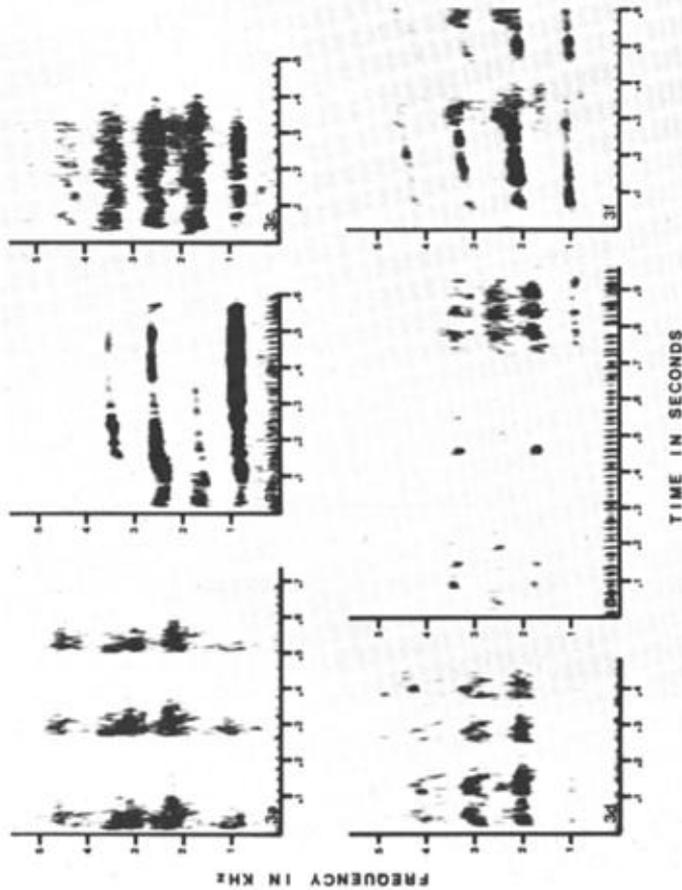


Figure 3. Gyrfalcon vocalizations. (a) Chup (three units) given by either sex during Ledge Displays, Food-Transferring, contact vocalizing. (b) Wail (one unit) given by either sex when motivated to change the social context. (c) Chitter (one burst) given by either sex during aggressive situations, by male before copulation, and probably by male during Mutual Ledge (d) Chatter (four units) given by either sex, especially by the female during Mutual Ledge Displays and Food-Transferring. (e) Copulation Solicitation (segment only) given by the female; first 0.6 sec. in figure is the Whine of initial solicitation followed by the first burst of primary solicitation. (f) Copulation Wail (segment only) given by the female during copulation (smudge at 0.3-0.4 sec. is the male vocalization).

tween the vertical and horizontal forms of the head-low postures. The threshold for assuming the more intense horizontal head-low posture is high in male Gyrfalcons, and females use the Head-Low Bow Display much less frequently than Peregrine females. Neither sex of Gyrfalcon shows the vigorous bowing so conspicuous in Peregrines. One of the most frequent contexts eliciting Head-Low Bow Displays in Peregrines is the approach of the mate or intention movements of approach. Use of the Display in this context was more frequent for males than for females in both species. The Gyrfalcons were less intense about the interaction, and intention movements rarely elicited display. Frequently the male did not display until the female was actually landing on his perch.

In our Gyrfalcon pairs there was no behavior pattern strictly parallel to the Agonistic Head-Low Bow observed in Peregrines. Female Copulation Solicitation has some characteristics in common with the Agonistic Bow, but, in general, orientation away from the male is necessary for mounting. Behavior comparable to the Extreme Head-Low Bow was not observed in the Gyrfalcons.

2. *Individual Ledge Displays.* The contexts in which these Displays occur are identical in both species. Visual contact with the mate is very important, reaction of the mate being a determinant of the Display intensity and duration.

The Male Ledge Displays of Gyrfalcons are nearly identical to those of Peregrines. The vocalization in Gyrfalcons is always a complete Chup as compared with a tendency of the Peregrine vocalization to degenerate. The reason may be that the basic Gyrfalcon vocal unit is a single syllable, whereas the Peregrine's is complex. There is a possibility that Male Ledge Displays are more frequent and more vocal in Gyrfalcons, but the sample size is too small to be certain.

Female Ledge Displays in both species show similar differences from Male Ledge Displays. These include less well-defined postures and a marked tendency to change into non-communicative activity. The female Gyrfalcon may more consistently maintain a head-low posture early in the Display.

3. *Mutual Ledge Display.* Although the functions and general characteristics of the Mutual Ledge Display are similar in Peregrines and Gyrfalcons, differences in movement, duration, and vocalization are conspicuous. In both species the Display is primarily organized around a potential nest-scrape and is frequently preceded by a Male Ledge Display. In Peregrines as well as Gyrfalcons, as the Mutual Display begins, both sexes are in a horizontal head-low posture.

In Peregrine Falcons there is considerable movement by one or both sexes around the scrape as well as pauses in the Display followed by renewed vigorous activity. In some Peregrine pairs the female is as likely as the male to terminate the Display by leaving the scrape. By contrast, Gyrfalcons tend to maintain stationary positions during the Mutual Ledge Display and rarely pause. It was extremely rare for our female Gyrfalcon to terminate a Mutual Display. Our male Gyrfalcon usually terminated the interaction after only five to ten seconds, resulting in Display durations shorter than was usual in Peregrines.

The greatest apparent difference between the vocalizations of Gyrfalcons and Peregrines is change in repetitiveness of vocalizations during the Display, rather than the obvious differences in the basic sound units. Male and female Peregrines give an Eechip vocalization with some variability depending on the intensity. In addition, Peregrines show considerable variability in the regularity with which successive units of the vocalizations are given. By contrast, male Gyrfalcons give very regular Chup vocalizations throughout the Display. In the female Gyrfalcon there is always a distinct change in vocalization as the male leaves her alone at the nest-scrape. During most of the interaction she gives a series of very fast Chup

units, but these increase in speed to a Chatter as the male departs (fig. 3d). When the female of either species remains in the scrape after the male has gone, vocalization diminishes, becoming sporadic, soft, and, in Peregrines, incomplete. The Gyrfalcons gave Mutual Ledge Displays only at the nest-scrape. Peregrines occasionally exhibited identical interactions at other locations, especially early in the courtship period. Billing was not observed during courtship in the successful pair of Gyrfalcons, but it has been seen in other pairs.

4. *Scraping*. The major characteristics of this behavior pattern are identical in the two species. The conspicuous "rocking" movement of Peregrines as they settle on eggs (Nelson 1970) are present in most scraping bouts by captive Gyrfalcons. This movement was observed in males and females beginning in January, when scraping activity first began. It was observed during Peregrine courtship only as the female did it a few days before laying.

5. *Food-Transferring*. The behavior patterns that comprise Food-Transferring are very different in Peregrines and Gyrfalcons although the function of the Display appears to be the same in both species. It is an important courtship interaction, expressed somewhat more frequently in the captive Gyrfalcons than in the Peregrines. The frequency of female-to-male transfer was low in both species, but unlike Peregrines the male Gyrfalcon rarely took food to the female's perch for transferring. It was more usual for him to prolong solicitation, waiting for the female to approach for the transfer.

Comparisons of vocalization are similar to those of the Mutual Ledge Display. Both sexes of Peregrine give a complete Eechip vocalization, and the male gives especially clear and sharp Eechips when soliciting a transfer. Gyrfalcons give Chup vocalizations through most of the interaction. The female increases the speed of repetition to a Chatter as the transfer occurs.

The postures of both sexes are different in the two species. In contrast to the upright posture of a male Peregrine, the male Gyrfalcon maintains a vertical to horizontal Head-Low Bow while soliciting a Food-Transfer. The male Gyrfalcon occasionally looks up at the female during solicitation, but on her approach he picks up the food in his beak and maintains a head-low posture until the transfer is complete or the female loses interest. Female Gyrfalcons approach in an entirely horizontal posture or slightly head-low. This mildly aggressive posture is maintained during the actual transfer and contrasts with the conspicuous head-low posture of female Peregrines throughout the Food-Transfer sequence. Males of both species tend to leave the area of transfer immediately after the interaction is complete, but the tendency is particularly pronounced in Gyrfalcons. Food-Transfer solicitation by the female is similar in the two species. As is usual, the Gyrfalcons tend to be more vocal, including a nearly continual vocal response by the female from the onset of male solicitation until the actual transfer.

6. *Male Precopulatory Display*. Male Peregrines and Gyrfalcons have distinctive postures used during precopulatory sequences. These are the Hitched-Wing and Curve-Neck Displays, respectively. The frequency with which these Displays appear is very different in the two species. The Hitched-Wing Display is first seen early in courtship and appears to function as a general signal. In Gyrfalcons the Curve-Neck Display was observed only when the male was motivated to copulate or just prior to a copulation attempt. Because of this specialized use of the Curve-Neck Display in Gyrfalcons, it always elicited some female response.

A close comparison is possible between Peregrine precopulatory Hitched-Wing Display and Gyrfalcon Curve-Neck Display. During these Displays the body is drawn up to maximum height, and the plumage is sleeked. Gyrfalcons direct the beak away from the female, and Peregrines often direct the beak toward the female. Body postures accentuate the head position in both species. Gyrfalcons extend and bend the neck into an inverted U shape;

Peregrines have their wings hitched over their backs, accentuating the head-low posture. When the female is very close, nonaggressive postures are added to or replace the above postures, at least in Gyrfalcons. Male Gyrfalcons either assume a head-low vertical posture at high intensities, or turn perpendicularly to the female, maintaining the Curve-Neck Display. When in close proximity to the female, male Peregrines present a profile, although the body may still be oriented toward the female. At higher intensities male Peregrines will frequently drop to a horizontal body posture, with Hitched-Wing and the Agonistic Head-Low position.

Males of both species use vocalizations during these Displays that are also used during clearly aggressive interactions. The male Peregrine frequently emits the Chitter vocalization (described by Cade 1960, Nelson 1970) just prior to mounting attempts. This vocalization has also been heard when the female was trying to pull food away, during exchanges for incubation, and while in Horizontal and Upright Threat. Male Gyrfalcon vocalizations just prior to mounting were difficult to resolve behind the overriding vocalization of the female. Recorded segments that have been analyzed appear similar to the agonistic vocalizations given during Horizontal and Upright Threat.

7. *Copulation Solicitation*. Some postural aspects of female Solicitation for Copulation differ between species, but the Display is similar in its progression and vocal characteristics. Generally there seems to be more of an agonistic component to Gyrfalcon solicitation. Although both females posture horizontally during primary solicitation, the female Gyrfalcon often approaches head-on in an entirely horizontal posture (i.e., components of horizontal threatening, fig. 1e), and the Peregrine female is stationary, usually oriented either perpendicular to or away from the male. Female solicitation in Peregrines is distinctly head-low. The female Gyrfalcon does turn perpendicularly when close to the male, and copulation proceeded in our pair when this orientation was maintained. In both species an initial solicitation was sometimes made from a vertical head-low posture, usually at some distance from the male.

8. *Copulation*. Female Peregrines and Gyrfalcons have distinctive Wail vocalizations given only during copulation. Their bodies are tipped forward to an angle of 45° , legs stiff and head in the body plane. The vocalization emitted by the male is variable even for an individual, but is usually given in bursts. This vocalization in Gyrfalcons appears to be the same as during the precopulatory sequence, although clear sonographs could not be made. The copulation posture of males is identical in Gyrfalcons and Peregrines. It is a vertical posture with the Curve-Neck head position (fig. 1f). In Peregrines, at least, the talons are balled up into a loose fist, weight on the tarsi (Nelson 1970; see also Mueller 1970). The talon position is difficult to see in Gyrfalcons owing to the dense plumage, but they appear to be balled up also; sometimes the male's hallux appears to be locked under the female's humerus.

9. *Aggressive Behavior*. The behaviors in this category are similar in the two species. Well-adjusted pairs rarely showed any agonistic behavior, and Upright Threat was not observed except in new and/or incompatible pairs.

Comments on the Courtship Behavior of Lanner and Prairie Falcons

Although Lanner and Prairie Falcons have not been subjected to the same detailed observation as our Peregrines and Gyrfalcons, we have enough incidental observations to know that all basic Displays discussed in the previous section are used by these species too. In most cases the forms of their Displays and vocalizations bear striking resemblances to those of Gyrfalcons and serve further to emphasize the close phylogenetic ties among these forms,

which are usually allied in a separate subgenus from the Peregrine. The displays and vocalizations of Prairie Falcons and, in particular, Lanners are more subdued and less conspicuous than the vigorous and loud displays of the Gyrfalcons, but otherwise there are few qualitative differences. One exception is the Chipping call of the Prairie Falcon, which is more similar to the Peregrine's "Eechip" than to the Gyrfalcon's "Chup" (fig. 4a). The Curve-Neck Displays of the males of all three species prior to copulation are strikingly similar and stand in marked contrast to the Hitched-Wing Display of the male Peregrine. One characteristic of Prairie Falcons that is different from the others is the high degree of female aggression, which often erupts into overt attack on the male during the early stages of pairing. As a consequence, Head-Low Bows and other forms of agonistic display occur more frequently and occupy a greater portion of the total courting period than in the case of the other species.

Seasonal Ontogeny of Reproductive Behavior

Owing to the individual variability in seasonal development and the small sample of paired Gyrfalcons, this discussion of seasonal ontogeny is limited to Peregrines.

Initial courtship interactions were observed earlier in each successive year of breeding for at least the first three years. Egg-laying also tended to begin somewhat earlier although the courtship period still lengthened each year. The earlier onset of copulation with respect to laying dates was especially consistent; all pairs showed this progression (table 1). There is some evidence to suggest that the seasonal ontogeny of behavior becomes stabilized after several years. The three experienced pairs (two breeding for the third time, one for the third and fourth times) showed striking similarities in courtship development. All pairs initiated courtship at about the same time, began copulation within one week of each other, and began to lay eggs within a period of ten days. The development of courtship outlined below uses the temporal progression characteristic of the pairs in their third or fourth breeding season (fig. 5). The actual dates used in this section are specific to our particular environmental conditions. They are expected to vary depending on local weather conditions, latitude, and photoperiod manipulation.

A gradual increase in activity on the nest-ledge by both sexes is the first indication that courtship is beginning. Ledge behavior is most conspicuous in the male, beginning in early January. He displays at several scrapes, often on more than one ledge. This pattern of maintaining a number of scrapes is exaggerated in the young pairs breeding for the first time. During this early period both sexes frequently use Head-Low Bow Displays or Mild Threat when approached closely or suddenly.

Toward the end of January, Mutual Ledge Displays and Food-Transferring begin to develop simultaneously. The female shows interest in Male Ledge Displays and also hesitates before getting food when it is first introduced. This hesitation permits the male initial access to the prey (see Willoughby and Cade 1964). Solicitation for Food-Transferring is displayed repeatedly by the male although if the female approaches, he tends to move away, resuming solicitation from a new perch.

Male Hitched-Wing flying becomes apparent about one month after the onset of courtship. For an additional two or more weeks the female responds directly to male Hitched-Wing flights over her or close by. This reaction is usually the Vertical Head-Low Bow accompanied by either Eechip or sometimes the Whine vocalization. Apparently the female becomes habituated to these Displays, as the male uses Hitched-Wing Displays for almost all

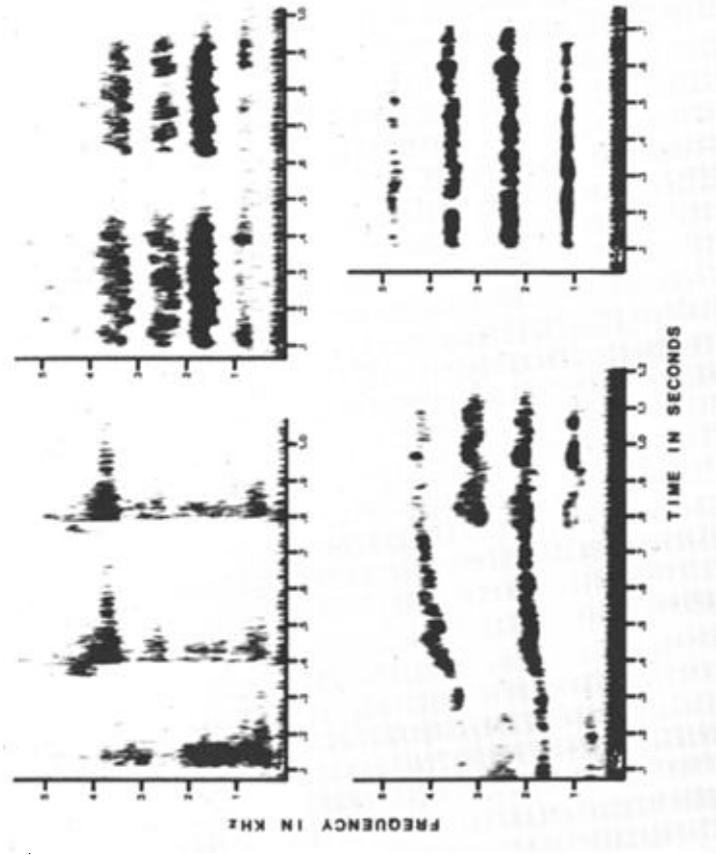


Figure 4. Prairie Falcon vocalizations. (a) Kuduchip (two units) given by either sex during Ledge Displays, Food-Transferring, contact vocalizing, aggressive interactions, and rarely by male during copulation (phonetics in figure: kudu chip, chip). (b) Chitter (two bursts) given by either sex during aggressive interactions. (c) Copulation Solicitation Whine (segment only) given by the female. (d) Copulation Wail (one unit) given by the female during copulation.

Table 1
**The relationship of breeding experience to the start
of copulation during courtship.**

Subspecies and year of breeding	Date of first observed copulation	Days prior to first egg
<i>F. p. tundrius</i>		
pair CC:		
first year (1972)	April 10	2
third year (1974)	March 5	15
fourth year (1975)	March 3	23
pair CH:		
first year (1973)	April 8	5
second year (1974)	March 7	10
third year (1975)	February 26	24
pair U8:		
first year (1975)	May 16	0
<i>F. p. pealei*</i>		
pair MP:		
first year (1973)	April 1	2
second year (1974)	March 22	4
third year (1975)	March 3	15

* This pair bred successfully for two years before 1973 at another breeding facility.

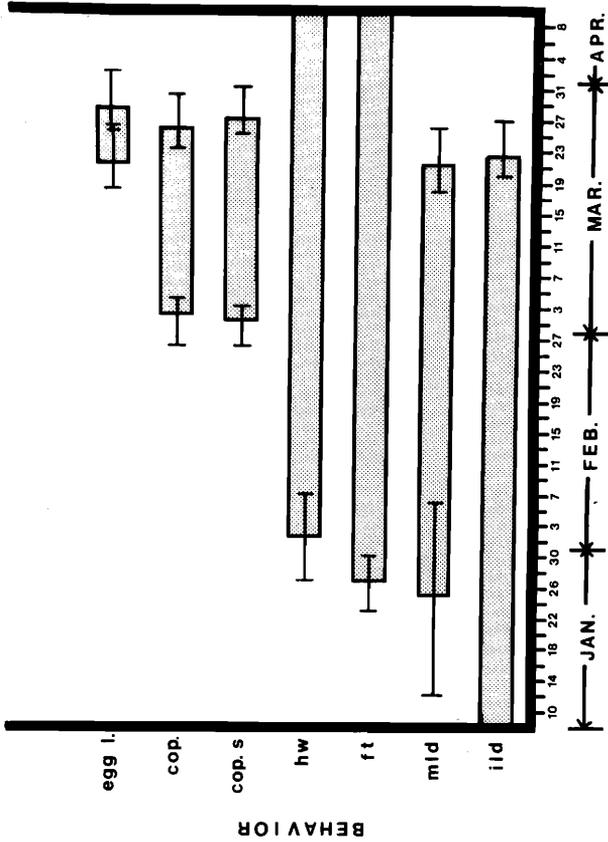


Figure 5. Seasonal ontogeny of Peregrine Falcon courtship (third or fourth year of breeding). Shaded bars represent the duration of behavior from the mean beginning date to the mean ending date; ranges are indicated. Behaviors: Individual Ledge Display (iild), Mutual Ledge Display (mld), Food-Transferring (ft), male Hitched-Wing Display (hw), female Copulation Solicitation (cop. s), Copulation (cop.) and egg laying (egg l.) (Based on three pairs breeding in 1975 (two *F. p. tundrius* and one *F. p. pealei*) plus one of the same *F. p. tundrius* in 1974.)

movements across the room, until the end of incubation. Young males are not as consistent in using the Hitched-Wing Display. Female reaction to this activity steadily decreases, and late in the courtship period her reaction initiates steps toward Copulation Solicitation. The Whine vocalization is almost always used in these situations.

For a period of about three weeks in February, Mutual Ledge Displays and Food-Transferring develop into frequent interactions, and Head-Low Bow Displays become less frequent. Mating behavior, including female solicitation for copulation and male precopulatory posturing, is first observed in late February to early March, about eight weeks after the onset of courtship. The females perform Copulation Solicitation Displays for a variable length of time before the males complete the sequence by mounting, usually in less than two days. In all cases the early mating behavior was identical to the precopulatory sequences observed later in the year. These involve female Copulation Solicitation with bowing, alternating with the male Vertical Head-Low Bow or, more often, the precopulatory Hitched-Wing. In both sexes the bowing is vigorous: a fast, jerky movement to the bow position, then up to the starting posture.

Initial Copulation Solicitation is observed about three weeks before laying. At first many copulation sequences are incomplete, and successful copulations are short, averaging five to six seconds depending on the pair. Two to three weeks before laying, copulation is already a regular interaction, with a duration of eight to ten seconds, occurring at a frequency of two to three copulations per hour during the most active period (first hour of light). One week before laying, copulation increases to a frequency of three to four per hour during the first hour of light. Copulation continues in most pairs until the third egg is laid. Although copulation was not observed in some pairs after the second egg was laid and very few pairs copulated after the third egg, full clutches were consistently fertile. A sudden increase in the frequency of copulation occurred on the day that the second egg was laid, either a few hours prior to, or after, laying.

The male shows little motivation to incubate the first egg and tends to continue Male Ledge Displays around the egg, sometimes moving the egg out of the nest-scape and then displaying in the empty space. The female incubates immediately if weather conditions require it although more often she only stands over the egg and does not begin continual incubation until the second or third egg.

Discussion

1. *Limitations of Studying Captives.* When behavioral data are based on the study of captive animals, extreme caution is necessary in extending conclusions to include wild situations or even other captive environments. In addition to other factors, the frequency with which certain behavior patterns occur can be very different in captive animals. There is also the temptation to consider as normal the behavior of captive animals that successfully reproduce. Such an assumption can be misleading. Highly unnatural pair-bonds and behavioral development may still result in fertilization, as in the case of interspecific crosses (e.g., Morris and Stevens 1971).

One factor that might contribute to such abnormality is the stimulus-deprived environment experienced by captive animals and the resultant responsiveness to suboptimal stimuli. A second bias may come from exaggeration of individual differences in behavior. Enforced pairing and limited or incomplete environments accentuate individual variations in behavior

that may or may not be significant in nature. Evaluating the importance of these behavioral differences can be helped by determining the causes of their expression in the captive situation.

The interpretation of behavior in captivity is dependent on study of the same behavior in nature, not vice versa. The only exception might be studies of organisms for which the entire range of environments experienced by the species within the cycle of behavior under study can be contained or accurately simulated in the study chamber.

The captive environment of our falcons cannot satisfy these requirements. The breeding chambers provide a minimal environment, satisfactory in that successful breeding can occur. The behavior of wild North American species of *Falco* has been studied to varying degrees. Peregrine Falcons, Prairie Falcons, and the American Kestrel (*Falco sparverius*) are best known, and the behavior of Gyrfalcons is just beginning to be described. Very little is known of the Lanner Falcon. Most of these studies include only incidental behavioral observations. A few have considered in more detail the repertoire and temporal patterning of reproductive behavior (e.g., for American Kestrels, Cade 1955; for Peregrines, Fischer 1968, Nelson 1970, Fyfe 1972, Wrege unpubl.; for Gyrfalcons, Platt 1976). Thus a small literature exists with which to gauge the behavior patterns of captive falcons.

Several basic differences are apparent when comparing the behavior of captive falcons with what is known of their behavior in the wild. The close proximity of the captive pair and the limited space have resulted in an emphasis on certain Displays, while others are deleted from the repertoire. Food-Transferring and especially Ledge Displays are much more frequent in captive Peregrines—probably because of the almost constantly available stimuli that elicit the behavior patterns. It is likely that other behaviors vary considerably in frequency when compared to wild falcons. Some courtship Displays observed in nature require considerable space, such as, territorial flight Displays, mutual defense Displays, and others (see Cade 1960, Nelson 1970). These behavior patterns are not observed in captivity, although some others may be modifications of them.

The contextual use of certain vocalizations is different in captive and wild falcons. Evidence suggests that many vocalizations of falcons communicate intensity of motivation, as opposed to direction of motivation to perform a specific action. The degree to which this might be true in wild falcons has not been determined. The close proximity of mates in captivity makes unnecessary vocalizations that may function in the wild as long-distance signals, and another vocalization is substituted (Platt pers. comm., Wrege unpubl.) For example, a wild male Peregrine will often solicit Food-Transferring with a Wail vocalization as he returns to the eyrie site. As the female approaches for the transfer, he begins to Eechip. In captivity the male solicits a transfer only with the Eechip vocalization, which continues until the Display is complete.

Individual behavioral characteristics of captive falcons greatly influence reproductive success. Continued close proximity and the difficulty of avoiding interactions are probably contributing factors. Observations of wild Peregrines and Gyrfalcons indicate that males may spend considerable time away from the females, either hunting or perching out of sight. No data are available to determine whether individual differences in behavior affect choice of mate and breeding success in wild falcons, but such influence seems likely (Cade 1960).

2. *The Function of Displays in Pair-Formation and Pair-Bonding.* The Displays and vocalizations of Peregrines, Gyrfalcons, Prairie Falcons, and Lanner Falcons can be divided roughly into three groups. First, nonaggressive behavior patterns include the following: All the head-low postures; Head-Low Bow Displays (excluding the agonistic form); Ledge Displays; Food-Transferring; Copulation Solicitation Whine; the Eechip vocalization and Ex-

treme Head-Low Bow in Peregrines; Chup and Chatter vocalizations in Gyrfalcons; Kuduchip in Prairie Falcons; and similar vocalizations in Lanner Falcons. These behaviors can be further subdivided into anti-aggressive or appeasement and approach-eliciting behaviors, according to the type of interaction. The uses of nonaggressive displays in these two forms are discussed in the section on the pair-bond and female dominance.

A second group of behavior patterns includes the male precopulatory postures in each species, female Copulation Solicitation in Gyrfalcons, and the Wail vocalizations in each species. It is difficult to label these behaviors as either aggressive or nonaggressive. In each case there appear to be aggressive components.

Finally, the remaining behavior patterns can be grouped as at least partly aggressive. These are the Agonistic Head-Low Bow Displays in Peregrines, any all-horizontal posture, Chitter vocalizations, and the Upright and Horizontal Threat Displays. Of course, none of the three groups of behavior patterns is rigid. In each species (and in some more than others) postures and especially vocalizations tend to intergrade depending upon changes in motivation.

Many courtship displays in falcons appear to integrate the pair and to ease co-inhabitation of a limited space. The effectiveness of a display and its frequency are probably related to the degree of sexual readiness of the mates. Male Ledge Displays stimulate reproductive behavior in females and initiate pair integration. Mutual Ledge Displays, Billing, and Food-Transferring all result in close, nonaggressive interactions. This does not imply that aggression and fear are never seen as part of the Displays; rather, it means that the outcome of the interaction is nonaggressive and helps to form a pair-bond.

Studies of captive and wild Kestrels suggest that copulation may function in pair integration very early in the reproductive season (Willoughby and Cade 1964). Fischer (1968) mentions copulation as the first interaction of the season in some wild Peregrine pairs, and Fyfe (1972) has described copulation in Prairie Falcons on the first day the pair was together at the eyrie. This association of copulation and initial pair-bonding was not observed in the four captive species of *Falco* studied here. Established pairs initiated copulation very early relative to egg-laying, but all other courtship patterns were well established at the time of first copulation. This pattern of pair-bond initiation, involving considerable courtship activity preceding first copulation, was also observed in captive Peregrines introduced to one another abruptly at the start of the breeding season (Nelson and Campbell 1973, 1974). Nonetheless, copulation probably does function importantly in strengthening the pair-bond. Copulation in the Gyrfalcon pair continued for 39 days before egg-laying, progressing from very short attempts that were terminated by female aggression through full-length copulations beginning 20 days before laying.

The Displays in each species of *Falco* can be characterized by the same name and include very similar postures, with the exception of the Hitched-Wing and Curve-Neck male precopulatory Displays. This likeness is suggestive of a similarity in function as well. Without the analysis of quantitative data, it is difficult to determine whether important interspecific differences exist in the function of various Displays in pair-bonding and integration. At this time, differences are not apparent, even when comparing the phylogenetic group of Gyrfalcons, Prairie Falcons, and Lanner Falcons to Peregrine Falcons. The major differences in behavior patterns are of frequency, intensity, and mate response. These differences, which may be intraspecific as well as interspecific, appear related to the nature of the pair-bond, especially the dominance relationship between the sexes.

3. *The Pair-Bond and Female Dominance.* The relationship of male and female in the pair-bond of falcons has been interpreted in different ways. In most cases, the interpretation

has been incidental to an explanation of reversed sexual size dimorphism, and this may account for the lack of data specifically bearing on the relationship. The following discussion about the pair relationship in captive falcons does not depend on any theory concerning the evolutionary pressures causing size dimorphism. Hagen (1942) suggested that female dominance was necessary to avoid filicidal behavior by the male. In most species of falcon, the male participates to some degree in incubation and care of the young. There is little evidence to suggest that a real threat exists, and strong selective pressure to eliminate such a tendency in the male's behavior would be expected. Cade (1960) placed importance on the division of labor that is very common in *Falco*, suggesting that female dominance might be necessary to maintain the male in his role as food provider. Amadon (1975) speculated that female raptors may be "more submissive or passive" relative to the male, at least during the initial pair interactions. To date there has been virtually no study of these initial interactions in any raptor. A different interpretation of the pair-bond resulted from the study of *pealei* in the Queen Charlotte Islands by Nelson (1970). He suggested that dominance was related to the location of the interaction, with the male being dominant in aerial encounters where his agility would be an advantage, and the female being dominant on the nest-ledge and during other close interactions where her size would be favorable. Observations on a captive pair of Arctic Peregrines led to the interpretation that the male dominated the female in the breeding chamber (Nelson and Campbell 1973).

There has been too little detailed behavioral analysis of wild falcons to determine the dominance relationship during reproduction. Our observations of four species of captive falcons indicate that the female is dominant in all species and in pairs that breed successfully. Unsuccessful breeding can often be correlated with either very dominant females, inhibiting almost any mutual behavior; with a lack of dominance by either sex; or, exceptionally, with a domineering male.

The relative frequency of aggressive and nonaggressive postures in each sex may be used as an indicator of the pair relationship. The use of these postures within ritualized courtship Displays as well as independently is important, and frequencies appear predictable on the basis of the degree of size dimorphism exhibited in the pair. A specific value for the relationship between size dimorphism and the relative frequencies of these behaviors would not be found in most captive falcons, for the following reasons. Differences in the history of each bird, primarily in its handling by humans and experience with conspecifics, result in a large variation in aggressiveness that influences the frequency of aggressive and nonaggressive behavior. We do feel, however, that a general pattern is demonstrable.

The Peregrine is the most dimorphic of the species studied and has been observed more intensively than the others. Possibly the most conspicuous behavior pattern throughout the reproductive season is the Head-Low Bow. Both sexes exhibit this Display, and intergradation is nearly continuous between the less intense vertical form and the extreme horizontal form. In most cases this Display appears to be anti-aggressive in meaning, rather than approach-eliciting. This distinction is important. An anti-aggressive posture is clearly one that inhibits aggression. Approach-eliciting postures signal the absence of aggressive motivation in the sender. It is quite possible for the same posture to take on either meaning, even when given by the same individual. The meaning depends on the relative dominance of the interacting animals in the context of that interaction or in anticipation of the interaction. The problem comes in deciding which meaning a given posture has and in trying to avoid shaping the decision on the basis of preconceptions. We would like to stress that all these comparisons are of relative frequencies. It is quite evident that each bird is intimidating to the other,

and both sexes must use postures that can be interpreted as anti-aggressive and as approach-eliciting.

The male Peregrine exhibits head-low posturing much more frequently than the female, often responding to female movements at a considerable distance. Female intention movements to approach the male elicit postures close to horizontal, and approach by the female frequently causes displacement of the male to another perch. Although the female also exhibits these postures, vertical positions predominate. Female displacement on male approach is not frequent.

In well-adjusted pairs, the very aggressive Upright and Horizontal Threat postures are rarely observed as interactions between the mates. With new pairs these displays may occur early in the season, but are observed less frequently as the pair-bond develops. Although the female may approach the scrape in an all-horizontal posture during a Mutual Ledge Display, she immediately assumes a head-low posture if the male looks up. It is unlikely that the horizontal posture in this case is really aggressive. Entirely horizontal approach to the scrape is usual in both sexes prior to Individual Ledge Displays—probably a relaxed posture for walking on a ledge or the ground. It is significant that the female's posture changes when the male looks at her; this is not seen in Gyrfalcons during some interactions (see below).

Postures and vocalizations that are apparently aggressive occur regularly in the copulation sequence of Peregrines. The female posture at this time is totally nonaggressive, as is her Whine vocalization. The male uses the Chitter vocalization and postures with aggressive components. There is little doubt of the aggressiveness of the Chitter, at least in some contexts. It has been observed during Upright Threat encounters, during forced (by female) Food-Transferring, and by both sexes when trying to force the mate off the eggs. The combination of this vocalization with the partly aggressive postures just before mounting is difficult to interpret. The female is not always intimidated by this behavior, although she is in a compromised position as the male mounts. Females do occasionally refuse mounting or aggressively displace the male after mounting, even when Copulation Solicitation occurred just prior to the mounting attempt. It is also unclear why the male sometimes continues the Chitter vocalization throughout copulation.

Willoughby and Cade (1964) describe for the American Kestrel a Chitter vocalization that is similar to the Peregrine Chitter in terms of its contextual use, but which apparently signals "friendly approach." The apparent difference in meaning may be related to the very slight size dimorphism in Kestrels. Because of similar size, the male may be more intimidating as he prepares to mount, and a nonaggressive signal might ease the interaction. Kestrels also use a Chitter vocalization during Food-Transferring.

The copulation sequence in Peregrines is characterized by a series of "testing" actions and responses. When the sequence is initiated, by male or female, the female assumes the Copulation Solicitation posture, often facing away from the male. An alternating series then proceeds, with the female looking up toward the male, the male responding with the Hitched-Wing Display and components of the Agonistic Head-Low Bow, and the female then responding with renewed head-low postures. The series may be repeated several times. In a completed sequence the female will maintain the soliciting posture as the male flies to mount. Female termination of the sequence involves a shift from the nonaggressive soliciting posture to an anti-aggressive Display, the Extreme Head-Low Bow. Although this usually caused the male to abort his mounting attempt, in two experienced pairs the male frequently mounted anyway, and copulation was usually completed.

Observations on the incubating behavior of wild Peregrines, especially by Nelson (1970), permit an interesting comparison with captive pairs, suggesting a difference in the pair

relationship that may be important. In nature, the female controls the schedule of incubation duty. If the male is incubating as the female arrives on the nest-ledge, he gets up almost immediately and leaves (Nelson 1970, Wrege unpubl.). The reverse situation does not necessarily elicit female withdrawal. Exchanges for incubation proceed very differently in captive Peregrines. Although the female's dominance is usually evident, either sex may approach the incubating mate and try to urge the mate off the eggs. The success of such an attempt is variable. Interactions of this form indicate a fairly close adjustment of the pair to one another. Although a dominance relationship develops, successful breeding requires that it be stable enough for overt female aggression to be minimal, so that the male is not constantly intimidated by the female. In the wild, where male avoidance may be a frequent response to female pressuring, interactions can be more agonistic. Interactions for the most part are very short in wild pairs.

Gyrfalcons are slightly less dimorphic than Peregrines. Differences are not great in the relative frequencies of head-low postures. These postures are rare in the female and can be interpreted as a reduction in the use of head-low postures as approach-eliciting signals. As mentioned previously for Kestrels, the male Gyrfalcon is intimidating to the female, probably more so than in Peregrines. As a result, definitely antiaggressive postures are more usual in some ritualized displays, as are aggressive components in others. For example, Mutual Ledge Displays are characterized by constant head-low postures by both birds. In contrast to male Peregrines, the male Gyrfalcon also maintains the head-low posture while soliciting a Food-Transfer. We interpret this posture as approach-eliciting for two reasons: the male rarely takes food to the female, at least early in the season; and the female approaches in a partly aggressive, horizontal posture, indicating a fear component. Male Peregrines have very rarely been observed in approach-eliciting postures.

Aggressive components are obvious in the female Gyrfalcon's primary Copulation Solicitation. When the male is at some distance, the female may initially solicit copulation with a horizontal head-low posture and a nonaggressive Whine. As the male shows intention movements to mount, the female assumes an entirely horizontal posture oriented toward the male and gives a vocalization with many similarities to the Chitter used in aggressive contexts (figs. 3c and 3e). Our male was intimidated by this Display, alternating between the Curve-Neck Display and anti-aggressive Head-Low Bow. Mounting proceeded only when the female was not oriented toward the male. These behavior patterns are consistent with a situation involving an intimidating male and preceding an action during which the female is in a compromised position. As with Peregrines, the male precopulatory postures involve aggressive components. Although the Curve-Neck Display stresses a lowered beak, the body posture is vertical and tall, accompanied by a vocalization apparently identical to the Chitter of aggressive situations. It is not clear why Gyrfalcons and Kestrels differ in the aggressiveness of male precopulatory behavior. The difference may well be related to the aggressive components in female Gyrfalcon solicitation.

Unfortunately, observations of Prairie Falcons are limited; comparison with Peregrines and Gyrfalcons is more difficult. In our captive pairs the pair-bond appeared strained, and it is well known among falconers that Prairie Falcons are the most aggressive of the North American species of *Falco*.

There is no question of the dominant position of the female in our captives. Frequent displacement of the male by the female is characteristic throughout the breeding season. During the nonbreeding season the mates avoid one another.

The extremely pugnacious temperament of Prairie Falcons is not easily explained in terms of the degree of size dimorphism, which is close to that of Gyrfalcons. However, a com-

parison of the relative frequencies of some behaviors is instructive in relation to the decided female dominance. It is possible that the pairs observed in this study were less well integrated than sometimes occurs. Fyfe (1972) observed a captive pair that was "at ease" with one another.

During Male Ledge Displays, even more than in the other species, the male Prairie Falcon is aware of the female's location in the room. Immediately upon her approach for a Mutual Ledge Display, an extreme head-low posture is adopted. During the Display the male constantly bows or presses himself almost flat on the ledge.

Female Solicitation for Copulation in Prairie Falcons involves an extreme head-low posture almost always oriented away from the male. Often solicitation is silent. Hitched-Wing approach by the male is usual, but aggressive postures just before mounting are not conspicuous.

Relative frequencies of aggressive, anti-aggressive, and approach-eliciting behavior exhibited by male and female falcons support an interpretation of female dominance. The degree to which this dominance can be initiated and maintained by "passive" intimidation as compared to more overt behavioral actions appears to depend on the difference in size between the mates. Intimidation of the mate owing to size difference is probably the major factor controlling relative frequencies of agonistic behavior. The ratio of these frequencies in a given pair depends on their specific degree of dimorphism and on their history, while the agonistic components of ritualized display behavior may be related to the size dimorphism characteristic of the species as a whole. Preliminary analysis of quantitative data tends to support these qualitative interpretations (Wrege unpubl.).

4. *The Function of Vocalizations in Social Communication.* Preliminary analysis of the vocalizations in these four species indicates that variability in the contextual use of vocalizations can be considerable. Intergradation from one vocalization to another is particularly striking in Gyrfalcons and Lanner Falcons. Many courtship vocalizations used by captive Gyrfalcons are based on a single sound unit, differing only in the speed with which the units are repeated (figs. 3a and 3c). The vocalizations of Lanner Falcons have not been analyzed; however, they sound very similar to Gyrfalcons. In Peregrines and Prairie Falcons the structures of some vocalizations are more complex. Variability of the vocalizations in these species is in the degree of completeness of the basic unit and is associated with the motivational level or intensity of the behavior, not with specific contexts.

Figure 2a shows the most common vocalization in Peregrine courtship. In its complete form the Eechip has three parts, but frequently one or more parts are deleted or repeated. The contexts in which this vocalization is elicited range from low intensity Individual Ledge Displays through agonistic encounters. With the exception of the territorial Cack vocalization and the female Copulation Wail, all vocalizations are used in numerous contexts.

Apparently the primary function of vocalizations is to communicate the intensity of motivation. As intensity increases, either the speed of unit repetition increases (Gyrfalcons and Lanners, especially), or the sound unit is fragmented, with some parts repeated before a new unit is initiated (Peregrines and Prairie Falcons).

Summary

The courtship behavior of Peregrine Falcons, Gyrfalcons, Prairie Falcons, and Lanner Falcons was studied for the purpose of describing their reproductive behavior, and, using comparative analysis, to characterize the pair relationship. Twenty pairs of falcons were studied for two to four years with an emphasis on Peregrine Falcons.

We found the behavioral repertoire very similar in the species studied, with at least 75 percent of the postures and displays common to all. Most interspecific differences were in the frequencies of certain Display postures, and in the specific characteristics of vocalization. The function of these behavior patterns in pair integration is apparently the same for all species, making these similarities important management tools for the captive breeding of falcons. Experimental work on species most available or amenable to manipulation can be used to predict, with some confidence, the outcome of similar manipulations on captive Peregrines or other endangered species.

The vocalizations of these species are also similar in their basic structure and function. All the vocalizations show high levels of frequency modulation, causing the "noisy" appearance of the audio spectrographs (figs. 2, 3, and 4). This basic structure may be related to the open habitats utilized by these species (Morton 1975). A more important similarity is the intergradation of some vocalizations and their nonspecific contextual use. In captivity, each species uses many vocalizations to communicate the intensity of motivation, and very few to communicate the motivation to perform a specific action. Copulation Solicitation and territorial defense calls fall into the latter group.

The seasonal ontogeny of reproductive behavior in Peregrines follows a predictable pattern, at least in experienced pairs. In pairs remaining together all year, courtship is initiated earlier each year for about three years. Copulation begins several weeks before egg-laying and probably helps to strengthen the pair-bond. The third and fourth eggs in a clutch can be fertilized by copulations just before and after the second egg is laid. This suggests that artificial insemination can be achieved with minimal disturbance to the pair, providing the technique ensures the placement of semen directly into the oviduct.

The frequency with which displays and postures are expressed is the major interspecific difference in the behavior of the captive falcons studied. Such a difference is consistent with the hypothesis that female dominance is a characteristic of the pair relationship in large falcons and is possibly necessary for successful reproduction. Apparently the primary factor that influences the relative frequency of aggressive and nonaggressive behavior is the degree of size dimorphism between the sexes.

The pugnacious nature of falcons and the potentially very serious injury from aggressive encounters may be the causes of a behavioral repertoire with the capacity to transmit finely tuned information about motivation and its intensity. The amount of information communicated through postures is probably very high. Frequently birds change their response to their mate when little or no change in posture was observed. The vocalizations in each species seem well suited to signaling the intensity of motivation.

Acknowledgements

We would like to thank James D. Weaver, Kathy Johnson, and Bill Heck for their assistance with the collection of data, and Mike Hopiak for help in the preparation of figures. This study was supported in part by grant number GB 31547 from the National Science Foundation and by contributions to The Peregrine Fund. Support was also received from the National Rifle Association, National Wildlife Federation, Wildlife Management Institute, and the American Petroleum Institute.

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