DENVER W. HOLT, *Owl Research Institute, P.O. Box 8335, Missoula, Montana 59807*; SCOTT M. MELVIN, *Massachusetts Division of Fisheries and Wildlife, Westboro, Massachusetts 01581*; AND BRIAN STEELE, *Dept. of Mathematical Sciences, Univ. Montana, Missoula, Montana 59806.* *Received 22 Aug. 1991, accepted 10 Dec. 1991.*

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**Frequency and timing of copulations in the Prairie Falcon.**—Several authors (Birkhead et al. 1987; Møller 1987a, b; Birkhead and Lessells 1988) have commented on the high copulation frequencies in birds of prey compared to other avian taxa. However, there is a scarcity of observations on the copulatory behavior of birds of prey. Møller (1987a) described the copulation behavior of the Northern Goshawk (*Accipiter gentilis*), Birkhead and Lessells (1988) investigated copulatory behavior of the Osprey (*Pandion haliaetus*), and Sodhi (1991) that of the Merlin (*Falco columbarius*). Here, I describe the copulation frequency and timing of the Prairie Falcon (*F. mexicanus*), a large monogamous falcon of western North America (Palmer 1988).

*Study area and methods.*—From 1984–1987, I observed 52 breeding pairs of Prairie Falcons in the Snake River Birds of Prey Area (BOPA) and Reynolds Creek watershed in southwestern Idaho for 613 days (9085 h). A pair was considered breeding if eggs were laid (Steenhof 1987). The study area is part of the western intermountain sagebrush steppe, characterized by cold winters and hot, dry summers (West 1983). The vegetation is dominated by big sagebrush (*Artemisia tridentata*), winterfat (*Ceratoides lanata*), and shadscale (*Atriplex confertifolia*) associations (U.S. Dept. Interior 1979, West 1983). Observations started up to seven weeks prior to incubation and continued until young were 30–35 days old or the nesting attempt failed. Blinds placed at an average distance of 147 m (range = 70–250 m) from the aeries were used to make observations, aided by 10–45 × telescopes and 10 × 50 binoculars. Each nesting territory was observed, on average, once every six days by two observers, each on a half-day shift. I used an entire day as the sampling unit to avoid sampling problems related to daily behavioral cycles of the falcons (Altmann 1974). Observations started half an hour before sunrise and were terminated half an hour after sunset. Behavioral data were collected continuously, using focal animal sampling (Altmann 1974). Copulations were recorded as single events. I was not able to distinguish between successful (i.e., cloacal contact between mating birds) or unsuccessful copulations. Sex was determined by the larger size of the female and position of the falcons during copulations. Females solicited copulations and begged for food, unlike males. Falcons were not individually marked, but stylized drawings of each nesting falcon's facial pattern aided identification of individual birds. The establishment of stable territorial boundaries early in the nesting season (Ogden and Hornocker 1977, Sitter 1983, Holthuijzen, unpubl. data) and the general openness of the terrain further facilitated the distinction between nesting pairs and intruding falcons. The data presented here were collected as part of a larger behavioral study on Prairie Falcons. More details on the sampling procedure can be found in Holthuijzen (1990) and Holthuijzen et al. (1990).

Hatching dates were calculated by back-dating ages of young, using a photographic aging key (Moritsch 1983). Start of incubation was based on a 34-day incubation period (Burnham 1983). Observation days were categorized in six-day intervals based on the approximate stage of the nesting cycle relative to the female's estimated clutch completion date and labelled by midpoints (pre-incubation, N = 91 days of observation [DO]: days −51, −45, −39, −33, −27, −21, −15, −9, and −3; incubation, N = 267 DO: days 3, 9, 15, 21, 27,

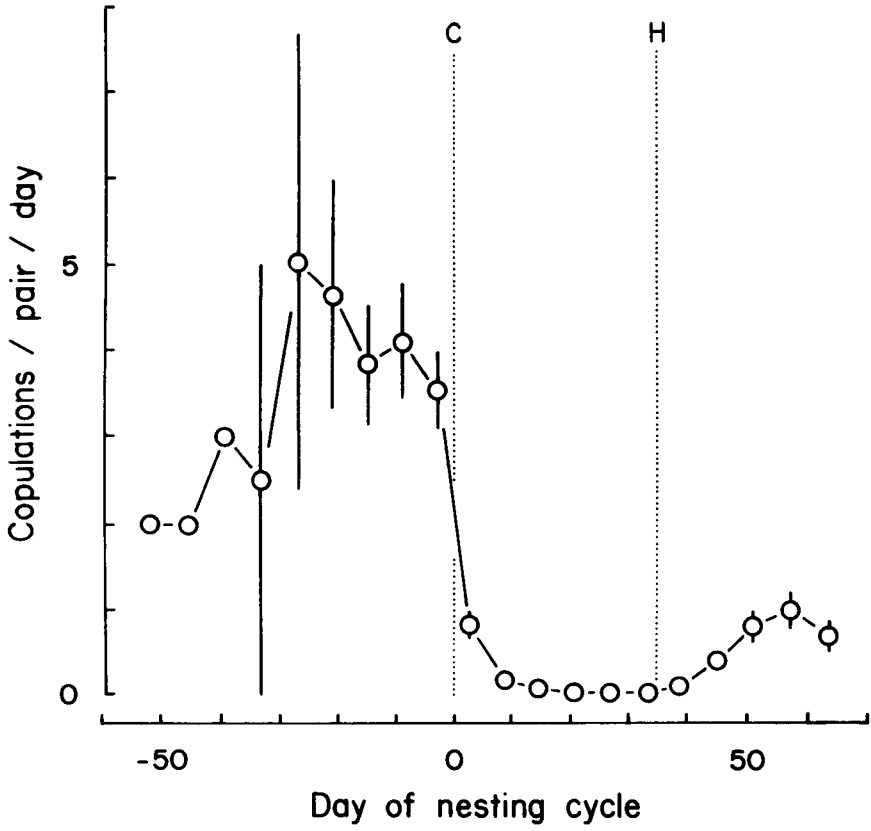


FIG. 1. Average number of copulations of Prairie Falcon pairs per day (±SE) during the nesting season (C = clutch completion, H = hatch).

and 33; and brood rearing, N = 255 DO: days 34, 39, 45, 51, 57, 63, and 69). Day 34 was included when falcons had newly hatched young (0–3 days).

The time of day when a behavior took place was standardized in hours after sunrise. Copulation frequency data were square root transformed (Sokal and Rohlf 1981). One-way analysis of variance (ANOVA) was used to determine differences in copulation frequency among nesting stages (copulations/day) and among hours of the day (copulations/h).

*Results and discussion.*—The total number of copulations over the 51-day pre-incubation period was estimated at 194 ± 15 (SE) copulations per clutch. On average, 28 ± 3 (SE) copulations per pair (N = 522 DO) occurred during incubation and brood rearing. The copulation frequency of the Prairie Falcon was high compared to the Osprey (59 copulations/clutch; Birkhead and Lessells 1988) and the Merlin (42 copulations/clutch; Sodhi 1991), but lower than the Northern Goshawk (500 copulations/clutch) (Møller 1987a), American Kestrel (*F. sparverius*; 690 copulations/clutch; Balgooyen 1976), and Eurasian Kestrel, *F. tinnunculus*; 374 copulations/clutch; T. Meijer in Birkhead and Lessells 1988).

None of the 553 observed copulations was identified as an extra-pair mating even though

the nesting densities of Prairie Falcons in the BOPA are the highest recorded for this species (U.S. Dept. Interior 1979). Birkhead and Lessells (1988) reported that EPC attempts occurred infrequently in Ospreys, but suggested that this may have been related to the low population density of Ospreys in the study area. Sodhi (1991) also recorded a small number of EPCs for the Merlin (3 of 41 copulations).

Copulations were observed at least 51 days prior to clutch completion, when falcons were already mated. Copulations peaked around 27 days before egg laying (Fig. 1) and remained high until clutch completion ($F = 29.59$, df = 21 and 591, $P = 0.0001$). Copulations averaged 3.8 ± 0.3 (SE) per day (N = 91 DO) during pre-incubation. Copulations then dropped off sharply and remained low throughout incubation (0.2 ± 0.04 [SE] per day [N = 267 DO]). During brood rearing the number of copulations per day increased again (0.6 ± 0.2 [SE] per day [N = 255 DO]). Most copulations (87.3%) took place during preincubation. To evaluate whether the copulation frequency peaked during the female's fertile period, I estimated the onset and duration of the female's fertile period (i.e., the period that sperm can be stored in the female's reproductive tract and remain viable up to oviposition of the last egg [Møller 1987a, Birkhead and Lessells 1988]). In captive, artificially inseminated Prairie Falcons sperm can remain viable for at least six days (Boyd et al. 1977). Fertilization of an ovum in these artificially inseminated females took place 50–60 hours prior to oviposition (Boyd et al. 1977). For an average clutch of 4–5 eggs in Prairie Falcons (U.S. Dept. of Interior 1979), I estimated the female's fertile period to be at least 12–14 days prior to clutch completion. Copulations were high 14 days before onset of the female's fertile period and remained high until clutch completion (Fig. 1).

During preincubation copulations per hour were highest in the first 2–3 hours after sunrise with a smaller peak in late afternoon to early evening ($F = 4.80$, df = 15 and 1408, $P = 0.0001$) (Fig. 2). During incubation copulation frequencies were similar among hours of the day ($F = 1.80$, df = 15 and 4176, $P = 0.03$). During brood rearing, however, copulation frequencies were higher during early mid-morning and early evening hours ($F = 2.77$, df = 15 and 3984, $P = 0.0003$).

To increase certainty of paternity, males can either guard their mates throughout the time that the females can be fertilized (Møller 1987c, Birkhead and Lessells 1988) or dilute sperm of possible competitors by frequent matings when they cannot guard the female (Birkhead et al. 1987). These predictions have been collectively referred to as the sperm competition hypothesis (Birkhead et al. 1987). Male Prairie Falcons provide for their mates (Holthuijzen 1990) and therefore, cannot guard the females continuously during the fertile period. In fact, Willoughby and Cade (1964) refer to the genus Falco as typical non-guarders. If sperm competition is an important factor determining copulation behavior, I would expect Prairie Falcons to have a high number of copulations per clutch, high copulation frequencies during the preincubation period, especially when the female is fertile, and optimal timing for fertilization during the day with peaks in the early morning and early evening (Birkhead et al. 1987, Birkhead and Lessells 1988). The results of this study are consistent with some of the predictions based on the sperm competition hypothesis. The number of copulations per clutch in Prairie Falcons is high compared to the number of copulations necessary for fertilization, a pre-requisite for the sperm competition hypothesis (Birkhead et al. 1987). Copulation frequencies in Prairie Falcons are high during preincubation, including the female's fertile period. Copulations also peaked in the early morning and late afternoon to early evening hours as predicted by the sperm competition hypothesis. There are significant deviations, however, in particular the absence of extra-pair copulations and no pronounced peak in copulatory activities during the female's fertile period. Several alternative explanations for high copulation frequencies in birds of prey have been proposed (Birkhead et al. 1987). Copulatory behavior during the preincubation period, before the female's fertile

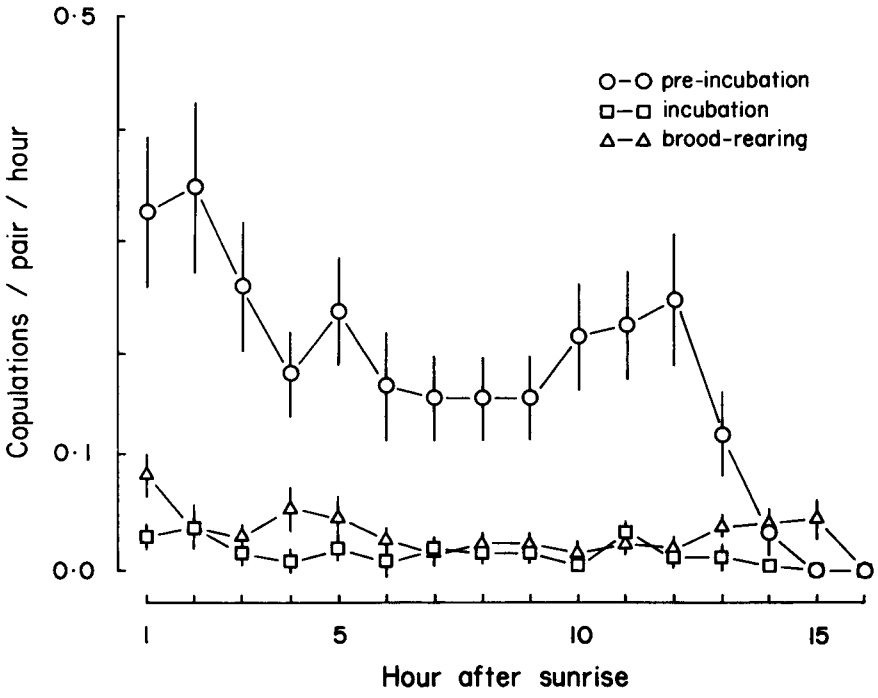


FIG. 2. Average number of copulations of Prairie Falcon pairs per hour (±SE) during the pre-incubation, incubation, and brood rearing stages.

period, can also be part of the mate assessment process, especially when the female solicits copulations (Birkhead et al. 1987), as is the case in Prairie Falcons. High copulation frequencies may be important in establishing the pairbond (Cade 1960, Newton 1979, Birkhead et al. 1987). Continued copulatory behavior after the female's fertile period suggests that this behavior may play an important role in maintaining the pairbond. In addition, increased copulatory activity during brood rearing may be related to a second nesting attempt. However, this explanation seems unlikely for Prairie Falcons nesting in the BOPA, because a second nesting attempt has never been recorded when the first one was successful (K. Steenhof, pers. comm.) (i.e., one or more young reached fledging age [Steenhof 1987]). No single hypothesis discussed here fully explains the observed copulatory behavior of Prairie Falcons. Maybe the copulatory behavior of the Prairie Falcon is driven by a combination of motivations. The data presented here cannot answer this question, but may be a starting point for further investigations.

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ANTHONIE M. A. HOLTHUIJZEN, *Idaho Power Co., Environmental Affairs Dept., P.O. Box 70, Boise, Idaho 83707.* *Received 1 Aug. 1991, accepted 20 Nov. 1991.*

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**Pairbond persistence and "divorce" in Black-capped Chickadees.**—Pairbond persistence over several years is common among parids including Black-capped Chickadees (*Parus atricapillus;* Odum 1942, Glase 1973); Carolina Chickadees (*P. carolinensis;* Brewer 1961, Dixon 1963); Mountain Chickadees (*P. gambeli;* Dixon 1965); and Plain Titmice (*P. inornatus;* Dixon 1949) in North America, and also in many European species, including the Great Tit (*P. major;* Hinde 1952) and others (reviewed in Perrins 1979). Occasionally, however, members of intact pairs may split up to form new alliances; Hinde (1952) and others have referred to this as "divorce." Among birds, divorce occurs when one member of an intact pair (two birds that bred together the last time breeding was possible) deserts its former mate to form a new pairbond with another bird; thus only birds that are at least one year old can be involved in divorce. Consequently, in birds such as Black-capped Chickadees, few, if any, birds with low winter rank can be involved in this process, since the vast majority of such birds (at least in most parid populations, including the chickadees in my study area) are less than one year old. In every divorce that I have observed, one bird moves and the other stays; I will consider the one that moves to be the bird that initiated the divorce.

This paper will examine all instances of divorce so far recorded in a small, color-banded population of Black-capped Chickadees in western Massachusetts, which I have been studying since the fall of 1979. During this time, the central winter population has varied from four to seven flocks, and the central breeding population, from 12 to 16 pairs (Smith 1988a, Smith 1991). This study population is not isolated physically from adjacent flocks or pairs, and for the purposes of the present paper, I also include data from banded members of peripheral chickadee groups.

Over the past ten years, I have recorded 15 instances of divorce among color-banded chickadees. During this same time period, 79 other intact pairs (just over 84%) remained together. Of the the 15 divorces, 10 were initiated by females and five by males. Three of these divorces occurred during winter; six occurred in spring (April and early May), and six occurred in late summer. All six of the spring divorces were early enough to permit breeding by the newly formed pair; by contrast, all of the summer divorces occurred too late for breeding to take place that year.

Fourteen of the 15 records involved clear rank increases for the divorce initiators (Table 1). Each male initiator went from beta to alpha male. Eight of the 10 female initiators went from second-ranked female to highest-ranked (in my study area, over the last 10 years, female winter rank has consistently reflected that of her mate; hence the top-ranked female is paired to the flock's alpha male). One female moved from third- to second-ranked female. Finally, one female (AlK KR; see Table 1) went from top-ranked female of a four-bird flock to top-ranked female of an eight-bird flock. Since most males rank above females during the nonbreeding season, a four-bird flock's highest-ranked female would rank above only one bird, whereas an eight-bird flock's highest female would rank above three other birds.