COPULATION AND MATE GUARDING IN THE NORTHERN FULMAR

SCOTT A. HATCH

Museum of Vertebrate Zoology, University of California, Berkeley, California 94720 USA and Alaska Fish and Wildlife Research Center, U.S. Fish and Wildlife Service, 1011 East Tudor Road, Anchorage, Alaska 99503 USA[1]

ABSTRACT.—I studied the timing and frequency of copulation in mated pairs and the occurrence of extra-pair copulation (EPC) among Northern Fulmars (*Fulmarus glacialis*) for 2 yr. Copulation peaked 24 days before laying, a few days before females departed on a prelaying exodus of about 3 weeks. I estimated that females were inseminated at least 34 times each season. A total of 44 EPC attempts was seen, 9 (20%) of which apparently resulted in insemination. Five successful EPCs were solicitated by females visiting neighboring males. Multiple copulations during a single mounting were rare within pairs but occurred in nearly half of the successful EPCs. Both sexes visited neighbors during the prelaying period, and males employed a special behavioral display to gain acceptance by unattended females. Males invested time in nest-site attendance during the prelaying period to guard their mates and pursue EPC. However, the occurrence of EPC in fulmars was largely a matter of female choice. *Received 29 September 1986, accepted 16 February 1987.*

THE occurrence and significance of extra-pair copulation (EPC) in monogamous birds has generated much interest and discussion (Gladstone 1979; Oring 1982; Ford 1983; McKinney et al. 1983, 1984). Because the males of monogamous species typically make a large investment in the care of eggs and young, the cost of being cuckolded is high, as are the benefits to the successful cuckolder. Males are expected to pursue opportunities for copulation outside the pair bond (Trivers 1972) and to reduce as far as possible the uncertainty of paternity for the young they help raise. The incidence of EPC may in general be higher in colonial species than in solitary nesters, and the threat of cuckoldry is postulated to be one of the principal disadvantages of colonial breeding (Alexander 1974, Hoogland and Sherman 1976).

Mate guarding may be defined as any behavior by a mated male whose principal function is to reduce the likelihood of encounters between his mate and other males during the time when fertilization of her eggs is possible. The importance of mate guarding in the monogamous male's reproductive strategy has been recognized in a variety of species (e.g. Beecher and Beecher 1979; Birkhead 1979, 1982; Power and Doner 1980; Power et al. 1981; Werschkul 1982a;

Bjorkland and Westman 1983; Buitron 1983; Birkhead et al. 1985).

I attempted to document the occurrence and behavioral context of extra-pair copulation and mate guarding in a colonial seabird, the Northern Fulmar (*Fulmarus glacialis*). Fulmars are among the longest-lived birds known, and fidelity to the same mate and nest site between years is high (Macdonald 1977, Ollason and Dunnet 1978, Hatch 1985). Only one egg is laid per clutch, and re-laying in the same season after the loss of a clutch is unknown. The sexes share about equally in incubation and chick-rearing duties (Hatch 1985). Thus, fulmars exhibit a highly conservative social system. Some features of the breeding biology make this species (and perhaps other Procellariiformes) particularly interesting from the standpoint of copulation behavior and potential sperm competition. At Pacific colonies, fulmars arrive synchronously some 6–8 weeks before the first eggs are laid. There is thus a considerable prelaying period for social interaction. Foraging occurs over large ocean areas in bouts of several days, and it is difficult for males and females to coordinate perfectly their attendance patterns at the nest site. Females are receptive to copulation over the whole prelaying period, and sperm are stored in special glands in the utero-vaginal (UV) region of the oviduct (Hatch 1983). Sperm remain viable in the UV glands for several

[1] Present address.

weeks, as frequently there is no contact between the male and female during the "prelaying exodus" (Warham 1964), a time of continuous foraging immediately before egg laying (lasting up to 38 days in fulmars; Hatch 1985). The combination of intermittent attendance patterns, sperm storage, and a prolonged receptive period in the female renders the male fulmar particularly susceptible to being cuckolded.

I studied the timing and frequency of copulation in mated pairs, both in relation to calendar date and relative to the laying dates of individual females. Social relations outside the pair bond, including EPC, were documented in a series of extended watches on a group of known individuals during 2 yr. Finally, I examined patterns of nest-site attendance during the prelaying period during 6 yr for evidence of mate guarding.

METHODS

The study was conducted on the Semidi Islands, Alaska (56°N, 156°W), where an estimated 440,000 fulmars breed (Hatch and Hatch 1983). The main study area on Chowiet Island contained 6–8 plots that were used to monitor colony attendance from 1976 to 1981. The plots comprised 500–700 nest sites. Monitoring began 4–8 weeks before egg laying and continued through the late chick stage in most years. Daily counts of single birds and pairs on the plots were made between 0900 and 1600. I also monitored several hundred sites individually, noting the attendance of adults and the presence of eggs or young each day. Both procedures provided information on nest-site attendance used in the present analysis (see also Hatch 1985).

All birds used in the study of social interactions (1980–1981) were sexed by their position in copulation, and their breeding status was determined by site attachment and egg laying. Fulmars occurred in a wide range of color phases, and most birds also had distinguishing black marks on the culmen. Thus, a combination of plumage differences and bill markings provided a reliable system for individual identification. Initially, I sketched each bird's bill markings on a template drawing of the head to provide a permanent record of individual identity. After memorizing the layout of nest sites and individual markers (an easy task because site-holding fulmars were relatively sedentary on land), all observations of behavior were ascribed to individuals according to sex and site number.

The basic unit of behavior I recorded was the visit, defined as the directed approach of one bird (the visitor) to within 0.5 m of another individual or pair at a nest site (the host). Visitors usually arrived on the wing, but close neighbors also moved between sites on the ground.

In May 1980 I made notes opportunistically on extra-pair visits and completed 21.3 h of dedicated observations on one plot of about 130 nest sites (plot Q). Observations on plot Q in 1980 encompassed the whole plot, without regard to particular focal pairs. For 3–6 h on each of 5 days I watched for interactions among known individuals and recorded on audiotape the characteristics of all visits detected. In addition, whenever I detected a visit involving known breeding birds during my daily rounds of other plots, I stopped to observe the encounter to its conclusion, and recorded information on duration, behavior of the sexes, and the visitor's identity. All visits involving breeding birds of opposite sex were placed in one of four categories for the purpose of presentation. In type 1 a breeding male visited an unattended breeding female, in type 2 a breeding male visited a breeding pair, in type 3 a breeding female visited a lone breeding male, and in type 4 a breeding female visited a breeding pair.

A standard copulation count was conducted each afternoon or evening (3–26 May). All occurrences of mounting in 1 h were noted, including both successful and unsuccessful copulations (see below), and the number of pairs on the plot was recorded at the beginning and end of the hour.

In 1981 all behavioral observations were confined to plot Q. Two observers worked alone or simultaneously, each observing a sample of 24–31 nest sites for 1–9 h daily from 17 April to 26 May, for a total of 176 h. The same sample of nest sites was observed throughout the season, but not all sites under observation at any one time were occupied. I sampled occupied sites for 4,173 site-hours, including 1,655 site-hours for singles and 2,518 site-hours for pairs. Again, the visit involving known breeding birds was the focal unit of behavior, and the large majority of occurrences probably was detected. Identity and breeding status were determined as necessary for birds that interacted with focal pairs. Information recorded on audiotape for each visit included time, identity and general behavior of the participants, duration of the visit, occurrence of EPC attempts or other physical contact, and presence or absence in the colony of the visitor's mate. All occurrences of copulation in focal pairs during behavior watches were recorded, and standard 1-h copulation counts were conducted daily in 1981.

Successful copulations were easily distinguished from unsuccessful attempts because the apposition of the birds' cloacae was a labored and conspicuous process, as was the final thrusting by the male (lasting several seconds) once cloacal contact was achieved. Copulation sequences that included cloacal contact and thrusting most likely resulted in insemination. I refer to those as "completed copulations." I use the
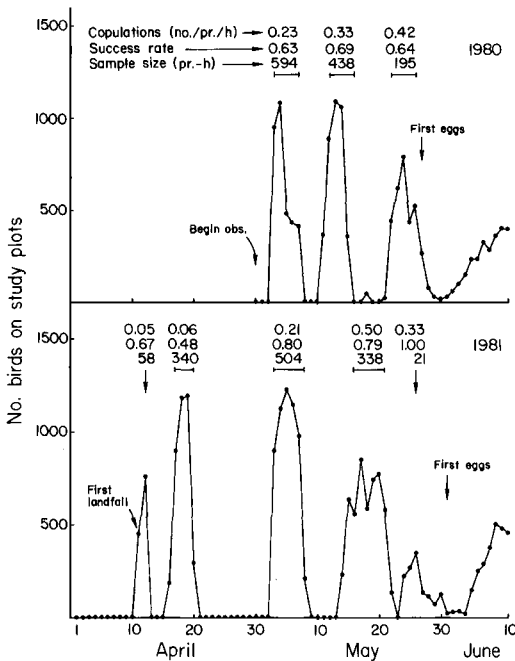
Fig. 1. Patterns of prelaying nest-site attendance in 1980 and 1981 and rates of attempted and successful copulation observed in the indicated time periods.

term "multiple copulation" for instances in which a male completed two or more successful copulations in a single mounting. In those instances, each copulation involved the full behavioral sequence, with distinct episodes of cloacal contact and thrusting.

In this paper, the term "nonbreeder" refers to any bird that did not regularly occupy a site in which an egg was laid. Two categories of nonbreeding fulmars were distinguished. Unattached nonbreeders had no steady partner and no particular site attachment. Most individuals in this group probably were prospecting birds that had never bred (prebreeders). They landed repeatedly in various places on the plot and, in fact, accounted for most of the visiting going on at any time. By contrast, established nonbreeders were site-holding pairs that behaved like breeders, except they produced no eggs. Some birds in this category probably had bred in a previous year. Of the 62 pairs included in the 1981 focal group, 57 were breeding pairs and 5 pairs were established nonbreeders. Except where stated otherwise, all observations on extra-pair relations reported below involved the males and females of the 57 breeding pairs and other known breeding birds with which they interacted.

The mean distance between neighboring nest sites on plot Q was 1.2 m (estimated visually). The laying times of individual females in this study were determined to within 24 h.

RESULTS

Behavior during copulation attempts.—The behavior of fulmars during copulation was described by Macdonald (1975). Pertinent features from my own observations are: (1) No pre- or postcopulatory displays ordinarily were associated with copulation in a mated pair. (2) Copulation was protracted, rarely lasting less than 1 min and sometimes 6–8 min or longer. (3) Female cooperation to the extent of allowing cloacal contact was essential for successful copulation. Contact was achieved as the female gradually raised and rotated her tail to meet that of the male, who appeared unable to effect contact unless he received this response. (4) Copulation always occurred on land and usually at the nest site; it was never observed on the water. (5) Failure of copulation was common, and appeared to be caused by the birds being in a poor position (e.g. a cramped nest site or uneven footing); poorly coordinated behavior; a low state of motivation, as some copulations were initiated but left unfinished; strong onshore winds that caused the birds to lose their balance; or the male being distracted by a bird (usually a nonbreeder) landing close by. There was little indication that visiting birds purposely disrupted copulations in progress; nonbreeders commonly landed near site-holding pairs at other times, and their behavior after landing was generally passive in any case.

Timing and frequency of copulations.—Nest-site attendance in the prelaying period was intermittent, with synchronous visits to land alternating with periods of several days when no birds were present (Fig. 1). I witnessed the first landfall of the season in 1981, when the prelaying period (first landing to first eggs) lasted 50 days. Fulmars copulated frequently during each peak in attendance, and the rate increased steadily as the onset of egg laying approached.

In 1981 the standard 1-h copulation count was divided into a 0.5-h morning segment (conducted between 0800 and 1030) and a 0.5-h afternoon segment (conducted between 1300 and 1700). Altogether, 753 pairs copulated 123 times in the morning hours (0.327 copulations·pair^{-1}·h^{-1}) and 747 pairs copulated 134 times in the afternoon (0.359 copulations·pair^{-1}·h^{-1}). Thus, there was no evidence that copulation frequency varied with the time of day ($G = 0.678$, $P > 0.3$). In calculating the total number of copulations per female, however, I assumed
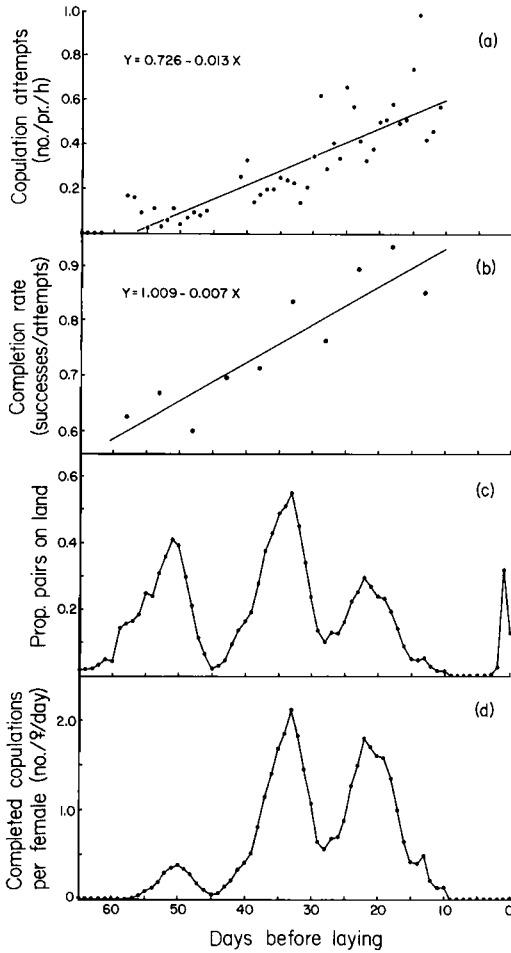
Fig. 2. Estimated rates of attempted and successful copulation in 1981 relative to individual laying schedules. (a) Linear regression of mounting frequency and day before laying in 57 breeding pairs on plot Q ($r^2 = 0.72$, $P < 0.001$). (b) Regression of copulation success rate (5-day means) over the same interval as above ($r^2 = 0.82$, $P < 0.001$). (c) Nest-site attendance by pairs during the prelaying period. The proportion of pairs at land on a given day is an estimate of the time pairs spent together at that stage. (d) Daily rate of completed copulation estimated for an individual female as the product of functions (a), (b), and (c) above. The vertical scale assumes that copulation occurred only during a 16-h period of daylight (see text).
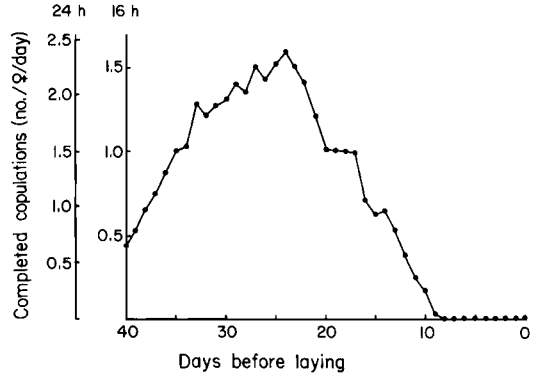

Fig. 3. Generalized pattern of copulation timing in relation to laying date obtained by combining 1981 mounting and success rates (Fig. 2) and averaged data on daily prelaying attendance by pairs in 6 yr. The two vertical scales assume effective day lengths of 24 h and 16 h.

the measured rates of copulation applied only during a 16-h period of daylight.

Within pairs, mounting frequency was positively correlated with the number of days remaining until egg laying (Fig. 2a), as was the rate of successful copulation attempts (Fig. 2b).

There were no copulations from 10 days until 2 days before egg laying, as attendance by pairs dropped to zero in that period (Fig. 2c). In fact, the interval between the last copulation and laying was usually longer than 10 days, because birds stayed at sea an average of 16.9 days (males) or 18.7 days (females) immediately before laying (the prelaying exodus). About one-third of the pairs were together at the nest site on the day before laying, but copulation was then extremely rare (pers. obs.).

The product of mounting frequency and success rate (Fig. 2a, b) was the hourly rate of completed copulations expected on each day of the prelaying stage. However, pairs spent less than half their time together before laying (Fig. 2c). Thus, the product of mounting frequency, success rate, and coincident attendance by the pair provided an estimate of the daily rate of completed copulations for an individual female (Fig. 2d). Because of the intermittent attendance of birds during prenesting (Fig. 1) and a high degree of breeding synchrony in the colony (SD of egg dates = 3.3 days), pair attendance and copulation rates both retained a strongly periodic pattern relative to individual laying dates.

The relationships in Fig. 2a and 2b probably apply approximately to all years. Therefore, I combined those functions with the 6-yr average attendance pattern of pairs from 40 to 1 day before laying to produce a generalized pattern of copulation frequency. The result indicated that effective copulation peaked an average of

TABLE 1. Extra-pair visits observed in 1980 and their outcomes.

Type	No. observed[a]	Duration (min)				EPC[b]		Multiple copula-tion[c]
		<1	1-5	6-60	>60	Attempts	Success	
1 (♂ → ♀)	16	1	3	4	8	11	3	1
2 (♂ → ♂♀)	1	1	0	0	0	1	0	—
3 (♀ → ♂)	16	0	12	3	1	5	3	2
4 (♀ → ♂♀)	0	—	—	—	—	—	—	—

[a] Nonrandom sample of visit types (see text).
[b] Multiple attempts to mount during a single visit counted as 1 EPC attempt.
[c] Multiple copulations during a single mounting counted as 1 EPC.

24 days before laying (Fig. 3). Integrating this daily rate over the whole prelaying period, I estimated that females were inseminated a mean of either 34 times (assuming a 16-h day) or 51 times (assuming a 24-h day).

The occurrence of within-pair multiple copulation was exceedingly low. I saw only two instances of apparently double insemination in nearly 800 copulations observed in 1981. One instance of four apparent inseminations during a single mounting was noted, but the status of the birds (whether mated or not) was unknown.

Extra-pair copulation.—Thirty-three visits involving breeding birds were observed in 1980, and included equal numbers of type 1 and type 3 visits (Table 1). EPC attempts occurred in 17 of the 33 visits (52%), and 6 EPCs (35%) were successful. Three of the 6 successful EPCs were multiple copulations, involving two apparent inseminations in each instance. The 1980 data comprised a decidedly nonrandom sample of extra-pair encounters because I detected the occurrence of those encounters almost solely by the observation of a characteristic male display (described below) that occurred frequently in the context of type 1 and type 3 visits.

Thirteen males, 12 females, and 13 different male-female pairings were involved in the 17 EPC attempts. The 6 successful EPCs included 5 different pairings. One male and female copulated successfully twice, once at the female's nest site and once at the male's site. Both of these were multiple copulations involving two apparent inseminations each. Thus, one female was inseminated up to four times by a breeding male other than her mate. In addition to the 17 EPCs among breeding birds, there was 1 successful and 1 unsuccessful copulation involving different nonbreeding males with breeding females, and 2 unsuccessful copulations were attempted by breeding males with nonbreeding females.

In 1981 I recorded 205 visits among breeders. Twenty-seven EPC attempts occurred, but only 3 (11%) were successful (Table 2). Two of the three successful EPCs involved the same male and female, and one was a double copulation. Thus, one female was inseminated up to three times by the same outside male.

The 27 EPC attempts among breeding birds in 1981 involved 13 males, 18 females, and 20 different pairings of males and females. There were, in addition, 9 EPC attempts (1 successful) involving a breeding male and a nonbreeding female, and 1 unsuccessful attempt by a non-breeding male to copulate with a breeding female.

A majority of EPC attempts occurred during type-1 visits, but the majority of successful EPCs occurred between a male at his own site and a visiting female (type 3). Ten (91%) of the 11 EPC attempts in 1981 that occurred when a male approached a breeding pair (type-2 visits) involved the same male. Over several days the bird made repeated attempts to force copulation by flying in and landing on the back of attended females (7 different individuals) in the vicinity of his nest site. In all cases, these attempts were brief and apparently futile, as the intruder was quickly routed by the host pair. One other male made a similar attempt in 1981, and there was one instance in 1980, both with similar results.

The frequency of visits and the frequency of attempted EPC increased from one prenesting cycle of colony attendance to the next (Fig. 4). In the final days of the prenesting period, however, visits to pairs (types 2 and 4) were limited by the scarcity of pairs in attendance.

Other behaviors outside the pair bond.—Observations in both years indicated that interactions among breeding birds were prevalent outside the pair bond, but did not necessarily involve attempted or successful EPC. Altogether, 40 (70%) of the 57 males observed and 44 (77%) of
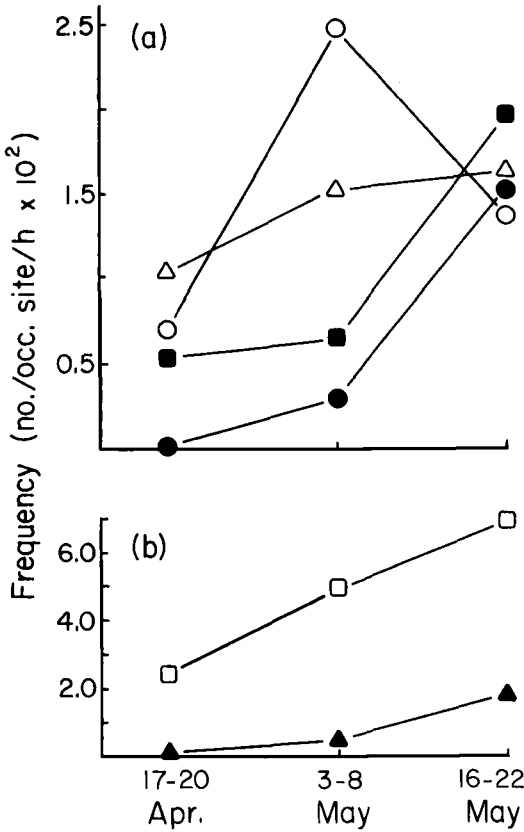
Fig. 4. Rates of visiting and extra-pair copulation (EPC) among breeders on plot Q in 1981. (a) Frequencies of type-1 (solid circles), type-2 (open triangles), type-3 (solid squares), and type-4 (open circles) encounters. (b) Total frequency of all encounter types (open squares) and frequency of EPC attempts (solid triangles). The three time periods on the abscissa correspond to prelaying peaks of colony attendance illustrated in Fig. 1.

the 57 females acted as a visitor or host at least once, and birds from 46 different sites (81%) were involved. Visits lasted from less than 1 min to more than 1 h (Table 2). Visits involving a single male and female generally lasted longer than threesomes, and in a few instances of extended absence by their mates, neighbors spent an entire day or parts of two or more days together.

The incidence of physical contact, such as billing or allopreening, between a host and visitor was related to the type of visit, and occurred most commonly when a female visited a lone male at his site. Contact between a visiting female and the male of a host pair also occurred

TABLE 2. Characteristics of 205 visits among breeding birds during the prelaying period (17 April–26 May) in 1981.

Type	No. observed	Participants[a]		Duration (min)				Physical contact[b]	EPC[c]		Multiple copulation[d]	Visitor's mate[e]	
		Visitors	Hosts	<1	1–5	6–60	>60		Attempts	Success		Present	Absent
1 (♂ → ♀)	33	25, 14	20, 17	11	8	12	2	7	9	1	0	3	30
2 (♂ → ♂♀)	57	23, 17	36, 23	40	15	2	0	1	11	0	—	15	42
3 (♀ → ♂)	50	20, 15	30, 20	18	22	8	2	33	7	2[f]	1	22	26
4 (♀ → ♂♀)	65	23, 19	47, 24	38	27	0	0	14	0	0	—	46	17

[a] Total number of different individuals (or pairs) engaged in one or more visits (first value), and number of focal individuals or pairs (of 57 under observation) participating (second value).
[b] Includes billing or allopreening, or both, but excludes EPC attempts that did not involve either behavior.
[c] Multiple attempts to mount during a single visit counted as 1 EPC attempt.
[d] Multiple copulations during a single mounting counted as 1 EPC.
[e] Presence or absence of visitor's mate in visitor's nest site at time of the encounter.
[f] Both successful copulations involved the same male and female (see text).

TABLE 3. Occurrence of unattended females during the last 40 days of the prelaying period in relation to their breeding status.

Status of pair	No. observations (nest-days)	No. singles	Single	
			No.	%[b]
Breeding	30,564	4,919	683	13.9
Nonbreeding[a]	3,390	353	81	22.9

[a] Established nonbreeders only (see Methods).
[b] $P < 0.001$ ($G = 19.2$, 1 df) for the difference between percentages.

frequently, whereas males that visited pairs almost never engaged in such activity with the host female.

A behavior pattern observed frequently during type-1 and type-3 visits was so nearly exclusive to those situations that I refer to the behavior as the extra-pair courtship display (EPCD). This display, performed only by the male, was characterized by intermittent soft cackling directed at the host female. Brief bursts of cackling (1–2 s) were spaced at fairly regular intervals ranging from about 3 to 8 s, suggesting a relative scale of intensity in the display. Males sometimes performed the EPCD almost continuously for 10–20 min and for more than 1 h in extreme instances. The EPCD was seen only during the prenesting stage and proved to be a reliable behavioral cue for sexing individuals, the only apparent one other than copulation itself. Only twice was a male seen directing this display toward his mate. In each instance it occurred, briefly and at low intensity, after the female returned from several days' absence during which the male had remained alone at the nest site.

In the course of an extended type-1 encounter there was frequently a progression of female responses toward passive acceptance of the outside male's presence at her nest site. If a female's initial reaction to the approach of a male was strongly agonistic (e.g. threatened or actual spitting of stomach oil), relations usually advanced no farther, despite persistent effort by the male. Sometimes, however, a type-1 visit that began with the female avoiding her visitor by moving to the far side of the nest site or flying out and staying away for brief periods progressed to nervous bill flicking or nibbling the male's breast feathers as he continued the EPCD, and finally to pairlike behavior. The male

then ceased his display and the birds sat side by side, occasionally billing or allopreening, and displaying together to other birds that landed nearby.

Males that attempted to mount usually were rebuffed as the female side-stepped the attempt, flew from the nest site, or reared up and dislodged the male if he succeeded in gaining the normal position for copulation. Brief fighting erupted occasionally, but the female apparently had the option to fly at all times, and she usually did so if the encounter became physically aggressive. A male that failed in an EPC attempt usually resumed the EPCD and did not attempt to mount again for some time, if at all.

Visits among breeding birds ordinarily involved close neighbors. This apparently was not due to a biased sample in which the only visits detected were those that occurred among neighbors. In some instances I first recognized an extra-pair encounter from behaviors such as the EPCD already described, not knowing the location of the visitor's nest site. When the visitor returned to its own site, it almost invariably proved to be a close neighbor.

Some females sought contacts with several males other than their mates. There were instances in which the same female visited three or four different males in the same day or season, spending up to several minutes with each and engaging in behavior normally associated with mated birds, such as billing or mutual vocal displays. The familiarity implied by these temporary associations carried over between years, as similar extra-pair interactions between known individuals were observed in 1980 and 1981.

Mate guarding.—Males behaved in several ways that tended to reduce the probability of type-1 encounters involving their mates. First, the proportion of occupied sites containing pairs was higher than the expected value (on the null hypothesis of independent attendance by the sexes) on all but 2 of 105 days in the prelaying period (Fig. 5). The exceptions occurred on 22–23 May 1980, when a high proportion of lone males present reduced the observed proportion of sites with pairs. Second, the disparity in male and female time investment followed a characteristic pattern with respect to a given cycle of prelaying attendance. The occupation of sites by pairs approached 100% (50:50 sex ratio) on days of peak attendance, but the proportion of
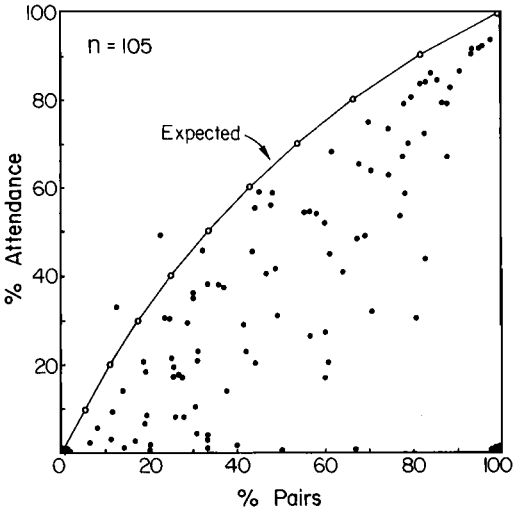
Fig. 5. Observed and expected relationships between the percentage of birds at the colony and the percentage of occupied sites containing pairs. The expected relationship assumes similar but independent attendance by males and females and was calculated as follows: % pairs = $[P/(200 - P)]100$, where $P = \%$ attendance/100 (see Coulson and Horobin 1972). The graph includes observations on 105 days with non-zero attendance during prelaying periods from 1976 to 1981. The analysis is conservative because it assumes equal amounts of prelaying nest-site attendance by males and females, whereas males actually spend more time on land than females (Hatch 1985).

lone males decreased before the peak and increased afterward (Fig. 6). That is, with respect to each episode of attendance in the prelaying period, males tended to be the first to arrive and the last to leave. Third, males tended to go visiting only when their mates were absent from the colony, whereas females went visiting whether their mates were present or not (last two columns of Table 2). Considering type-1 and type-3 visits, for instance, females were more than twice as likely as males to go visiting when their mate was present. Finally, the females of established nonbreeding pairs were unattended by their partners more frequently than the females of breeding pairs ($P < 0.001$; Table 3), consistent with the hypothesis of male nest-site attendance as mate guarding.

The temporal component of sex differences in nest-site attendance varied during the prelaying period. Relative to individual laying dates, nest-site attendance was highest from about 35 to 23 days before egg laying, after which
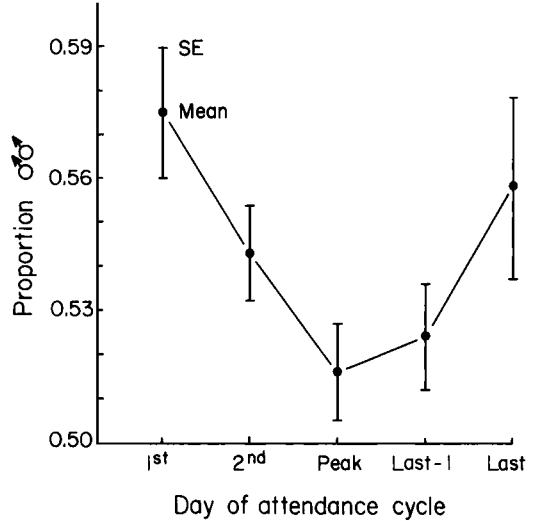

Fig. 6. Changes in the sex ratio among birds at nest sites during a typical cycle of prelaying attendance. Included are data from 7 peaks of prelaying attendance observed from 1977 to 1981 (see Fig. 1 and Hatch 1985). Only cycles that attained near-maximal values for the season and an approximately equal sex ratio at their peak were used (e.g. 3–7 May and 11–15 May 1980, 16–20 April and 3–8 May 1981, Fig. 1).

it steadily declined as birds departed on the prelaying exodus (Fig. 7a). As the laying date approached, the sex ratio of birds on land was increasingly biased toward males, approaching 100% in the last 10 days (Fig. 7b). Moreover, although the occurrence of pairs at nest sites was consistently higher than expected throughout the prelaying period (Fig. 5), it was relatively highest at times when nest-site attendance was low, i.e. earlier than 35 days and later than 20 days before laying (Fig. 7c). That is, females that delayed departure on the prelaying exodus, and those that visited the colony in the 3 weeks before they laid, were rarely unattended by their mates.

DISCUSSION

The incidence of EPC in fulmars was lower than has been reported in some other colonial species (Bray et al. 1975, Gladstone 1979, Roberts and Kennelly 1980, Fujioka and Yamagishi 1981, Werschkul 1982b), lower also than in ducks (McKinney et al. 1983), and possibly lower than in some territorial passerines (Ford 1983, Alatalo et al. 1984; but see Monnett et al. 1984).
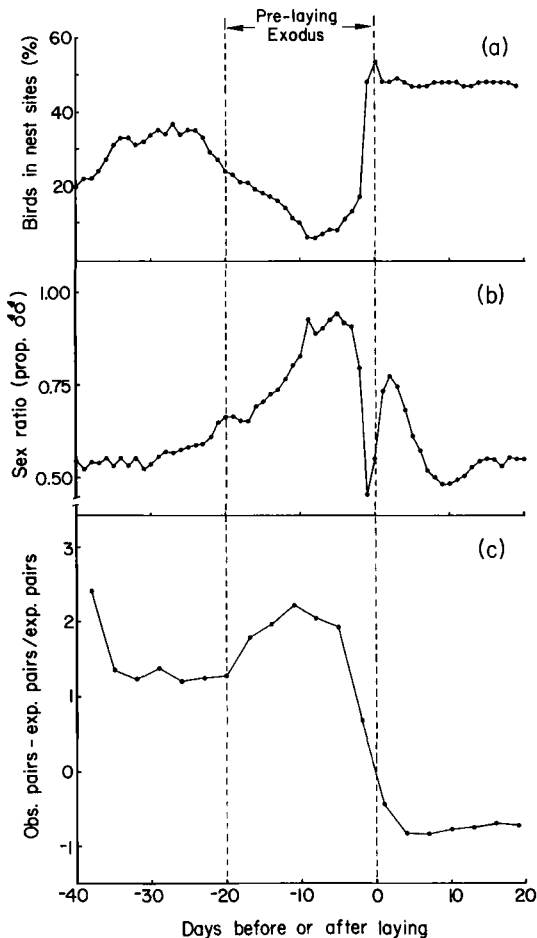
Fig. 7. Patterns of nest-site attendance during prelaying and early incubation stages, combining data collected in 6 yr, 1976–1981: (a) overall percentage of birds in nest sites, (b) sex ratio among birds present at a given stage, and (c) standardized difference between observed and expected numbers of pairs (3-day means) on the null hypothesis of independent attendance by males and females. Expected values are calculated as $(M \times F)/N$, where M = number of males present during a count, F = number of females present, N = number of nest sites observed. Here, unlike Fig. 5, there is no assumption that males and females spend equal amounts of time at the nest site.

Thus, the potential noted previously for a high incidence of cuckoldry in fulmars appeared to be largely unrealized. The existence of special behaviors associated with EPC pursuit and defense, however, suggests that the threat of cuckoldry has been, and remains, an important factor influencing fulmar behavior during the prelaying period.

Among Procellariiformes, EPC has been reported only in albatrosses (Tomkins 1983, McKinney et al. 1984), but male prelaying attendance patterns suggestive of mate guarding have been reported widely (Davis 1957; Tickell 1962, 1968; Harris 1966; Imber 1976). Also, the behavior of breeders visiting and spending time with other breeding birds has been noted in various species of petrels (Richdale 1963, Tickell and Pinder 1966, Beck and Brown 1972, Imber 1976). Of particular interest in fulmars was the bilateral character of relations outside the pair bond, with females commonly initiating the contacts.

Sperm competition.—Copulation occurred over the whole prelaying period and peaked about 24 days before egg laying. Even the earliest copulations probably involved the transfer of sperm, as indicated by the presence of sperm in an oviduct collected on 18 April 1981, 5 weeks before the first eggs appeared in the colony (Hatch 1983). Thus, fulmars exhibit two features, sperm-storage organs in the female and a prolonged receptive period, that predispose this species to sperm competition (as defined by Parker 1970).

In the event a female is inseminated by more than one male, the outcome of sperm competition will depend greatly on the system of sperm precedence, i.e. whether sperm from the first mated male predominate, sperm from the last male supersede earlier deposits, or random sperm mixing occurs (Wade and Arnold 1980). In mammals, modes of sperm precedence may be highly species specific (Dewsbury and Baumgardner 1981, Oglesby et al. 1981). There is little comparative information available for birds, but experiments with domestic fowl and captive Mallards (*Anas platyrhynchos*) generally have shown that the most recent sperm have an advantage in fertilizing eggs (e.g. Compton et al. 1978, Cheng et al. 1983). However, in an experiment that simulated in some important respects the situation in fulmars, the sperm of a second male chicken (*Gallus gallus*) superseded that of the first only if the second male had continued access to the female (Warren and Kilpatrick 1929). Eggs laid more than 24 h after removal of the second male were equally likely to be fertilized by sperm from either one. These results seem especially relevant to the interpretation of copulation behavior in birds that inseminate repeatedly and have delayed fertilization. I postulate that the usual delay of 10–

30 days between the last insemination and fertilization in fulmars promotes sperm mixing and reduces the last-male advantage.

Male reproductive strategies.—Sperm mixing and a reduced last-male advantage may explain the seemingly high frequency of insemination (34–51 times before laying) in this species, in which only one egg is laid. A male that copulates so frequently with his mate may be all but assured of paternity even if the female has engaged in EPC. He would, of course, also increase the likelihood of being the last male to copulate. The relatively high incidence of multiple copulation during EPC suggests outside males attempted to increase the proportion of their sperm in the storage glands.

The strategy of flooding a female with sperm to increase the likelihood of paternity has been suggested to explain the high copulation frequency observed in the White Ibis (*Eudocimus albus*; Benshoof and Thornhill 1979). Indeed, there may be a correlation between copulation frequency and the relative threat or consequences of cuckoldry, but few data are available on the frequency or total number of inseminations per reproductive cycle in wild birds. The range appears to be once (as in certain lekking species; Wiley 1973, Oring 1982) to dozens of times (Brown 1967, Burger 1976, Gochfeld 1980, this study).

The abundance of sperm introduced into the female reproductive tract may thus be one element of the male strategy, but in addition males invested more time in prelaying nest-site attendance than females, which I interpret as mate guarding. It can scarcely be viewed as site defense as there was little fighting or other agonistic behavior except in the context of EPC. Other birds rarely spent time in unoccupied nest sites, even in the most crowded portions of the colony. Macdonald (1980) also noted the apparent lack of necessity for strong nest-site defense in a colony of fulmars.

Mate guarding and the pursuit of extra-pair copulations may be mutually exclusive male activities (Beecher and Beecher 1979, Mineau and Cooke 1979, Barash 1981, Werschkul 1982b). This was only partially true for fulmars; by spending time in or near his nest site, a male effectively guarded against the unaccompanied return to land of his mate but was also free to visit neighboring females or be visited by them.

Female reproductive strategies.—An alternative explanation for the prolonged receptive period and large number of copulations in fulmars postulates an advantage to females of this behavior. Lumpkin (1981, 1983) suggested that females of monogamous species may deceive their mates about the timing of their fertile period by soliciting copulation well ahead of the time when effective (fertilizing) inseminations can occur. The tactic is viewed as a means to elicit more guarding behavior from the male, on the premise that females benefit from increased levels of male guarding. Critical data for evaluating this hypothesis are lacking in my study, because the maximum length of the fertile period in fulmars is unknown. Presumably, it averages no shorter than about 4 weeks to accommodate normal variability in the prelaying exodus.

The male's ability to restrict access to his mate clearly was limited by the female's tendency to associate with other males away from the nest site. Inasmuch as 5 of 9 successful EPCs occurred during type-3 visits (females visiting males), and successful EPC appeared to require female cooperation in any case, relations outside the pair bond appeared to be largely a matter of female choice. The view that most EPCs in monogamous birds are forced on unwilling females has generally prevailed (Gladstone 1979, McKinney et al. 1984), and the phenomenon I observed of mated females soliciting copulation from outside males has rarely been reported (McKinney et al. 1983). The behavior runs counter to most theoretical treatments of female reproductive tactics in monogamous species (Trivers 1972, Gladstone 1979).

There are at least three ways a female might benefit by copulating with males other than her mate. First, she may confer on her offspring the genes of an especially fit male whose quality she has been able to assess (Trivers 1972). Second, she increases the lifetime genotypic variability of her offspring and therefore possibly her own fitness (Williams 1975). Third, the female whose mate is derelict in his prelaying attendance and copulation in the current season, or that has experienced infertility with her partner in the past, may attempt to prevent its recurrence by copulating with other males.

The criteria involved in female choice in this system could include the attendance patterns of a neighboring male as an indicator of his individual quality. I have attempted, with some success, to relate these patterns to breeding suc-

cess (Hatch 1985), and female fulmars poten-tially have much more information on this point than I. More directly, females have information on their neighbors' records of success in raising young, and on their survival from one breeding season to the next. In fact, the combined effects of adult mortality and changes of mate or nest site resulted in a turnover among neighbors of only about 6% per year (Hatch 1985). Thus, the wide range of female responses to the approach of outside males may in part reflect the number of years particular neighbors had interacted, and instances of successful EPC may represent a cul-mination of several years' effort by a breeding male to establish familiarity and the required level of acceptance by a neighboring female.

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