Forced extra-pair copulation and mate guarding in the white-cheeked pintail: timing and trade-offs in an asynchronously breeding duck

LISA GUMINSKI SORENSON
Bell Museum of Natural History and Department of Ecology, Evolution & Behavior, University of Minnesota, Minneapolis, MN 55455, U.S.A.

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Abstract. Males employing a mixed reproductive strategy may increase their fitness through extra-pair copulations (EPCs), but also risk lost paternity when they leave their own mate unguarded. How males maximize the effectiveness of forced extra-pair copulation (FEPC) attempts while minimizing the risk of cuckoldry was studied in a non-migratory population of the white-cheeked pintail, Anas bahamensis, a tropical species with extended breeding seasons. Despite substantial asynchrony in the laying dates of females, males directed FEPC attempts primarily at females in fertile condition. The rate of pair copulations also peaked during the female's fertile period, but 23.1% of all successful copulations with laying females were FEPCs. Males guarded their paternity by vigorously defending their mates from males attempting FEPC, by escorting females to their nests, by defending a territory, and by forcing copulation on their own mates after they had been subjected to an FEPC attempt by another male. Contrary to expectation, males did not temporally partition mate guarding and FEPC activity but pursued FEPCs primarily during the period when their own mates were fertile. There was no evidence, however, of a trade-off between FEPC activity and the quality of male mate guarding. Females paired to males with the highest FEPC rates were rarely subjected to FEPCs themselves. In addition, although females that abandoned nesting efforts suffered a high frequency of FEPC attempts, their mates were much less active in FEPCs than the mates of females that nested successfully. These results suggest substantial variation in male quality: some males excelled at both guarding their mates and achieving FEPCs, while others neither pursued FEPCs nor mate-guarded effectively.

Extra-pair copulation or EPC is a common feature of the reproductive biology of many so-called monogamous bird species (reviewed by Ford 1983; McKinney et al. 1984; Birkhead 1988; Birkhead & Möller 1992). In addition to helping their own mates raise offspring, males take advantage of opportunities to inseminate other females via extra-pair copulations. This behavior pattern, known as a mixed reproductive strategy, is expected to occur in males because their reproductive success is limited primarily by the number of females they can inseminate, and not by the number of sperm they produce (Trivers 1972). Observational studies have shown that males direct EPCs at fertile females (reviewed by Birkhead & Möller 1992) and genetic studies have confirmed that EPCs in the wild can result in fertilizations (e.g. Westneat 1987b; Alatalo et al. 1989; Burke et al. 1989; Graves et al. 1992). Thus, in at least some species, EPC functions as a secondary reproductive strategy that may increase the reproductive success of individual males above that possible through monogamous mating alone.

A direct consequence of EPCs is sperm competition, defined by Parker (1970) as the competition between the sperm of two or more males to fertilize the eggs of a single female. Studies of sperm competition in several species (reviewed by Birkhead & Möller 1992) have shown that last male sperm precedence occurs if copulations are separated by more than 4 h, but that paternity is proportional to the number of sperm from each male if the copulation interval is less than 4 h. In addition, it has been shown for captive waterfowl that sperm from copulations occurring within 1 h after the previous egg is laid have the greatest chance of fertilizing the next egg (the 'insemination window', Cheng et al. 1983). Thus, for...
maximum effect, males should copulate with their mates and attempt EPCs following egg laying (most birds lay one egg per day) resulting in a diurnal pattern in the timing of both pair copulations (PCs) and EPCs. The effectiveness of an EPC will also be determined by the relative frequency of EPCs and PCs because frequent copulations of one type may transfer enough sperm so that one copulation of another type has little chance of fertilizing the egg, even if that copulation is the last one (Birkhead 1988).

Because EPCs can result in parental investment in young that are not their own, males are under strong selection to protect their paternity. The most common means by which they do this is (1) mate guarding (Buitron 1983; Gowaty & Plissner 1987) which may involve territory defence (Moller 1987a), and (2) frequent copulation (McKinney et al. 1984; Birkhead et al. 1987). Other anticuckoldry tactics include a male copulating forcibly with his mate immediately after an EPC as an antidote insemination (forced pair copulations, Barash 1977; McKinney et al. 1983), cloaca-pecking (in dunnocks, Prunella modularis, Davies 1983) and a male rejecting a female that had been courted and possibly inseminated by another male (Zenone et al. 1979). Despite the recent increase in field studies addressing EPCs, detailed information is still lacking for many species on the relative frequency, success and temporal patterns of EPCs and PCs, and on the tactics used by individual males to achieve EPCs while also guarding their paternity.

Forced extra-pair copulation (FEPC) has been recorded in 39 species of waterfowl (McKinney et al. 1983) and extra-pair paternity has been verified in two species (Evarts & Williams 1987; Lank et al. 1989), but detailed behavioural observations have been conducted on only a few migratory species breeding in temperate and sub-arctic North America. The breeding seasons of these species are short and the laying periods of females are relatively synchronous. In lesser snow geese, Anser caerulescens (Minea & Cooke 1979) and mallards, Anas platyrhynchos (Evarts 1990), males guard their mates while they are fertile and then neglect them during incubation to pursue FEPCs. In lesser scaup, Aythya affinis (Afton 1985), both activities occur at the same time. With the exception of these three species, very little is known about how males accomplish the conflicting objectives of mate guarding, territorial defence and FEPC. In general, however, there is an inverse correlation between the degree of territoriality (which is associated with strong mate defence) and FEPC activity (McKinney et al. 1983; Gauthier 1988). In other words, FEPC is observed frequently in species in which paired males do not defend territories (e.g. northern pintail, Anas acuta, Smith 1968; Derrickson 1977) and it appears to be rare in highly territorial species (e.g. northern shoveler, Anas clypeata, Seymour 1974a, b; c; Afton 1979), suggesting trade-offs in reproductive effort (Westneat et al. 1990).

FEPCs have not been investigated in wild populations of tropical and southern hemisphere waterfowl where mild climates and irregular rainfall can result in great variation in the duration and timing of breeding seasons (Siegfried 1974; Frith 1982). Asynchrony in the laying dates of females might be particularly advantageous to males pursuing a mixed reproductive strategy because it would enable them to guard their paternity while their own mates are fertile, but pursue FEPCs when the danger of cuckoldry is passed. A temporal separation of mate guarding and FEPC activity could enable males to increase their fitness through additional extra-pair matings without trading off their own parental investment or paternity.

I studied FEPC and mate guarding behaviour in a non-migratory, tropical duck, the white-cheeked pintail, Anas bahamensis bahamensis, a species with an extended breeding season in much of its range (McKinney & Bruggers 1983). Observations of captives breeding in flight pens suggested that males were highly territorial as well as active in pursuing FEPCs (McKinney & Bruggers 1983). In this paper, I examine how males maximized the effectiveness of FEPC attempts while minimizing the risk of cuckoldry by documenting (1) how well male white-cheeked pintails time their FEPC attempts in relation to the reproductive status of females, (2) how the timing, frequency and success of FEPCs compares with pair copulations and (3) how males in an asynchronously breeding population allocate time to mate guarding and FEPC.

STUDY AREA AND NATURAL HISTORY

This study was conducted from January to June in 1985 and from March to July in 1986 and 1987 on
the Paradise Island golf course, north of Nassau, New Providence, Bahamas. These dates encompassed most or all of the breeding season each year. The study site included five ponds which ranged in size from 0.37 to 3.6 ha. Two of the ponds were partially surrounded by vegetation, predominantly native shrubs and grasses, while the other three were relatively open. A more detailed description of the study site is given in Sorenson (1992).

Prior to the start of the breeding season, white-cheeked pintails are gregarious and actively engage in social courtship. Once breeding begins, however, aggression between males increases: males of breeding pairs establish territories approximately 2 weeks before their mates initiate egg laying. Females nest on Salt Cay, a rocky island with no surface water, located 1.4 km north of Paradise Island. Each day after egg laying and for incubation recesses, nesting females return to their mates' territories on the golf course for all other activities (e.g. feeding, preening). Swimming across the ocean, females lead their broods back to the golf course ponds within 24 h of hatching and raise them there. Most males pair monogamously, but a small percentage have two mates each year (Sorenson 1992). Like northern hemispheric Anas, males do not provide parental care. They do, however, provide substantial indirect parental investment by defending their mates from courtship and harassment by other males before and during egg laying and throughout the incubation stage. Detailed information on territorial behaviour, the mating system, and the general breeding ecology of white-cheeked pintails is provided in Sorenson (1990, 1992).

METHODS

Field Procedures

Pintails were captured in mist nets and individually colour-marked with nylon nasal markers (Lokemoen & Sharp 1985). A total of 156 birds (80 males and 76 females) were marked over the course of the study, including 12 birds marked as yearlings (hatched in the previous breeding season) and 23 as ducklings (hatched in the present breeding season). Yearling birds were distinguished from adults by the presence of notched tail feathers (Bellrose 1980).

Behavioural observations were conducted from blinds or hidden vantage points on each of the four ponds used by breeding pairs. Observation periods lasted from 1 to 8 h and alternated between morning, midday and afternoon. Observing several birds simultaneously (focal sub-group sampling, Altman 1974), I recorded on tape-recorder all social interactions, including copulations, occurring among the marked pairs and unpaired males on a pond. The times that marked birds moved out of sight of the observer (i.e. behind vegetation) while still on the pond were also recorded. My two assistants and I usually conducted simultaneous watches on different ponds and maintained contact via walkie-talkies. This system enabled us to follow local movements of marked birds and document the outcomes of territorial and FEPC chases that involved travel from one pond to another. In 1987, early morning observations were also conducted from a blind erected at the nesting area on Salt Cay (6 mornings for a total of 20 h). A total of 8835 bird-hours of observation was completed during the 3 years of the study. Only data from pairs that were observed regularly throughout the breeding season and in which at least one member was marked are included in my analyses. Fifteen pairs in 1985, 34 in 1986 and 47 in 1987 met these criteria. In addition, nine to 13 marked, unpaired males were under observation each year.

I distinguished three types of copulation (McKinney et al. 1983). (1) Pair copulations (PCs) involve cooperation of both mates. PCs are preceded by mutual head-pumping, after which the female adopts a prone posture and is mounted by the male. PCs were considered to be successful (i.e. likely to have transferred sperm) if the male was well positioned on the female's back, there was a pronounced tail bend and thrust, and the copulation was followed by post-copulatory display (see Johnsgard 1965). (2) Forced extra-pair copulations (FEPCs) are characterized by the grasping and mounting of a female by a male other than her mate, followed by copulation despite resistance by the female. No pre-copulatory displays are performed before the male attempts to mount the female and the female does not adopt the prone posture. (3) Forced-pair copulations or FPCs are identical to FEPCs except that they occur between mates.

I used criteria similar to Barash (1977), Burns et al. (1980), and Afton (1985) to estimate FEPC success. In 'FEPC attempts', the male chased the female and made physical contact by grasping her
neck and mounting or attempting to mount. FEPC attempts were considered to be successful when the male achieved a tailend and thrust. Post-copulatory display was not considered to be a necessary indicator of a successful FEPC because (1) the male attempting FEPC was often chased off by the female's mate immediately after the tailend/thrust and presumably before he had a chance to perform post-copulatory display, and (2) in some cases where the female's mate was not present, there was a pronounced tailend/thrust and immediate departure by the male without post-copulatory display, consistent with McKinney et al.'s (1983) suggestion that the link between intromission and post-copulatory display is weak in copulations involving birds that are not paired to one another.

I also recorded 'sexual chases', in which a male chased and sometimes attempted to grasp a female but never made physical contact. Sexual chases involved a male leaving his territory to chase a female on a neighbouring territory or a female that was visiting the pond (i.e. she was not a resident) and were distinct from territorial chases in which a male chased an intruding female or pair out of his own territory and then immediately returned to it.

Analysis

I used 10 reproductive-condition categories in the analysis. (1) Pre-breeding: the time period prior to 10 days before egg laying. (2) Pre-laying: from 10 days to 1 day before egg laying. (3) Laying: from the day before the first egg up to and including the day of the penultimate egg. Laying dates were observed directly for nests found in the laying stage or were determined by backdating from hatching date assuming a 25-day incubation period. (4) Apparent pre-laying: pairs that established territories and whose behaviour indicated they were in the pre-laying or laying stage (e.g. nest-prospecting at Salt Cay) but then were not known to initiate a nesting attempt (some of these pairs may have abandoned a nesting attempt before I found the nest). (5) Incubation: from the day of clutch completion until hatch. (6) Post-failed nest: the 10 days following the loss of a nest during laying or incubation. Only two females were known to initiate a second nest after the first nest failed (Sorensen 1990). The only female in which pre-laying and post-failed nest categories overlapped (16-day interval between nest loss and re-nesting) was classified as post-failed nest for 6 days and pre-laying for 10 days. (7) Post-hatch: pairs with broods. (8) Non-breeding: pairs that apparently made no attempt to breed. On average, 31% (range=19-50%) of marked females did not breed each year (Sorensen 1990); non-breeding pairs remained gregarious and used pond areas not occupied by territorial breeding pairs. (9) Unpaired: males that did not obtain a mate for the breeding season (see Sorensen 1992). (10) Moulting: the flightless period during wing-moult. In 1986 and 1987, a few birds began moulting on the study site ponds while some pairs were still breeding.

Given that viable sperm can be stored in the female reproductive tract for, on average, 10 days in mallards, Anas platyrhynchos (Eider & Weller 1954), I considered birds in pre-laying, laying and apparent pre-laying condition as 'fertile' and those in all other categories as 'non-fertile'. All my observations suggest that apparent pre-laying pairs actually did initiate breeding attempts but abandoned their efforts due to harassment and repeated FEPC attempts (see Results).

PC rates (frequency/h) were calculated using only the time that focal pairs were in sight because PCs could have occurred while the pair was temporarily out of view. Because it was highly unlikely that an FEPC could have occurred behind vegetation and not have been detected by the observer, FEPC attempt rates (frequency/h) and sexual chase rates (frequency/h) were calculated using the time that focal males and females were present on the pond. Repeated FEPC attempts on the same female by one male during an observation period probably cannot be considered independent events. I therefore used a maximum of one FEPC attempt per hour per male to calculate FEPC rates. Similarly, a series of chases of a given female by the same male were considered as one chasing bout when calculating the rate of chasing by males.

I used data only from the 'breeding season' to calculate PC and FEPC attempt rates. The 'breeding season' began 17 days (the maximum sperm storage period in mallards, Elder & Weller 1954) before the first female of the season began laying and ended when the last nest of the season hatched. This restriction limits any bias in comparisons of copulation rates between fertile and non-fertile conditions that would be due to
including many hours of observation of non-fertile birds before and after the breeding season. Some PCs, but no FEPC attempts were observed outside of the breeding season.

Categorical data were analysed using the G-test for goodness-of-fit and G-test for independence, applying William’s correction for small sample size (Sokal & Rohlf 1981).

**RESULTS**

**Frequency and Timing of Forced Extra-pair Copulations**

Over the 3 years of the study, I recorded 139 FEPC attempts. Excluding repeated FEPC attempts by a given male on the same female within an hour, the total was 96 FEPC attempts. I knew the reproductive condition of the female in 71 of these 96 cases (74%). Females in laying, apparent pre-laying, and post-failed nest reproductive conditions were subjected to the highest frequencies of FEPC attempts (Table I). Overall, the rate of FEPC attempts on fertile females was 7.2 times the rate on non-fertile females \((G_{adj}=65.1, df=1, P<0.001)\). FEPC attempt rates for individual females that were observed in both fertile and non-fertile conditions were almost always higher when they were fertile (sign test, \(N=25, T=18, P=0.022\)). The frequency of FEPC attempts on fertile females was 0.79 per day (using 13 h of daylight) while the frequency on non-fertile females was 0.11 per day. Most of the FEPC attempts directed at non-fertile females involved females in the post-failed nest condition and all of these FEPC attempts occurred less than 8 days after females had nests destroyed during laying \((N=2)\) or early incubation \((N=1)\).

Additional evidence of male ability to discriminate between fertile and non-fertile females was found by examining 14 FEPC attempts in which (1) both the male and female involved were ‘resident’ on the same pond (a ‘resident’ was defined as a bird that had a territory on the given pond or had been using the pond for at least 5 days prior to the FEPC attempt) and (2) resident females in both fertile and non-fertile condition were present at the time of the FEPC attempt. Assuming that males randomly chose an FEPC target from all the females present on his pond, 6.7 and 7.3 FEPC attempts on fertile and non-fertile females, respectively, would be expected, given the reproductive stages and numbers of females present in each of these 14 cases. The observed number of 13 FEPC attempts on fertile females was significantly greater than expected \((G_{adj}=12.8, df=1, P<0.001)\).

**Frequency and Timing of Pair and Forced-pair Copulations**

I observed 84 PCs during the 3 years of the study, 62 of which occurred during the breeding season. The reproductive condition of the female was known in 45 of these 62 cases (73%). Although non-breeding pairs and pairs in the pre-breeding stage copulated relatively often, PCs were most frequent during the laying stage (Table II). Overall, the rate of PCs for pairs in fertile condition was 2.3 times the rate for pairs in non-fertile condition \((G_{adj}=6.79, df=1, P<0.01)\).
Table II. Pair copulation rates (frequency/h) in relation to female reproductive condition

<table>
<thead>
<tr>
<th>Reproductive condition</th>
<th>PCs</th>
<th>Hours observed</th>
<th>PC rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-breeding</td>
<td>15</td>
<td>530.7</td>
<td>0.028</td>
</tr>
<tr>
<td>*Pre-lying</td>
<td>5</td>
<td>150.2</td>
<td>0.033</td>
</tr>
<tr>
<td>*Laying</td>
<td>8</td>
<td>131.7</td>
<td>0.061</td>
</tr>
<tr>
<td>*Apparent pre-lying</td>
<td>7</td>
<td>267.9</td>
<td>0.026</td>
</tr>
<tr>
<td>Incubation</td>
<td>0</td>
<td>214.3</td>
<td>0</td>
</tr>
<tr>
<td>Post-failed nest</td>
<td>1</td>
<td>57.0</td>
<td>0.018</td>
</tr>
<tr>
<td>Post-hatch</td>
<td>0</td>
<td>241.2</td>
<td>0</td>
</tr>
<tr>
<td>Non-breeding</td>
<td>9</td>
<td>545.7</td>
<td>0.016</td>
</tr>
<tr>
<td>Moultiing</td>
<td>0</td>
<td>9.2</td>
<td>0</td>
</tr>
<tr>
<td>*Fertile</td>
<td>20</td>
<td>549.7</td>
<td>0.036</td>
</tr>
<tr>
<td>Non-fertile</td>
<td>25</td>
<td>1541.1</td>
<td>0.016</td>
</tr>
</tbody>
</table>

The frequency of PCs for fertile females was approximately 0.47 per day (using 13 h of daylight) while the rate for non-fertile females was approximately 0.21 per day. No copulations were observed during the incubation or brood-rearing stages or in pairs that were moultiing.

I also recorded seven FPCs during the study. I knew the reproductive condition of the female in five of these cases; three were in the laying stage, one had just abandoned her nest after laying five eggs and one was classified as apparent pre-laying. In four of the seven cases (three involving laying females), the FPC occurred less than 80 min after the female had been subjected to an FEPCC attempt in the presence of her mate. Three FPCs occurred just after an observation period began so I did not know whether the female had recently been subjected to an FEPCC attempt, but in two of the three cases, the FPC occurred during a 7-day period in which the females were frequently chased and subjected to at least two and six FEPCC attempts, respectively.

Diurnal Timing of Copulations

The frequency of PCs peaked between 0700 and 0900 hours and again between 1200 and 1400 hours (Fig. 1). Peaks in FEPCC rates occurred after the peaks in PC activity in both the morning and afternoon. Overall, the PC rate was 2.3 times higher in the morning (0500–1200 hours) than in the afternoon (1200–1900 hours), while the FEPCC rate by males was 1.3 times higher in the morning than in the afternoon.

During the laying stage, the timing of PCs and FEPCC attempts was influenced by patterns of female nest attendance. Laying females returned from Salt Cay to Paradise Island later and later in the day with each egg laid (Fig. 2). All six PCs that involved females in the last half of the laying stage occurred in the afternoon (after 1200 hours), whereas five of seven PCs that involved females in pre-laying condition or in the first half of the laying stage occurred in the morning. Similarly, nine of 10 FEPCC attempts that involved females in the last half of the laying stage occurred in the afternoon, while three of seven FEPCC attempts that involved females in pre-laying condition or in the first half of the laying stage occurred in the morning. Although few direct data on the time of egg laying are available, patterns of nest attendance (Fig. 2) suggest that females may lay each successive egg a little later each day. One female that nested on Paradise Island and therefore could be monitored more closely, laid the third egg of a nine-egg clutch between 1100 and 1200 hours and

Figure 1. FEPCC attempt rate by focal males (●), FEPCC attempt rates on focal females (■) and PC rate (O) in relation to hour of day (EST). Rates are calculated using only copulation records from fertile reproductive condition categories.
Figure 2. Arrival times of laying females returning from Salt Cay to their territories in relation to the proportion of clutch laid ($Y=7.62+8.95p$, where $Y$ equals arrival time at the territory and $p$ equals proportion of the clutch laid, $r^2=0.78$, $P<0.001$, mean clutch size $\pm se=8.3 \pm 0.3$).

laid the fourth egg between 1100 and 1400 hours. Both PCs and FEPCs occurring in the afternoon during the last few days of laying may therefore coincide with the insemination window.

Success of Copulations

The FEPC success rate was 19% (18 of 96), significantly lower than the PC success rate of 80% (67 of 84; $G_{adj}=71.1$, $df=1$, $P<0.001$). Four out of seven FPC attempts (57%) were successful. Although one might predict that males would expend more effort and achieve greater success when attempting FEPC with a fertile female, FEPCs attempted with fertile females were no more successful (17%, 8 of 48) than FEPCs attempted with non-fertile females (13%, 3 of 23; $G_{adj}=0.15$, $df=1$, $P>0.2$). Similarly, PC success did not differ between fertile (85%, 17 of 20) and non-fertile females (77%, 24 of 31; $G_{adj}=0.43$, $df=1$, $P>0.2$). All four successful FPCs involved fertile females.

Mate Guarding by Males

Most males aggressively defended their mates during FEPC attempts. Typically, a male whose mate was being subjected to an FEPC attempt directly attacked the assaulting male and tried to dislodge him by beating him with his wings while pushing against him with his breast. Males were often able to prevent a male intent on FEPC from even reaching their mate by chasing him off as he approached the territory. Once FEPC attempts began on a male’s mate he became extremely alert and aggressive and frequently patrolled the boundaries of his territory. Territorial defence peaked during the laying stage, supporting the hypothesis that one function of territoriality is protection of paternity (Sorenson 1990).

The much lower rate of success for FEPCs compared with PCs presumably reflects the combined effectiveness of mate defence and female escape tactics (females actively resisted FEPC attempts by diving, flying away and hiding; Sorenson 1994). The importance of mate guarding per se is suggested by a higher frequency and greater success of FEPC attempts when a female’s mate was absent (i.e. not on the pond). The frequency of FEPC attempts on females was 3-4 times higher when they were alone than when their mates were present ($G_{adj}=9.30$, $df=1$, $P<0.005$, Table III). FEPC success was significantly higher when the female was alone (33%, 8 of 24) than when the female’s mate was present (14%, 10 of 72; $G_{adj}=3.91$, $df=1$, $P<0.05$).

Males were also observed guarding their mates on Salt Cay while they were nest-prospecting and during the early part of laying. Males chased off any nearby males and then returned to their mates. If a female was aerially pursued, her mate followed and tried to deflect the chasing male, sometimes making physical contact on the wing. This mate defence was probably highly effective because I never observed a male force a female down onto the ocean when her mate was present (unpublished data). Males escorted their mates out to Salt Cay in the early morning, but escorted
Table IV. FEPC attempt rates (frequency/h) by males in relation to their mate’s reproductive condition

<table>
<thead>
<tr>
<th>Reproductive condition</th>
<th>FEPC attempts</th>
<th>Number successful</th>
<th>Hours observed</th>
<th>FEPC attempt rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-breeding</td>
<td>6</td>
<td>3</td>
<td>788.1</td>
<td>0.008</td>
</tr>
<tr>
<td>*Pre-laying</td>
<td>9</td>
<td>2</td>
<td>225.1</td>
<td>0.040</td>
</tr>
<tr>
<td>*Laying</td>
<td>27</td>
<td>7</td>
<td>310.8</td>
<td>0.087</td>
</tr>
<tr>
<td>*Apparent pre-laying</td>
<td>10</td>
<td>2</td>
<td>395.6</td>
<td>0.025</td>
</tr>
<tr>
<td>Incubation</td>
<td>15</td>
<td>2</td>
<td>802.1</td>
<td>0.019</td>
</tr>
<tr>
<td>Post-failed nest</td>
<td>5</td>
<td>1</td>
<td>117.5</td>
<td>0.034</td>
</tr>
<tr>
<td>Post-hatch</td>
<td>1</td>
<td>0</td>
<td>403.9</td>
<td>0.002</td>
</tr>
<tr>
<td>Non-breeding</td>
<td>0</td>
<td>0</td>
<td>748.5</td>
<td>0</td>
</tr>
<tr>
<td>Unpaired</td>
<td>11</td>
<td>1</td>
<td>1172.4</td>
<td>0.009</td>
</tr>
<tr>
<td>Moulting</td>
<td>0</td>
<td>0</td>
<td>48.2</td>
<td>0</td>
</tr>
<tr>
<td>*Fertile</td>
<td>46</td>
<td>11</td>
<td>931.4</td>
<td>0.049</td>
</tr>
<tr>
<td>Non-fertile</td>
<td>37</td>
<td>6</td>
<td>4077.7</td>
<td>0.009</td>
</tr>
</tbody>
</table>

Timing of Mate Guarding and FEPC by Males

Instead of partitioning mate guarding and FEPC activity seasonally, males attempted FEPC primarily during the period when their own mates were fertile. FEPC attempt rates were highest for males whose mates were laying, and overall, the rate by males whose mates were in fertile condition was 5.4 times that for males whose mates were in non-fertile condition (G_{adj} = 55.6, df = 1, P < 0.001, Table IV).

By pursuing FEPCs while his own mate is fertile, a male risks cuckoldry by leaving his mate unguarded and vulnerable to attacks from other males. I recorded five cases of a female being subjected to an FEPC attempt while her own mate was attempting FEPC with another female. Males were apparently able to minimize this risk, however, by philandering more when their mate was absent (usually on the nest). The FEPC rate was 3.5 times higher for males when they were alone than when their mate was present on the territory (G_{adj} = 25.9, df = 1, P < 0.001, Table V). Males also may have reduced their chances of being cuckolded by pursuing FEPCs primarily on their own ponds and with neighbouring females (Sorensen 1994). By doing so, a male remained close enough to his own territory to keep watch on his mate and return to defend her if she was attacked. In all five cases mentioned above, the male attempting FEPC with another female returned immediately to his own mate after she was attacked, and through aggressive defence was able to repel the assaulting male.

Individual Variation and Trade-offs in FEPC and Mate-guarding Behaviour

There was a great deal of variability among males and females in observed rates of FEPC activity. Many males were never observed to attempt FEPCs, while several males had FEPC attempt rates up to eight times the average rate for all males. Similarly, some females were never subjected to an FEPC attempt, while other females were subjected to FEPC attempts at rates up to seven times the average rate for all females.

If there is a trade-off between FEPC activity and a male’s ability to effectively guard his mate,

Table V. FEPC attempt rates (frequency/h) by males in relation to the presence or absence of the male’s mate

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<tr>
<th></th>
<th>FEPC attempts</th>
<th>Hours observed</th>
<th>FEPC attempt rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male’s mate present</td>
<td>38</td>
<td>2760.5</td>
<td>0.014</td>
</tr>
<tr>
<td>Male alone</td>
<td>33</td>
<td>672.5</td>
<td>0.049</td>
</tr>
</tbody>
</table>

Observation hours and FEPC records for males in the post-hatch stage are excluded because males did not always escort their mates with broods and only one FEPC attempt was recorded during this period.
there should be a positive relationship between an individual male’s FEPC attempt rate and his mate’s, i.e. the most promiscuous males may guard their mates less carefully than males that do not pursue FEPCs (Birkhead et al. 1985). Consistent with this prediction, the males of many pairs never attempted FEPCs and their mates were never subjected to FEPCs. Contrary to this prediction, however, there was no significant correlation between the FEPC rate of a male and that of his mate ($r_s=0.21$, $N=32$, $P>0.1$, Fig. 3). A high rate of FEPC activity by a given male did not necessarily result in a high rate of FEPC attempts on his mate.

There was also no evidence of a trade-off between a male’s FEPC activity and his mate’s ability to initiate and incubate a nest, a measure of the quality of male mate guarding (Sorenson 1992). Although females that abandoned a nesting attempt (i.e. those classified as apparent pre-laying, $N=17$) suffered a higher frequency of FEPC attempts and sexual chases than females that completed clutches and initiated incubation (Mann–Whitney $U=259$, $N=23$, $P=0.054$, Fig. 4), philandering by males did not influence the breeding success of their mates. In fact, the mean FEPC activity rate of males whose mates nested ($N=22$) was significantly greater than that of males whose mates abandoned a nesting attempt.

**DISCUSSION**

**Sperm Competition and the Timing and Frequency of Copulations**

Despite substantial asynchrony in the laying dates of females (females in fertile condition were available for up to 101 days or longer; Sorenson 1992; Sorenson et al. 1992), male white-cheeked pintails clearly discriminated between fertile and non-fertile females and directed FEPC attempts primarily at fertile females. Given that white-cheeked pintail pairs copulate most frequently during the laying stage (unlike most birds which copulate most frequently during pre-laying and infrequently or not at all during laying; Birkhead...
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& Møller 1992, 1993), sperm from an FEPC must be deposited during the female's laying period to compete effectively with sperm from pair copulations. Within fertile categories, the higher FEPC rate on laying females than pre-laying females (Table 1) suggests that males maximize the effectiveness of FEPCs by timing them to occur during the period when their sperm would be most competitive.

Copulations should also occur at the time of day when chances of successful fertilization are highest. Ducks, like most birds, are generally thought to lay eggs early in the morning and because an insemination window occurs during a relatively short time period after egg laying (Cheng et al. 1983), copulations were predicted to occur during the morning hours. Both PCs and FEPC attempts were more frequent in the morning, supporting the insemination-window hypothesis. FEPC attempts were also more frequent during the morning in lesser scaup (Afton 1985) and captive mallards (Cheng et al. 1982). The assumption that egg laying and the insemination window occur during the morning throughout the laying period may not be valid for all waterfowl species, however. Time-lapse photography suggested that female redhead, Aythya americana, and canvasback, A. valisineria, ducks laid each successive egg a little later in the day (M. D. Sorenson, personal communication). Female blue-winged teal, Anas discors, were sometimes found to contain a fully shelled egg in the uterus when flushed off their nests in the afternoon hours (F. Rohwer, personal communication). Arrival times of laying white-cheeked pintail females returning from Salt Cay (Fig. 2) suggest that female white-cheeked pintails may also be on a greater than 24-h laying schedule. If so, both PCs and FEPCs that occur later in the day may coincide with the insemination window, thereby explaining the afternoon peaks in copulation activity (Fig. 1). Data on the timing of PCs and FEPCs in relation to the stage of egg laying are also consistent with the possibility of both a morning and an afternoon insemination window. Regardless of when eggs are actually laid, however, male opportunities for either PCs or FEPCs are constrained by patterns of female nest attendance, such that copulations during the last half of the laying stage occur in the afternoon.

The frequency of PCs as well as their timing may have evolved as a male strategy to reduce the probability of fertilization by sperm deposited by FEPCs (Cheng et al. 1983; Birkhead & Møller 1992). Birkhead et al. (1987) suggested that PCs should be frequent in species in which FEPCs are common and define a high PC rate as being greater than two copulations per female per day during the fertile period. By this definition, white-cheeked pintails have a low PC rate (0.47 copulations per day during the fertile period). Given the relatively high FEPC rate for fertile females (0.79 FEPC attempts per day), it is somewhat surprising that the PC rate was not higher. It is possible, however, that the diurnal timing of PCs is more important than their frequency; if males time their pair copulations optimally, then frequent copulations may not be necessary. Pair copulations peaked before FEPC activity for both the morning and afternoon and PC rates were highest when FEPC rates were low. This pattern suggests temporal partitioning on a very fine scale, males copulate with their mates before attempting to secure extra-pair fertilizations. Because the number of ejaculates a male is capable of delivering per day is limited (Dewsbury 1982; Møller 1988; Aguilera 1989), males may be ensuring the fertilization of their own mate's eggs first with this timing. The potential for sperm depletion is significant for male white-cheeked pintails because extra-pair copulations and pair copulations are not broadly temporally separated.

Male white-cheeked pintails occasionally forced copulation on their own mates, particularly after they had witnessed them being subjected to an FEPC attempt by another male. The close temporal link between FPCs and FEPC attempts suggests paired males can devalue the extra-pair copulation by diluting the sperm of the extra-pair male. Such 'retaliatory' copulations have also been observed in the zebra finch, Poephila guttata (Birkhead et al. 1989), rook, Corvus frugilegus (Goodwin 1955), and many other waterfowl species (McKinney et al. 1984; Afton 1985).

Mate Guarding

Male white-cheeked pintails guarded their paternity by aggressively defending their mates from males attempting FEPC, defending territories, escorting their mates to and from the nesting area on Salt Cay during pre-laying and the early part of laying, and by forcing copulation on their own mates after they had been subjected to an FEPC. 'Natural' removal experiments
simulated by the occasional separation of pair members showed that FEPC attempts were significantly more likely to be successful if the female was alone, indicating that mate guarding was effective in preventing FEPCs. The high frequency of FEPC attempts for females whose mates were absent suggests that males take advantage of FEPC opportunities with unguarded females. Similar results have been reported for the pied flycatcher, *Ficedula hypoleuca* (Björklund & Westman 1983), common murre, *Uria aalge* (Birkhead et al. 1985) and barn swallow, *Hirundo rustica* (Møller 1987b).

As the amount of time the female spent on the nest increased during laying, males stopped waiting for their mates and stopped escorting them from Salt Cay back to Paradise Island. Although males risked loss of paternity by not escorting females on the return flight, the cost of waiting for the female at Salt Cay and not defending the territory on the golf course would increase as laying progressed. This trade-off between territorial defence, one function of which is to guard paternity, and direct mate guarding is imposed by the unusual separation of the nesting area and breeding territories in this population.

**Timing of FEPC and MateGuarding: Conflicting Demands on Males**

Males pursuing FEPCs may suffer a cost of cuckoldry because unguarded females were subjected to a higher frequency of FEPC attempts than guarded females. Males were apparently able to minimize this cost to some degree by philandering more when their mate was absent and by pursuing neighbouring females (so that they could quickly return to their mates and defend them if necessary).

Males might also be expected to partition FEPC activity and mate guarding on a seasonal time scale. Surprisingly, however, males pursued extra-pair copulations primarily while their own mates were fertile. This pattern is in direct contrast to that of most other species in which males have been found to partition mate guarding, paternal care and EPC activity. For example, male indigo buntings, *Passerina cyanea*, pursued EPCs during incubation, a time when they contribute little to care of the young (Westneat 1988). Similarly, male lesser snow geese (Mineau & Cooke 1979; Lank et al. 1989) and male rock ptarmigan, *Lagopus mutus* (Brody 1988) attempted EPCs primarily after their mates had begun incubating. Why has selection not favoured the temporal separation of the two activities in white-cheeked pintails, a species in which asynchronous breeding should provide ample opportunity for such separation?

One possibility is that males may be constrained by other activities during their mate's non-fertile period. During the pre-breeding period, males continuously guarded their mates in order to allow their mate to feed efficiently and meet the energetic demands of egg production; such guarding appeared to be essential to successful reproduction (Sorenson 1990, 1992). Although the intensity of mate guarding was no less during the laying stage, males had blocks of time available for FEPC activity once their mate started spending time on the nest. In contrast, there were few constraints on the time of males whose mates were incubating or tending broods. Males escorted and guarded their mates during the daily 2- to 3-h incubation recess, but the rest of the day could have been spent pursuing FEPCs with no risk of cuckoldry or harassment of their mates. None the less, FEPC activity by males abruptly ceased during the first few days of their mate's incubation period. Similarly, males with brooding mates rarely attempted FEPCs even though they provided no parental care and escorted their mates, at most, on a part-time basis (Sorenson 1992). Instead, males spent time feeding, resting or courting other females during these periods.

An alternative explanation for the lack of temporal separation in mate guarding and FEPC activity was suggested by Afton (1985) for male lesser scaup, a species with a very short, synchronous breeding season. He suggested that males used their mates' reproductive condition as an index to the fertility of other females and as a result, attempted FEPCs primarily when their own mates were laying, a pattern similar to what I observed in white-cheeked pintails. In the asynchronously breeding white-cheeked pintail, however, the reproductive condition of a male's mate is a poor index to the reproductive condition of other females. This hypothesis also predicts that males would attempt FEPC with all available and vulnerable females they encounter during their own mate's fertile period. There was no evidence for this in white-cheeked pintails: males discriminated between fertile and non-fertile females and
were never observed attempting FEPC with non-breeding females.

Finally, the temporal partitioning of mate guarding and FEPC activity may be constrained by the costs of maintaining high levels of testosterone and aggressive behaviour for an extended period (e.g. reduced survival, injury; Marler & Moore 1988; Dufty 1989). FEPC is a highly aggressive behaviour (males must overtake and subdue a struggling female as well as fight off her defending mate) that may, like other patterns of aggressive behaviour in birds (Wingfield et al. 1987), require elevated testosterone levels. An extension of FEPC activity and elevated testosterone levels might be particularly costly to males that, by the time the female begins incubation, have already spent several weeks establishing and defending a territory and guarding a mate. The energetic costs of mate defence (i.e. chasing away intruders, defending the female from harassment and FEPC attempts) and a modified activity budget (i.e. increased time spent alert at the expense of foraging time; Aschoff 1976; Sorensen 1990) probably reduce the physiological condition of males.

On a proximate basis, copulation behaviour in males may depend on the sexual receptivity of their mates. For example, palsa androgen levels in male white-crowned sparrows, Zonotrichia leucophrys, increase in response to the solicitation displays of their mates during pre-laying and laying, then decrease rapidly at the onset of incubation (Wingfield & Farner 1980; Moore 1982, 1983). A similar mechanism may operate in white-cheeked pintails. Sexual receptivity of females and the relatively high rate of pair copulation during egg laying may maintain a high testosterone level in males, facilitating not only mate guarding, but perhaps also FEPC behaviour.

Individual Variation and Trade-offs in Male FEPC and Mate-guarding Behaviour

Individual males varied greatly in their involvement in FEPCs. One source of this variation may be due to individual differences in strategy. For example, certain males may forego FEPC opportunities in favour of mate guarding: in many pairs neither the male nor his mate were involved in FEPCs (Fig. 3). This strategy may be particularly advantageous for males with little breeding experience that may have little chance of successfully completing an FEPC attempt. In addition to protecting paternity, mate guarding in white-cheeked pintails and other ducks represents an indirect form of parental investment. A trade-off between mating and parental effort in males has been suggested as an important factor contributing to patterns of paternal care and EPC involvement across species (Maynard Smith 1977; Westneat et al. 1990). It may also be useful in explaining individual variation in behaviour within a species.

Interestingly, however, there was no evidence for a trade-off between mate guarding and FEPC activity for males attempting FEPCs. There was no correlation between a male’s FEPC rate and the rate of FEPC attempts on his mate. In fact, females paired to males with the highest FEPC rates were rarely subjected to FEPCs, while some females paired to males with low FEPC rates were not well guarded. A similar observation was reported for common murres (Birkhead et al. 1985) and white ibis, Eudocimus albus (Frederick 1987) and parentage analysis in red-winged blackbirds, Agelaius phoenicus, confirmed a positive relationship between a male’s paternity on his own territory and neighbouring males’ territories (Gibbs et al. 1990). Moreover, males of pairs that nested successfully had higher FEPC activity rates than males of pairs that abandoned a nesting attempt, and females that abandoned a nesting attempt suffered more FEPC attempts and harassment than females that nested. These results strongly suggest individual variation in male quality: some males were capable of both mate guarding and pursuing FEPCs, while others neither pursued FEPCs or guarded their mates effectively.

Male aggression is essential to protecting the pair bond, maintaining a territory and successfully guarding a mate, and some males were clearly more aggressive than others. The most aggressive and dominant males guarded their mates most effectively from FEPC attacks and disturbance throughout breeding, enabling them to feed undisturbed and nest successfully. These males were also most active in pursuing FEPCs, were older (unpublished data), and a few were also polygynous (Sorensen 1990). Older males performed most EPCs in purple martins, Progne subis (Morton et al. 1990) and rooks, Corvus frugilegus (Roskaft 1983) and EPC activity by individual male white ibis was correlated with
fighting ability (Frederick 1987). That some males excel at both mate guarding and FEPC will result in greater variance in male reproductive success and thereby intensify sexual selection.

Significance of FEPC as a Secondary Reproductive Strategy of Male White-cheeked Pintails

Although it is difficult to assess precisely the importance of FEPC as a secondary reproductive strategy without paternity data, the behavioural evidence on the timing, frequency, and success of FEPCs and the tactics used by males to detect fertile females and achieve FEPCs (Sorensen 1994) strongly suggest that it is a well developed strategy that likely results in extra-pair fertilization and increased reproductive success for certain males. Studies combining field observations of behaviour with paternity analysis have shown that behavioural observations sometimes underestimate the frequency of extra-pair fertilization (Moller 1987b; Westneat 1987a, b). Westneat (1987a) attributes this discrepancy to chance, but it is also possible that some EPCs are not observed, particularly if the birds involved behave surreptitiously (Birkhead 1987; Sherman & Morton 1988) or copulate in a visually occluded habitat. Because white-cheeked pintails copulate on open water, my behavioural estimates of the relative number of EPCs and PCs is probably unbiased. Thus, unless extra-pair copulations differ greatly in potency from pair copulations, the proportion of eggs fertilized by FEPCs is potentially quite high: 27-6% of all successful copulations during the fertile stage were FEPCs. The fact that some females abandoned breeding as a result of FEPCs, however, probably reduced the rate of extra-pair paternity. Considering copulation records from breeding females only, 16-7% of all successful copulations during pre-laying and laying combined were FEPCs, and 23-1% of all successful copulations during the laying stage were FEPCs. Data on extra-pair paternity are needed to support the validity of these estimates (Dunn & Lifjeld 1994).

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