

FORCED EXTRA-PAIR COPULATION IN THE WHITE-CHEEKED PINTAIL: MALE TACTICS AND FEMALE RESPONSES¹

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Abstract. I studied tactics used by males to detect fertile females and achieve forced extra-pair copulations (FEPC) and female responses to FEPCs in a non-migratory, asynchronously breeding population of White-cheeked Pintails (*Anas bahamensis*) in the Bahamas. Males assessed female reproductive status by (1) monitoring behavior of neighboring pairs, (2) visiting the island nesting site and observing laying females directly, and (3) chasing females. FEPC attempts directed at neighboring females were more likely to occur during the female's fertile period than FEPC attempts directed at non-neighbors and a large proportion (44%) of FEPC attempts involved neighboring pairs. Sexual chases of fertile females were more frequent and of longer duration than chases of non-fertile females suggesting that males gain information on female reproductive status in initial chases. Males employed sophisticated tactics to achieve FEPCs, including waylaying females as they left their nests, approaching females surreptitiously by swimming "submarine" style, and capturing and mounting females underwater. Females vigorously resisted FEPC attempts by repeatedly diving, flying away and hiding and were sometimes chased to exhaustion. The high costs of resistance and observations that females resisted copulations from all extra-pair males, regardless of quality, make "resistance-as-a-ploy" and "genetic-quality" hypotheses unlikely explanations for why females resist EPCs. I argue that females resist EPCs to preserve the pairbond and investments of their mates, which in turn protects their investment.

Key words: *Anas bahamensis*; extra-pair copulation; mixed reproductive strategy; reproductive tactics; sperm competition; White-cheeked Pintail.

INTRODUCTION

Males of many monogamous birds pursue a mixed reproductive strategy in which they seek copulations with other females while helping their own mate raise offspring (Trivers 1972). The recent profusion of studies concerning extra-pair copulations (EPC) in birds has increased our understanding of sperm competition and its implications for the evolution of mating systems and parental investment patterns (reviewed by Westneat et al. 1990, Birkhead and Møller 1992). Detailed information on how EPCs occur and on female responses to EPCs, however, is still lacking for many species. In particular, few studies have investigated cues that males use to discriminate between fertile and non-fertile females or the tactics used by males to achieve EPCs. This deficiency is due in part to the difficulty of observing EPC behavior in visually occluded hab-

itats, but also because individuals involved may behave secretively. Determining whether females actively solicit, cooperate with, or resist EPCs also is difficult, but data on female responses are necessary to address the question of costs and benefits of EPCs to females (Westneat et al. 1990).

Forced extra-pair copulation (FEPC) is well known in waterfowl and is particularly common in dabbling ducks (*Anas* spp., reviewed by McKinney et al. 1983). Males chase females and copulate with them despite female resistance and male mate guarding. Aerial pursuits associated with FEPC attempts often are wide-ranging (covering several km) and may last for many minutes before the male forces the female down onto land or water. Extra-pair copulations can lead to extra-pair fertilizations (Burns et al. 1980, Evarts and Williams 1987, Lank et al. 1989). The question of why female ducks always resist EPCs (McKinney et al. 1983) has not been resolved.

I studied forced extra-pair copulation (FEPC) behavior in the White-cheeked Pintail (*Anas bahamensis*), a non-migratory, tropical duck with extended breeding seasons. Despite substantial asynchrony in laying dates of females (Sorenson

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et al. 1992), males direct FEPC attempts primarily at fertile females. Males do not, however, temporally partition mate guarding and FEPC activity on a seasonal basis as might be expected; they attempt FEPCs primarily during the period that their own mates are fertile (Sorenson, in press). Because FEPC activity is energetically costly and because the pursuit of EPCs entails leaving their own mates unguarded at a time when they are most vulnerable to being cuckolded, males should have highly developed behavioral tactics that increase the likelihood of obtaining a successful EPC (McKinney et al. 1983, Afton 1985). I report here on tactics used by individual males to assess the reproductive status of females and achieve FEPCs, responses of females to FEPC attempts, age and pair status of males attempting FEPC, and reproductive strategies of unpaired males.

METHODS

STUDY AREA AND NATURAL HISTORY

I studied White-cheeked Pintails (hereafter pintails) on Paradise Island golf course, north of Nassau, New Providence, Bahamas from January to June 1985 and from March to July 1986 and 1987. I also made a brief visit to the study area in September 1984 to capture and mark birds. My study area included five ponds, ranging in size from 0.37–3.6 ha. Native shrubs and grasses partially surrounded two ponds, while the other three were relatively open. The study site is described in more detail in Sorenson (1992).

This population of pintails breeds seasonally but the timing and duration of breeding seasons is variable. Approximately two weeks prior to egg laying, males of breeding pairs establish territories. During my study, almost all females nested on Salt Cay, a dry, rocky island located 1.4 km north of Paradise Island. Each day after egg laying and during incubation recesses, females flew back to their mates' territories on the golf course for all other activities (e.g., feeding, preening). Females led their newly hatched broods back to the golf course ponds (swimming across the ocean) and reared them there. Although males provide no parental care to ducklings, they do provide indirect parental investment by defending the female and territory throughout the breeding cycle. Detailed information on the mating system, timing and success of FEPC attempts, mate guarding, and general breeding ecology of

pintails is provided in Sorenson (1990, 1992, in press).

FIELDWORK

I captured pintails with mist nets and individually color-marked them with nylon nasal markers (Lokemoen and Sharp 1985). A total of 156 pintails (80 males and 76 females) were marked during the study, including 12 birds marked as juveniles or yearlings (hatched in previous breeding season) and 23 as ducklings (hatched in present breeding season). Ten juvenile and two yearling birds captured in September 1984 and March 1986, respectively, still retained notched tail feathers and could be distinguished from adults by this characteristic (Bellrose 1980).

I conducted behavioral observations from blinds or hidden vantage points on each of the four ponds used by breeding pairs. A total of 8,856 bird-hours of observation was completed during the three field seasons. I analyzed data only from pairs which were observed regularly throughout the breeding season and in which at least one pair member was marked. Fifteen pairs in 1985, 34 in 1986 and 47 in 1987 met these criteria. Marked, unpaired males ($n = 9-13$) also were under observation each year. I used focal sub-group sampling (Altmann 1974) to record on tape all social interactions and copulations occurring among marked pairs and unpaired males on the pond. Times that marked birds moved out of sight of the observer (i.e., behind vegetation) while still on the pond also were recorded. Two assistants and I usually conducted simultaneous watches on different ponds, maintaining contact via walkie-talkies. This system enabled us to follow local movements of marked birds and document outcomes of territorial and FEPC chases that involved travel among ponds. In 1987, six morning observations (total of 20 hr) also were conducted from a blind erected at the nesting area on Salt Cay.

A forced extra-pair copulation attempt (FEPC attempt) consisted of a male other than the female's mate grasping and mounting the female in spite of her resistance. No pre-copulatory displays are performed by males before FEPC attempts, and the female does not adopt the prone posture (as in pair copulations). FEPC attempts were considered to be successful when the male achieved a tailbend and thrust (postcopulatory display, used as a criterion of success in other studies [e.g., Afton 1985], was not used in this

study for two reasons; see Sorenson, in press). Typically, the male chased the female a number of times before grasping and mounting. Chases associated with FEPC attempts were distinguished from "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 in order to (1) chase a female on a neighboring territory, (2) chase a female that was visiting the pond, or (3) join in an ongoing chase involving 1 or more males chasing a female. Sexual chases were distinct from territorial chases in which a male chased a female or pair that intruded into his territory *out of his territory* and then immediately returned to it. Any chases that were ambiguous (e.g., a male chasing a female out of his territory and not immediately returning to the territory) were excluded from the analysis.

DATA ANALYSIS

Sexual chase rates were calculated for 10 reproductive-condition categories. (1) Pre-breeding: the period prior to 10 days before egg laying. (2) Pre-laying: from 10 days to one day before egg laying. (3) Laying: from the day before the first egg up to and including the day of the penultimate egg (range of clutch size = 6–10 eggs). Laying dates were observed directly for nests found in the laying stage or determined by backdating from hatch assuming a 25 day incubation period. (4) Apparent-prelaying: pairs that established territories and whose behavior 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. (7) Post-hatch: pairs with broods. (8) Non-breeding: pairs which apparently made no attempt to breed (i.e., they did not establish territories and were not observed making trips to Salt Cay). On average, 31% (range 19%–50%) of marked females did not breed each year (Sorenson 1990); these pairs remained gregarious and utilized pond areas not occupied by territorial breeding pairs. (9) Unpaired: males that did not obtain a mate for the breeding season (see Sorenson 1992). (10) Molting: the flightless period during wing-molt. In 1986 and 1987, a few birds began molting 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* (Elder and Weller 1954), I considered birds in pre-laying, laying and apparent-prelaying condition as "fertile" and those in all other categories as "non-fertile." Use of the maximum sperm-storage duration of 17 days (e.g., Afton 1985) to classify fertility status would result in an inflated estimate of extra-pair fertilization frequency (Birkhead 1988).

During three years of study, I recorded 139 FEPC attempts and 278 sexual chases. To maintain independence of data points, I calculated FEPC attempt rates (freq/hr) using a maximum of one FEPC attempt per hour per male ($n = 96$ FEPC attempts). Similarly, a series of chases of a given female by the same male were considered as one chasing bout when calculating the rate of sexual chases by males ($n = 126$ sexual chase bouts). I used data only from the "breeding season" to calculate FEPC attempt and sexual chase rates. I defined the "breeding season" as beginning 17 days before the first female of the season began laying (17 days is the maximum sperm storage period in Mallards [Elder and Weller 1954]; also, males established territories, on average, 17 days prior to egg laying [Sorenson 1990]) and ended when the last nest of the season hatched (females were still chased and subject to FEPC attempts during incubation). This restriction limits any bias in comparisons of copulation rates between fertile and non-fertile conditions that would be due to including observations of only non-fertile birds long before or after the breeding season. Sexual chases and pair copulations, but no FEPC attempts, were observed outside of the breeding season.

Associations between FEPC attempt and sexual chase frequencies and fertility, pair or residence status were analyzed using the G -test for goodness of fit and G -test for independence, applying William's correction for small sample size (Sokal and Rohlf 1981). The duration of chasing between fertile and non-fertile females was compared with the Mann-Whitney U test. Differences in the percent time females were in sight on the pond during pre-breeding and laying were tested with the Wilcoxon signed-ranks test.

RESULTS

MALE TACTICS

Detecting fertile females. There are several cues males may use to discriminate between fertile

and non-fertile females. First, males could assess a female's reproductive condition by monitoring the behavior of neighboring pairs. Males were apparently better at judging the reproductive condition of a female if she was resident on the same pond: FEPC attempts directed at resident females were more likely to occur during the female's fertile stage (34 of 39) than FEPC attempts directed at non-resident females (nine of 23; $G_{adj} = 6.28$, $df = 1$, $P < 0.025$, $n = 62$ FEPC attempts for which the male's and female's resident pond and female's reproductive stage were known). In addition, a large proportion of all FEPC attempts (44%, 42 of 96) involved males and females resident on the same pond. Males, however, also took advantage of opportunities to copulate with non-resident females that visited their pond (22%, 21 of 96) and they were occasionally observed attempting FEPCs off their resident ponds (16%, 15 of 96). In eight cases, a male was observed making excursions to the female's pond prior to the FEPC attempt, during which he swam around the pond peering into the vegetation, apparently searching for the female.

Second, males may gather information on the reproductive condition of females by chasing them. Sexual chases on the study site ponds were common throughout the breeding season, but females in laying and apparent-prelaying condition were chased most frequently (Table 1). Overall, the chase rate for fertile females was 5.4 times higher than that for non-fertile females ($G_{adj} = 83.1$, $df = 1$, $P < 0.001$). The duration of chasing also differed: the mean number of chases per chase bout was significantly higher for fertile females ($\bar{x} \pm SE = 2.40 \pm 0.30$, $n = 76$) than for non-fertile females (1.62 ± 0.17 , $n = 50$; Mann-Whitney $U = 2,340$, 2-tailed test, $P = 0.016$).

Third, males may directly observe laying females at the nesting area on Salt Cay. Males escorted their mates to Salt Cay in the early morning during pre-laying and laying and remained at the cay until mid-morning (return time [EST] to Paradise Island during prelaying, $\bar{x} \pm SE = 0934 \text{ hr} \pm 15 \text{ min}$, $n = 13$ flights; laying = $0817 \text{ hr} \pm 10 \text{ min}$, $n = 16$ flights). While their mate was on the nest or walking through the vegetation (prospecting for a nest site), males stood on the rocks nearby, remained alert and surveyed their surroundings. During 20 hr of observation, I observed 63 flights and chases by males of other birds (both male and female) around the cay and to and from Paradise Island. It was difficult to determine the outcome of these chases because

TABLE 1. Sexual chase rates (chasing bouts/female-hr) in relation to female reproductive condition. The category "fertile" contains summary data for pre-laying, laying and apparent-prelaying reproductive conditions, "non-fertile" contains summary data for all other reproductive conditions.

Reproductive condition	Sexual chases	Hours observed	Sexual chase rate
Pre-breeding	21	734.3	0.028
*Pre-laying	15	213.2	0.070
*Laying	21	209.8	0.100
*Apparent-prelaying	40	363.0	0.110
Incubation	17	290.7	0.058
Post-failed nest	5	94.1	0.053
Post-hatch	1	814.1	0.001
Non-breeding	6	742.9	0.008
Molting	0	34.1	0
*Fertile	76	785.9	0.097
Non-fertile	50	2,710.1	0.018

the birds disappeared from view out over the ocean or behind the cay, but two sexual chases culminated in a successful FEPC after the male forced the female down onto the ocean. Both cases involved the same marked female (but two different males) that was left unguarded by her mate on her first and sixth day of egg laying.

Males may use additional behavioral cues from the female. During pre-laying and especially laying, females became very secretive: they tended to remain in the deepest corner of the territory, they swam inconspicuously (close to the shoreline rather than out in the open water), and they spent significantly more time out of sight in the vegetation on their territory (percent time in sight during pre-breeding: $\bar{x} \pm SE = 81.8\% \pm 3.2\%$, during laying: $61.8\% \pm 6.8\%$; Wilcoxon signed-ranks test, $z = -2.55$, $P = 0.01$; analysis is on 13 individual females in 1986 that were observed in both pre-breeding and laying stages; time out of sight does not include time spent on the nest because females nested away from their territories on Salt Cay). I also observed 16 instances of a female suddenly freezing into a low, crouched posture (head and neck parallel to the water) in response to a pintail flying overhead, 13 of these females had been subjected to FEPC attempts and sexual chases in the preceding 24 hr. This behavior was never observed in non-breeding females.

Achieving FEPCs. Including repeated FEPC attempts by a given male on the same female, most FEPC attempts (76 of 139) involved a single male pursuing a single female. In a typical attempt, the male either flew directly to the target



FIGURE 1. Male White-cheeked Pintail swimming in submerged posture towards prospective FEPC target female and her mate.

female or swam towards her until he was within approximately 10 m of her before making a dash for her. He then grasped the feathers on the back of her head or neck in his bill and attempted to mount. Only 6% of initial FEPC attempts (six of 96) resulted in a successful FEPC because the female escaped (see below). Most males were very persistent, however; of 90 FEPC attempts in which males were initially unsuccessful, 71% repeatedly chased the female. If the female dived, the male either dived and pursued her underwater or else waited above the water scanning back and forth to see where she would surface. In 27% of FEPC attempts (26 of 96), the male captured the female underwater and came to the surface mounted on her back. Males made an average of 6.0 chases (± 0.91 SE, range 1–45, $n = 96$ FEPC attempts) per FEPC attempt and spent an average of 5.8 minutes (± 0.83 SE, range 1–38, $n = 96$ FEPC attempts) actively chasing

the target female. This time spent chasing does not include time spent searching for (swimming around the pond peering into the vegetation) or trying to approach the female, which sometimes lasted for up to an hour and rarely longer.

Males also approached females by sneaking through shoreline vegetation or swimming with the body submerged and only the top of the head and back showing (Fig. 1). Surreptitious approaches, observed in 12% of FEPC attempts ($n = 96$), were adopted after direct approaches failed due to strong mate defense. The behavior of one male, GYy (who had the highest FEPC attempt rate among males in 1986), illustrates the persistence and apparent “cunning” of some males.

In April 1986, GYy made two FEPC attempts and 24 approaches to female W+o on the day she laid her second egg. He first attempted to reach her by swimming or flying at her directly. Before he was able to grasp her neck, her mate

(Govy) chased or escorted him off the territory. While being escorted, GYy would abruptly take flight and turn back toward W+o. After seven unsuccessful approaches, GYy retreated to his territory on the opposite corner of the pond and began a surreptitious approach. He swam with the submerged profile along the perimeter of the pond, staying close to the shore and underneath the overhanging vegetation. Govy, now apparently very wary, spotted him when he was about 20–25 m away and aggressively chased him off three times. On the fourth try, GYy approached within a few meters and lunged at the female. Capturing W+o underwater, GYy came to the surface mounted on the female. W+o dived again and was apparently able to evade GYy underwater, after which GYy was seen swimming away from the pair in the submerged posture, presumably to avoid being attacked and chased by Govy. GYy persisted in his unsuccessful attempts to copulate with W+o (~1.5 hr) until his own mate arrived from Salt Cay. He then abandoned his FEPC activity to escort and guard his laying mate.

Two or more males were involved in 63 of 139 FEPC attempts (each male's attempt scored separately). All multi-male attempts began as single male attempts; the chasing and splashing during FEPC attempts attracted the attention of other males in the area. Males that joined in an FEPC attempt tried to mount the female simultaneously, resulting in a pile of males on the female's back, each grasping the head or neck of the bird below. The weight of these males, all struggling and fighting to stay mounted as well as dislodge each other, forced the female completely underwater, only her head occasionally appearing above water as she struggled. Most multi-male attempts involved two males ($n = 16$) but instances involving three, four and five males also were documented ($n = 2, 5, 1$, respectively). Per male FEPC success was lower in multi-male (four of 63) vs. single male attempts (14 of 76, $G_{adj} = 4.61$, $df = 1$, $P < 0.05$), perhaps because of interference between males.

AGE AND PAIR STATUS OF MALES ATTEMPTING FEPC

Eighty-seven percent of FEPC attempts (72 of 83) were by older, paired males. The FEPC attempt rate by paired males was 2.0 times higher than that of unpaired males ($G_{adj} = 5.38$, $df = 1$, $P < 0.025$, Table 2). Among unpaired males, all 11 FEPC attempts involved males that were at

TABLE 2. FEPC attempt rates (freq/hr) and success by males in relation to their pair status.

Male status	FEPC attempts	Number successful	Hours observed	FEPC attempt rate
Paired	72	16	3,836.7	0.019
Unpaired	11	1	1,172.4	0.0094

least two years of age. Seven of these attempts (including one successful FEPC) occurred in 1987 and involved two males that were at least three and at least four years old, respectively. One of these males also was unpaired in 1986 when he was first marked, while the other was paired in both 1985 and 1986. The behavior of these two males differed markedly from that of other unpaired males in that they appeared to actively search for FEPC opportunities. They moved from pond to pond (often together) and repeatedly intruded on the territories of breeding pairs, chasing and trying to mount fertile females. The FEPC attempt rate of the over four-year-old male (0.110 frequency/hr) was third highest among individual males in 1987 and 1.9 times the average rate for paired males that year (Sorenson 1990). Although other unpaired males also were quite mobile, they were active primarily in social courtship (Sorenson 1992) and were seen intruding on territories and chasing females only five times. Seven yearlings under observation (257 hr), six of which were unpaired, were never observed making FEPC attempts.

The FEPC success rate of paired males (22%, 16 of 72) did not differ significantly from that of unpaired males (9%, 1 of 11; $G_{adj} = 1.10$, $df = 1$, $P > 0.2$), although sample size for unpaired males was small. The proportion of FEPC attempts directed at fertile females by paired males (71%, 37 of 52) and unpaired males (44%, four of nine) also did not differ significantly ($G_{adj} = 2.19$, $df = 1$, $P > 0.1$).

RESPONSES OF FEMALES TO FEPC

With two exceptions (see below), females appeared to actively resist FEPC attempts by vigorously trying to escape, usually by diving. In 57% of sexual chase bouts and chase bouts associated with FEPC attempts (152 of 265), females dived in response to being chased. They surfaced from a dive with only the top of the head and back showing in 22% of dives and then swam to cover on the shoreline where they re-

mained hidden in a crouched posture. Crouching occurred in 23% of chase bouts (61 of 265). Females also flew or skittered short distances (<10–15 m) across the water or across or around the pond to evade males (37%, 98 of 265). Flying completely off the pond to another pond occurred in only 9% of chases (24 of 265). This resulted in “three-bird flights” which involved a male chasing a female around the golf course with the female’s mate following and the female often making abrupt twists and turns in the air to evade the male.

Diving rather than flying may have been a better escape tactic for several reasons. Aerial chases may attract other males that are likely to join in the FEPC attempt: 22% of three-bird-flights ($n = 197$) around the study area typically resulted in one or more males flying up to join the chase. By flying, the female also risks becoming separated from her mate, thereby losing the defense he provides. Finally, although males were sometimes able to capture the female underwater (see above), females were able to evade an assaulting male in 31% of unsuccessful FEPC attempts ($n = 78$) by diving and then swimming submerged to cover.

I never observed females to seek extra-pair copulations by, for example, deliberately entering another male’s territory or making herself available by swimming on the edge or outside her own territory. The only two FEPCs in which the female did not appear to resist occurred on the ocean (described above). In both cases, the female’s mate was absent and the first mount ended in an apparently successful FEPC without the repeated diving and chasing characteristic of all other FEPC attempts. The female’s lack of escape behavior during these copulations may be explained by higher costs of resistance on the ocean, particularly those associated with diving (i.e., difficulty in swimming underwater in ocean currents and waves).

Costs of FEPC attempts to females such as increased energy expenditure and injury were probably greatest during multi-male attempts. When two or more males repeatedly chased and tried to mount a female and she was unable to escape, she eventually came out of the water and onto land (10 of 96 FEPC attempts). Once on land, she continued to resist copulation by sitting against the shoreline bank and pressing her tail to the ground. Males appeared to have difficulty mounting on land but continued to peck and

grasp the back of the female’s head and neck. No successful FEPCs were seen out of the water, although in one case a male was able to pull the female back into the water, where he then mounted. Moving onto land appeared to be a last resort for females because by this time their plumage was wet and in disarray. Although I observed two females that were clearly exhausted (unable to walk without collapsing) by a multi-male FEPC attempt, both recovered and no female deaths attributable to injuries inflicted by males occurred (see Titman and Lowther 1975, McKinney and Stolen 1982, McKinney et al. 1983).

DISCUSSION

MALE TACTICS FOR DETECTING FERTILE FEMALES AND ACHIEVING FEPCs

Males may use the following cues to discriminate between fertile and non-fertile females: monitoring the behavior of neighboring pairs, chasing females, and visiting the nesting area on Salt Cay. Males were better at assessing the reproductive status of females if they were resident on the same pond, and they directed a large proportion of FEPC attempts at resident females. A possible behavior that neighboring males monitor is the intensity of territorial aggression exhibited by the breeding male: male aggression and intolerance of other pintails in or near the territory as well as territory size increased during pre-laying, reached a maximum during egg-laying, then declined gradually during incubation (Sorenson 1990). Mates of females that abandoned a nesting attempt (i.e., those classified as apparent-pre-laying) also were territorial, and these females were subjected to a high rate of FEPC attempts (Sorenson, in press). In contrast, mates of non-breeding females did not defend territories and FEPC attempts on these females were never observed. Thus, as suggested for swallows (*Hirundo rustica*, Møller 1987a) and several other species (e.g., Frederick 1987; Hatch 1987; Westneat 1987a, 1987b), the intensity of male mate guarding could provide a reliable cue to female fertility status that neighboring males can monitor. Several other studies report that EPC activity usually involves neighboring pairs and the use of similar behavioral cues has been suggested.

Males attempting FEPC when away from their resident ponds may rely on the same mate guarding cues. It seems likely, however, that the greater investment of time and energy required to gather

information on female reproductive status as well as the increased risk of cuckoldry when a male leaves his own mate unguarded (Sorenson, in press) may explain the lower frequency of FEPC attempts by males while away from their resident ponds.

Males also might monitor the behavior of neighboring females. Laying females spent more time out of sight in the vegetation and they may inadvertently signal their reproductive status by hiding and skulking within the territory. Although secretive behavior is presumably effective in concealing a female's presence much of the time, experienced males may learn to recognize this behavior. Similar hiding behavior has been observed in wild Mallards (Titman 1973) and captive Green-winged Teal (*Anas crecca*, McKinney and Stolen 1982).

Data on the frequency and timing of sexual chases suggest that males also may use sexual chases to assess the reproductive status of females, as hypothesized by McKinney et al. (1983). Chase bouts involving fertile females were more frequent and involved more individual chases than chases of non-fertile females, suggesting that males abandoned the pursuit with non-fertile females or became more persistent with fertile females after gaining information on the female's reproductive status in the initial chases. Jones (1986) showed experimentally that flight performance of female Bank Swallows (*Riparia riparia*) was affected by the increased body mass typical of laying females, and that males used flight behavior as a cue to fertility. Female White-cheeked Pintails also were heaviest during their fertile period (Sorenson, unpubl. data), and a female with an egg in the oviduct has a distinctly "dropped" profile. Sexual chases associated with FEPC activity have been recorded in several other species including the White-fronted Bee-eater (*Merops bullockoides*, Emlen and Wrege 1986), Purple Martin (*Progne subis*, Brown 1978), swallow (Møller 1987a, 1987b) and many ducks (McKinney et al. 1983).

While escorting their own mates at Salt Cay, males chased other laying females and attempted to force them down onto the ocean for an FEPC. Two FEPC attempts in only 20 hours of observation suggest a high frequency of FEPC activity at the nesting area. Male ducks in captivity (Cheng et al. 1982) and in the wild (Stewart and Titman 1980, Evarts 1990) have also been reported to chase and attempt FEPC with females after they

leave their nest. Although they were not always successful in waylaying a female as she left her nest, visiting the cay also may have allowed males to learn which females were laying.

My observations indicate that FEPC is not a simple behavior that occurs on an opportunistic basis only. Rather, males employ remarkably sophisticated behaviors to attain FEPCs and often are successful despite vigorous female resistance and strong male mate guarding (23% of successful copulations with laying females were FEPCs; Sorenson, in press). Males were skilled at diving and frequently succeeded in capturing and mounting the female underwater (reported also for several other species; McKinney et al. 1983, Evarts 1990). They also actively searched for females which had eluded them by swimming along the shoreline and peering into the vegetation. If males were at first unsuccessful in their FEPC attempts by rushing directly at the female, they adopted a surreptitious approach, sneaking through the vegetation or swimming "submarine" style. Secretive behavior by males seeking EPCs has been reported in several other species (e.g., Black-billed Magpie, *Pica pica* [Buitron 1983]; Pied Flycatcher, *Ficedula hypoleuca* [Björklund and Westman 1983]; Yellow Warbler, *Dendroica petechia* [Ford 1983]). This behavior seems exceptionally well-developed in White-cheeked Pintails.

REPRODUCTIVE TACTICS OF UNPAIRED MALES

Although one might expect unpaired males to pursue EPCs as an alternative reproductive strategy (Barash 1977), most studies of extra-pair copulation in birds have shown that it is resident, paired males that pursue EPCs (Mineau and Cooke 1979, Fujioka and Yamagishi 1981, Afton 1985, Frederick 1987, Westneat 1987a). I also found that most unpaired White-cheeked Pintail males did not pursue FEPCs. Most unpaired males were yearlings (Sorenson 1992) and, given their inexperience, may have had difficulty identifying fertile females and successfully completing an FEPC (Afton 1985). Paired, territorial males seemed to recognize this factor and behaved as if unpaired yearlings were not a paternity threat; they tolerated their presence in or near their territory boundaries much more than they would a paired adult male (Sorenson 1990). Unpaired males were very active, however, in social courtship (Sorenson 1992). As suggested

by Afton (1985) for Lesser Scaup (*Aythya affinis*), pair formation is probably a more profitable strategy for unpaired males, especially given that mate switches were common throughout the breeding season in my study population (Sorenson 1992).

Frequent FEPC activity was documented, however, in two older, unpaired males. The FEPC attempt rate of one of these males was well above the average rate for all paired males. FEPC therefore may be an important alternative reproductive tactic for a few older, experienced males who for some reason were unable to obtain a mate that year (see also Afton 1985).

COSTS AND BENEFITS OF EPCS TO FEMALES

In theory, females also may benefit from EPCs (reviewed by Westneat et al. 1990, Birkhead and Møller 1992). Females may gain by mating with a male genetically superior to their own mate, they may increase the genetic diversity of their offspring, or EPCs may provide insurance against sterility of the mate. Such benefits are perhaps most likely in species in which females either solicit or at least cooperate with EPCs (Hatch 1987, Møller 1988, Smith 1989, Wagner 1991). White-cheeked Pintail females, however, vigorously resist FEPC attempts by hiding, flying away or repeatedly diving, and were never observed to actively seek an extra-pair copulation. The fact that females so vigorously resist EPCs suggests that the costs of EPCs for females are high and almost certainly outweigh possible benefits. What are the costs of EPCs for females and why do females not accept EPCs to avoid harassment and possible injury?

One possibility is that female resistance of EPCs may actually be a ploy to test male quality: presumably the best males would be successful at achieving the EPC (despite female resistance, male mate defense and male-male competition) and their good genes or ability to achieve EPCs would be inherited by the female's offspring (Christoleit 1929, in McKinney et al. 1983, Westneat et al. 1990). Females, however, were sometimes chased until they were wet and exhausted, and prolonged attempts by one male typically turned into risky multi-male attempts with each male pecking at and trying to mount the female simultaneously. Most importantly, females that suffered a high frequency of FEPC attempts often abandoned their breeding efforts

for the season (Sorenson, in press; see also Koenig 1982, Afton 1985, Davies 1985). Although not observed in this study, female dabbling ducks may be killed during FEPC attempts (McKinney et al. 1983). Clearly, the costs of resistance are very high, making the "resistance-as-a-ploy" hypothesis unlikely for White-cheeked Pintails (and other waterfowl, Birkhead and Møller 1992).

A second possibility is that females resist EPCs because they are already paired to a high-quality male; by resisting, they avoid the costs of copulating with a male of inferior or unknown quality (Westneat et al. 1990, Birkhead and Møller 1992). This is an attractive hypothesis for waterfowl because females choose their mates directly from a group of courting males (pairbonds are formed prior to territory establishment and so territory quality is not a factor in mate choice). However, every female cannot be mated to the best male (Gladstone 1979, Møller 1992) and the quality of White-cheeked Pintail males (as evidenced by mate-guarding ability; Sorenson 1992, in press) varies greatly. Thus, one prediction from the genetic-quality hypothesis is that females should accept EPCs from certain males and avoid them with others. For example, female Black-capped Chickadees (*Parus atricapillus*) performed EPCs only with males that were of higher dominance rank than their own mate (Smith 1989) and female Zebra Finches (*Taeniopygia guttata*) engaged in EPCs with males that were more attractive than their own mate (Burley and Price 1991). My data indicated that high quality males attempted EPCs most frequently and often with females paired with low quality males (Sorenson, in press), but contrary to the genetic-quality hypothesis, females always resisted these attempts. In addition, contrary to the suggestion of Birkhead and Møller (1992), there is no evidence that female White-cheeked Pintails (or females of other duck species) avoid EPCs with unpaired males but accept them from paired males: females resisted EPC attempts from males of both categories and I did not observe variation in resistance in relation to a male's pair status.

Finally, a female may resist EPCs to preserve the pairbond and investment of her mate (Gladstone 1979), which in turn protects her investment (Trivers 1972, Dawkins 1976). If a female cooperates in an EPC and her mate witnesses the copulation, he may defend her less vigorously or even desert her. Afton (1985) described how mate

defense in a male Lesser Scaup gradually declined and eventually ceased as the number of FEPC attempts on his pre-laying mate increased. This female abandoned her nest after three days of incubation; without male protection she was continuously chased and harassed and presumably was unable to feed. White-cheeked Pintail females which were subjected to many FEPC attempts and chases also abandoned their nesting attempts (Sorenson 1992, in press). Abandonment may have been due to male inability to defend the female and territory from other more dominant males. Alternatively, abandonment may have been the result of the male withholding investment in the current breeding effort because his confidence of paternity was low.

Abandonment of the current breeding attempt may seem like an extreme response given that males do not provide parental care, and the probability of breeding again in the same season is low (Sorenson et al. 1992). Males do, however, provide substantial indirect parental investment by courting the female, defending the territory and guarding their mates from courtship, disturbance and FEPC attempts by other males before and during egg laying and throughout incubation. The energetic costs of this investment (i.e., reduced foraging time at the expense of time spent alert and involved in aggressive interactions; Sorenson 1990, 1992) may make the costs of cuckoldry high (Gladstone 1979). It is possible that benefits such as increased survival, experience, and dominance in the following year outweigh the costs to the male of investing in young that have a low probability of being his own. Adult male White-cheeked Pintails were more successful at pairing and breeding and were dominant compared to yearlings (Sorenson 1990, 1992). A reduction in reproductive effort in favor of such benefits may be advantageous for certain males. Data on paternity and reproductive success over the lifetime of individual males are needed to test this idea.

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