VARIABLE MATING SYSTEM OF A SEDENTARY TROPICAL DUCK: THE WHITE-CHEEKED PINTAIL (*ANAS BAHAMENSIS BAHAMENSIS*)

Lisa Guminski Sorenson[1]

Bell Museum of Natural History, Department of Ecology, Evolution and Behavior, University of Minnesota, 10 Church Street S.E., Minneapolis, Minnesota 55455, USA

Abstract.—I studied the breeding chronology, courtship activities, pair-bond relationships, and parental-care behavior of a sedentary population of White-cheeked Pintails (*Anas bahamensis bahamensis*) in the Bahamas from 1985 to 1987. The timing and duration of breeding seasons was variable and associated with variation in the onset and amount of winter and spring rainfall. Year-around courtship, mate switches, courtship of brood females, and the formation of extrapair liaisons all reflected intense and continuous competition for quality mates. Most White-cheeked Pintails paired monogamously, but a low level of polygyny occurred regularly: each year, 4 to 9% of paired males had two mates during the breeding season, despite a strongly skewed sex ratio in favor of males (1.45:1). Polygynous males were particularly effective at guarding their mates during the breeding season, an important determinant of female breeding success. The term "male-quality polygyny" is proposed to characterize this form of polygyny. Both long-term pair bonds and mate changes between years were recorded: 10 of 23 marked pairs (43%) stayed together for two or more breeding seasons, while 13 pairs (57%) divorced. Mate retention in the second year was not related to breeding success in the first year. Only females provided parental care, but some males continued to escort and guard their mate for at least part of the brood-rearing period. Although highly variable, male attendance declined with both hatch date and duckling age. Some birds associated as pairs year around, and several pairs stayed together during the wing molt. The sedentary lifestyle in this subtropical climate and the potential for variable and extended breeding seasons appear to be the key ecological factors influencing the complex and variable mating system of this species. *Received 3 April 1991, accepted 8 November 1991.*

Because of their worldwide distribution and great diversity of social systems, dabbling ducks in the genus *Anas* (Anatidae, tribe Anatini) are excellent subjects for study of how ecological factors shape social behavior. Northern Hemisphere species, which have been studied extensively, are migratory and have a short annual breeding season in the temperate or subarctic zones. Each year, new pair bonds form on the wintering grounds and each male follows his mate back to the female's natal area in spring. Males escort and defend their mate through late winter, spring migration, and the early part of the nesting season. Although the duration of the pair bond varies among species, the male generally abandons the female soon after she has begun incubating and moves to a safe area to undergo the wing molt. Females raise the ducklings alone and do not molt until after leaving their broods. Following the wing molt, both sexes migrate to the wintering grounds where the cycle begins again. This seasonally monogamous mating system varies little among Northern Hemisphere *Anas* and, presumably, has evolved in response to the seasonal climate of the temperate and subarctic breeding grounds, and the migratory lifestyle of these species (McKinney 1985, 1986, Rohwer and Anderson 1988, Oring and Sayler 1992). Forced extrapair copulation is a secondary reproductive strategy for males of some species (McKinney et al. 1983), but polygyny has not been documented.

Tropical and Southern Hemisphere dabbling ducks face entirely different ecological pressures than migratory northern species. Mild climates and/or irregular rainfall result in considerable variation in the duration and timing of breeding seasons (Siegfried 1974, Frith 1982), which in turn may lead to greater diversity in mating systems and the reproductive strategies of individuals. For example, extended breeding seasons may result in marked asynchrony of

[1] Present address: Smithsonian Institution, Conservation and Research Center, National Zoological Park, Front Royal, Virginia 22630, USA.

female breeding schedules, providing oppor-
tunities for males to monopolize more than one
mate (McKinney 1985). Climate also affects
movement patterns: many tropical/Southern
Hemisphere species or populations are seden-
tary or travel relatively short distances, while
others are nomadic and move in response to
water availability (Johnsgard 1978). These
movement patterns could in turn affect various
aspects of the mating system. For example, mate
retention and polygynous pair bonding may be
more feasible in a sedentary species.

Although very few detailed behavioral stud-
ies of individually-marked birds have been con-
ducted, the social systems of tropical and
Southern Hemisphere *Anas* appear to differ
markedly from those of their Northern Hemi-
sphere counterparts. Pair bonds may persist
throughout the year and over a period of several
years (McKinney et al. 1978, Siegfried et al. 1976),
and polygyny has been documented in captive
birds (McKinney and Bruggers 1983, McKinney
1985). Males of certain species provide parental
care by guarding and/or escorting ducklings,
while males of other species sometimes accom-
pany females and broods, but appear to show
no parental behavior (Kear 1970, Siegfried 1974,
McKinney 1985, Buitron and Nuechterlein 1989,
McKinney and Brewer 1989).

The White-cheeked Pintail (*Anas bahamensis
bahamensis*), previously not studied intensively
in the wild, is a tropical/Southern Hemisphere
species that inhabits brackish or salt-water ponds
and mangrove marshes (Johnsgard 1978, Mc-
Kinney and Bruggers 1983). A pilot study of
White-cheeked Pintails in captivity (McKinney
and Bruggers 1983) indicated that this was an
especially intriguing species: males were ex-
tremely territorial throughout the breeding sea-
son, forced extrapair copulation attempts were
common, and a polygynous relationship (one
male simultaneously paired to two females) was
documented. In addition, males occasionally es-
corted their mates and broods, but the role of
the male, if any, in parental care was unclear.
The objectives of my field study of a sedentary
population of White-cheeked Pintails in the Ba-
hamas were to: (1) document the breeding chro-
nology, courtship activities, pair-bond relation-
ships, and parental-care behavior; and (2)
examine how ecological factors influence the
timing of breeding, the mating system, and the
reproductive strategies of individuals.

STUDY AREA AND NATURAL HISTORY

I studied White-cheeked Pintails from January to
June in 1985 and from March to July in 1986 and 1987
on the Paradise Island golf course, located due north
of Nassau, New Providence, Bahamas (Fig. 1; 25°N,
77°W). The study site included five ponds, which
ranged in size from 0.37 to 3.60 ha. Two of the ponds
were partially surrounded by vegetation, predomi-
nantly casuarina (*Casuarina litorea*), sea grape (*Coccolo-
ba ivifera*), coconut palm (*Cocos nucifera*), mangroves,
cattail (*Typha* spp.), and sedge (*Cyperus* spp.), while
the other two were relatively open. Pintails were also
studied on "Flamingo Pond," a natural basin sur-
rounded by native vegetation, located about 1 km
west of the golf course. The golf-course ponds receive
water from the Paradise Island sewage treatment fa-
cility and, thus, are organically enriched, but there
also is salt-water intrusion into the ponds from the
nearby ocean (B. Carey, pers. comm.). The use by
waterfowl and other avian species of such nutrient-
rich, waste-stabilization ponds is well known (e.g.
Swanson 1977). A small population of pintails has
inhabited these ponds since at least 1982 (D. Bruggers,
pers. comm.).

The Paradise Island study site was chosen over a
more natural site because of two important advan-
tages: (1) It was designated a wild-bird reserve by the
Ministry of Agriculture and Fisheries. Widespread
poaching on other islands in the Bahamas (P. Maillis,
pers. comm.) would hinder a long-term study of
marked birds. (2) The ponds were highly accessible,
the birds were accustomed to people, and marked
birds could be observed easily from the pond shore-
lines. Conditions for observation are much more dif-
ficult on other islands, where shooting has made the
birds wary, and dense mangrove growth impedes
travel and reduces visibility (D. Bruggers, pers. comm.).

Natural saline ponds on Rose Island, located 5.7 km
from Paradise Island, served as a secondary study site
(Fig. 1). Because some marked birds used ponds on
both islands, pintails were censused on Rose Island
at least biweekly throughout the breeding season in
1986 and 1987, and some behavioral observations were
conducted there as well. The size of the study pop-
ulation on the two islands ranged from approximately
40 to 120 birds over the three years. The mean density
of the birds using the Paradise Island ponds was 5.8
birds per hectare of water (range 2.7–10.6 birds/ha,
$n = 132$ censuses). Densities of breeding White-
cheeked Pintails in more pristine habitats have not
been reported. A density of territorial, breeding pairs
similar to that on the golf course was observed, how-
ever, on one of the smaller Rose Island ponds.

White-cheeked Pintails were gregarious prior to
the start of the breeding season, but males of breeding
pairs defended territories during the prelaying, lay-
ing, and incubation stages of their mates. All terri-
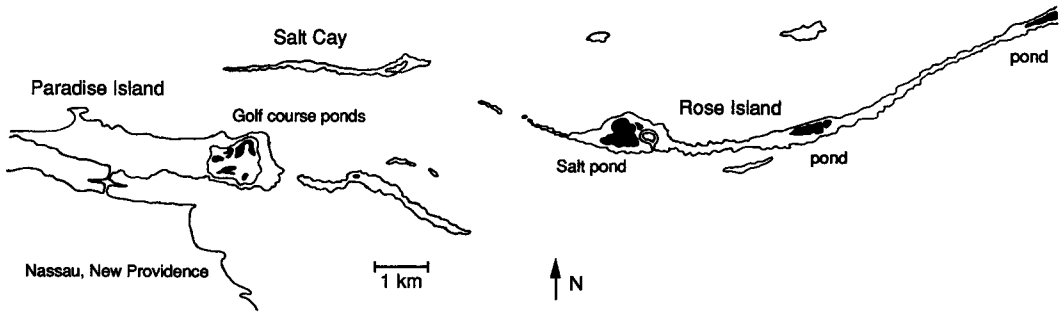tories were established following pair formation. Fe-

Fig. 1. Location of golf-course study site on Paradise Island, Rose Island, and Salt Cay.

males nested on Salt Cay, a rocky island with no surface water located 1.4 km north of the golf course (Fig. 1), but returned daily to their mate's territory for all other activities (e.g. feeding, preening) after egg laying and for a 2 to 3 h incubation recess. Males remained vigilant and strongly defended their mates throughout the breeding cycle from courtship, harassment, and forced extrapair copulation (FEPC) attempts by other males. Mate guarding is particularly important to female ducks during egg production when time spent feeding must be increased, and during incubation when they have a limited amount of time to feed (Wishart 1983). Within 24 h of hatching, females led their downy broods from Salt Cay back to the golf-course ponds and raised them there. Nonbreeding was a regular occurrence in my study population. Each year, an average of 31% of females (range 19–50%) apparently made no attempt to breed (Sorenson 1990). The mates of these nonbreeding females did not defend territories; nonbreeding pairs utilized pond areas that were not occupied by territorial breeding pairs. The mates of an additional 16% (range 6–24%) of females established territories, and these females showed signs of breeding (e.g. trips to Salt Cay), but they apparently abandoned the breeding attempt before incubation began. More detailed information on territoriality, forced extrapair copulation behavior, and general breeding biology of the White-cheeked Pintail is presented in Sorenson (1990, unpubl. manuscript).

METHODS

Pintails were captured in mist nets and "drop nets" (a piece of mist net, suspended over bait or loafing spots, that was released with a trigger line), and individually marked with nylon nasal markers (Lokemoen and Sharp 1985). A total of 156 birds, including 80 males and 76 females, were marked during the study. Twelve of these birds were marked as yearlings and 23 as ducklings. Yearling birds were distinguished from adults by the presence of notched tail feathers (Bellrose 1980).

I conducted behavioral observations from blinds or hidden vantage points on each of the four ponds used by breeding pairs. Observation periods of 1 to 8 h were alternated among morning, midday and afternoon. I used focal subgroup sampling (Altmann 1974) to record on tape recorder all courtship activity and social interactions of marked pairs and unpaired males on the pond. Pairs were recognized by several types of behavior, including inciting by the female, synchronization of activities, defense of the female by the male, mutual displays (e.g. head-pumping, belly-preens; see Johnsgard 1976, McKinney 1992), copulation, and continuous close proximity of pair members. Including only pairs that were observed regularly throughout the breeding season and in which at least one member was marked, 15 pairs were studied in 1985, 34 in 1986, and 47 in 1987. In addition, 9 to 13 marked, unpaired males were under observation each year. With the aid of assistants, a total of 8,856 bird-h of observation was completed. Also, I made brief visits to the study area in September 1984, November 1985, October 1986, April 1988, and April 1989 to obtain additional information on courtship activity and pair-bond duration.

Local movements and the sex ratio of my study population were documented by conducting a daily census of all birds present on the study-site ponds. Only censuses conducted in the afternoon (when females were least likely to be on the nest) during the first few weeks of each field season (before all or most females had begun nesting) were used to estimate the population sex ratio ($\bar{x} \pm 1$ SE).

Seasonal changes in courtship frequency were quantified by calculating, on a biweekly basis, the number of courtship bouts per hour of observation. The biweekly mean number of courtship displays (down-ups) performed per male for each display group was used as a measure of courtship intensity. The number of males in a display group included all males that appeared "interested" in courting (swimming about jockeying for position and giving introductory headshakes), although all did not necessarily perform down-ups. Courtship rates for individual males and
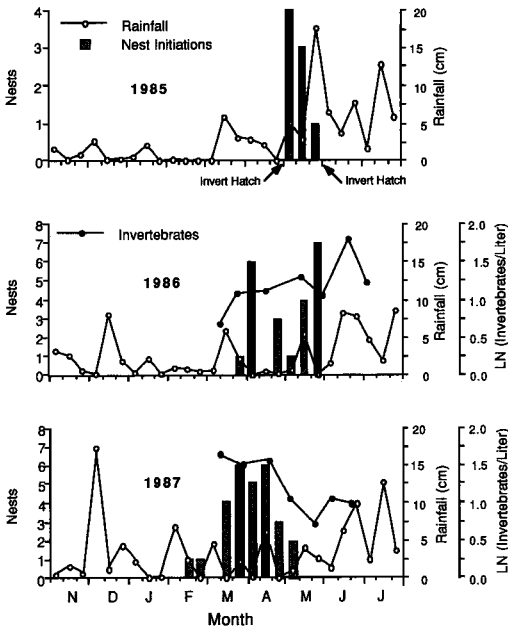
Fig. 2. Relationship between rainfall (10-day rainfall totals for New Providence Island), invertebrate abundance, and timing of breeding in the White-cheeked Pintail. The dominant invertebrate taxa sampled included shorefly larvae (Ephydridae), brine shrimp (*Artemia* spp.), and water boatman (Corixidae). Although invertebrates were not sampled in 1985, shorefly larvae and brine shrimp hatches were noted in early May and early June, respectively (indicated by arrows in 1985 graph).

females were calculated as the number of females courted (displayed to) per hour of observation and the number of males courting per hour of observation, respectively. Each male and female was counted only once per observation period, and only individuals with greater than 9 h of observation were included in the analysis. Courtship rates of paired versus unpaired males were compared using data from the first half of the breeding season only (when courtship activity was greatest). A comparison of the courtship rates of brood-rearing versus nonbreeding females included data from the day the first brood of the season hatched to the end of the field season.

The amount of time males spent with their mate throughout the brood-rearing period was quantified by recording the presence or absence of the mate for each brood female based on daily census data. The proportion of sightings with the male present was used as a measure of male attendance. Similar analyses using observation-hour data (i.e. the amount of time the male spent with his mate and brood during observation periods) yielded very similar results. Proportions were arcsin transformed (Sokal and Rohlf 1981) and analyzed with parametric statistics.

A combined rate of chasing and FEPC attempts (frequency/female-h) by males was calculated for females during their prelaying (10 days before laying) and laying period using a maximum of one chase or FEPC attempt per hour. Time spent feeding was recorded with instantaneous scan sampling (Altmann 1974) of all marked birds on the pond every 5 to 10 min, depending on density. Feeding data presented here are for 21 pairs studied in 1986.

Seasonal changes in invertebrate populations were documented in 1986 and 1987 by taking 5 to 10 invertebrate samples from the Rose Island ponds on a biweekly basis. Samples were obtained from both the water column and substrate with a water-column sampler (Swanson 1978) and were immediately run through a sieve (#35 U.S. Standard, 0.5-mm mesh), identified (to family and size class), counted, and then discarded. The natural logarithm of the number of invertebrates per liter was used as an index of invertebrate density. Samples were also taken from the golf-course ponds (to study the importance of food in territory defense; Sorenson 1990), but were not used in this analysis because of the artificial water management. Rainfall data for New Providence Island were obtained from the Bahamas Meteorological Department in Nassau, Bahamas.

RESULTS

Timing of breeding.—Variation in the timing and duration of breeding seasons was associated with variation in the onset and amount of winter and spring rainfall. Following heavy rains in winter and spring, pond water levels rose, invertebrate hatches occurred, and females began nesting (Fig. 2). A period of drought (monthly rainfalls from November to February averaged 4.4 cm below long-term averages) in the winter of 1984/1985 caused two ponds on Rose Island to dry up, and no invertebrate hatches were noted until late in the season. The first nests were not initiated until May. Moderate rainfall (monthly rainfalls from November to February averaged 0.8 cm above long-term averages) in the winter and spring of 1986 was followed by invertebrate hatches and nest initiation in late March. In 1987, females began nesting in February following the highest rainfall on record in December. Invertebrates were abundant at the start of my field season. The duration of the breeding season similarly was related to the timing and amount of winter and spring rainfall. Nests were initiated during an interval of 29, 66, and 86 days in 1985, 1986, and 1987, respectively.
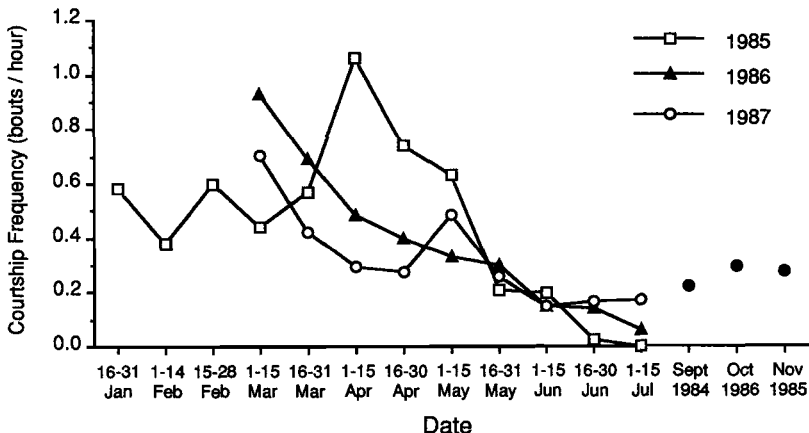
Fig. 3. Seasonal changes in courtship frequency. Total of 654 courtship bouts recorded during 1,745 h of observation.

Sex ratio.—The mean population sex ratio from 128 censuses conducted over three years was 1.45 males to 1 female (± 0.02 SE). Sex ratios did not vary significantly between years ($F = 0.48$, df = 2 and 25, $P > 0.1$).

Courtship, pair formation and within-season mate switching.—The winter and early spring months were characterized by frequent social courtship, which peaked each year just as the birds began breeding (Fig. 3). Courtship intensity peaked in April in 1985 and 1986, and in March in 1987 (Fig. 4). Typically, 2 to 10 males surrounded 1 to 4 females and, while jockeying and jostling for position, performed "down-ups," the major courtship display of the White-cheeked Pintail. The skewed sex ratio resulted in intense competition among males for mates. Aggression between rival males in the form of pecks, open-bill threats, swim-offs, chases, fights, and parallel-swims/flights occurred throughout each courtship session (Sorenson, unpubl. data). Males also used the down-up display as an aggressive signal to other males (see McKinney et al. 1990).

Courtship activity occurred year around. Although not as frequent or intense as during the winter and spring, I documented social courtship during June and July, when breeding activity had ended and some birds were beginning the wing molt (see below), as well as during brief visits to the study area in September, October and November (Figs. 3 and 4).

Both unpaired and paired birds engaged in social courtship, but unpaired males were most active: the courtship rate of unpaired males ($\bar{x}$

$\pm$ SE = 0.47 ± 0.06 females courted/h, $n = 14$) was significantly higher than the courtship rate of paired males (0.16 ± 0.02, $n = 31$; Mann–Whitney U-test, $U = 393$, two-tailed, $P < 0.001$). Unpaired males frequently swam or flew across the pond to join courting parties in progress, or approached females and pairs (often after they
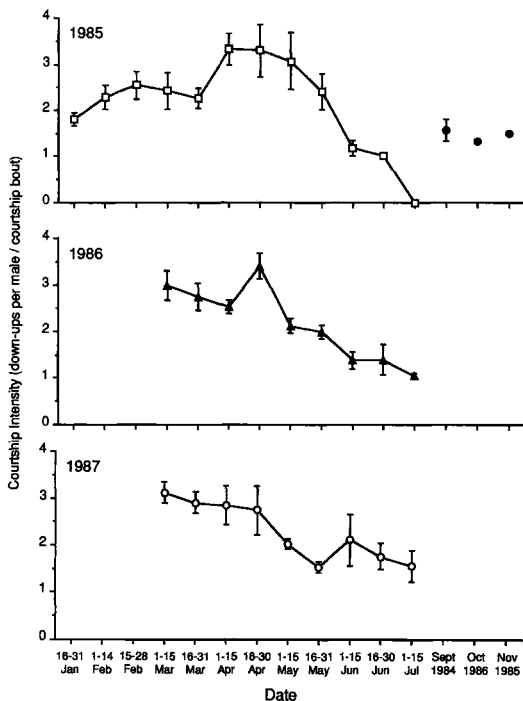

Fig. 4. Seasonal changes in courtship intensity (mean $\pm$ SE).

TABLE 1. Frequency of within-season mate switching in the White-cheeked Pintail.

Year	No. pairs initially observed[a]	Both pair members re-pair	Female re-pairs, male remains unpaired	Female re-pairs, male status uncertain	Male re-pairs, female status uncertain	Female re-pairs, polygynous male becomes monogamous	Total
1985	15	1	3	—	—	—	4
1986	33	1	3	2	—	1	7
1987	46	2	1	3	2	1	9

[a] Pairs (determined by female inciting) recorded at beginning of field season.

had flown onto the pond) and initiated court-ship. Paired males directed courtship displays to their mates, as well as to other females, and were most active early in the season. If their own mate was courted, paired males usually defended their pair bond by chasing and at-tacking rival males, and by trying to lead the female away from the courting group. If the pair bond was strong, the female followed her mate away from the group, inciting vigorously.

Mate switches and temporary liaisons prior to and throughout the breeding season were common. I found 20 to 27% of the marked pairs at the beginning of each field season switched mates within the season (Table 1). The female re-paired in all 18 switches in which her sub-sequent pairing status was known, while the male obtained a new mate in only 6 of 13 cases in which his subsequent pairing status was known. Mate switches seemed to occur most commonly when a male left his mate unguard-ed, even if only for a short period of time (e.g. for less than 30 min). Unattended females were courted and followed frequently, and females sometimes began inciting beside and associat-ing with a new male following such attention. Several females associated with a series of males before settling down with one mate, and both paired males and females occasionally formed

TABLE 2. Proportion of males pairing polygynously and number of unpaired males in the White-cheeked Pintail.

Year	Proportion of paired males that were polygynous (%)[a]	No. marked unpaired males
1985	1/14 (8.3)	9
1986	3/34 (8.8)	11
1987	2/45 (4.4)	13

[a] Data include monogamous pairs and polygynous trios with at least one mate marked.

temporary liaisons with another individual out-side the pair bond.

It was apparent during social courtship that certain males and females were preferred over others. Some males were consistently rejected as mates by all females, and some females were courted much more frequently than others. Be-cause of the male-biased sex ratio, however, all females (with one exception) eventually ob-tained a mate; in 1985, all females were paired by April, while in 1986 and 1987, all females were already paired when my field seasons be-gan in early March. The only female that re-mained unpaired appeared to be in very poor condition, was very secretive, and disappeared in April 1985.

Among other factors (see below), a male's age and experience apparently influenced his abil-ity to form a pair bond. Of 54 males that could be classified as yearlings or adults (≥ 2 yr), only 1 of 7 yearling males was paired (with a yearling female), while 42 of 47 adults were paired (G_{adj} = 15.1, P < 0.001). Moreover, 11 of 13 males that changed pair status between years switched from being unpaired in one year to paired in the next, while only 2 switched from paired to unpaired.

Monogamy and polygyny. —Most White-cheeked Pintails in my study population were monogamous, but I documented a low level of polygyny in the form of bigamous relationships and one short-term trigamous relationship. Us-ing records from monogamous pairs and po-lygynous trios with at least one mate marked, from 4 to 9% of paired males had two mates each year (Table 2). In four of the six trios stud-ied, the male divided his time between his two mates, spending more time with one female that was in prelaying or laying condition, and then switching attention to the second female when the first was incubating or tending her brood. A fifth trio was formed when a male (male G),

TABLE 3. Frequency of mate retention and mate changes between years in White-cheeked Pintails.

Year	No. marked pairs under observation[a]	Status of pairs in following year			
		Pair bond intact	Pair divorced[b]	One member of pair with new mate, old mate not sighted	Neither member of pair sighted
1985	10	2	5	3	0
1986	27	8	8	10	1
1987[c]	37	5	5	12	15
1988[c]	9	2	2	1	4

[a] Only pairs with both mates marked included in this analysis.

[b] For divorces, both mates known to be alive in following year.

[c] Data shown for 1987 and 1988 not used to calculate proportion of birds maintaining pairbonds, etc., because some living pairs and individuals probably not resighted during the short visits to study area in 1988 and 1989.

while still maintaining the pair bond with his first mate who was raising a brood, courted and paired with another brood female whose mate had been killed. In each of these five cases, aggression between the two females was evident whenever the trio was together.

In the sixth and best-studied trio, all three individuals synchronized their activities and associated closely with one another with very little aggression between the two females. At the beginning of the field season, the male of this trio (male Y) was simultaneously paired to three females. He copulated with all three females and was engaged in almost constant mate defense, as many unpaired males repeatedly attempted to approach and court his three mates. Initially, the three females rejected these courting males with pecks, open-bill-threats, chases, and inciting, but after several weeks, one of the females (whose pair bond appeared to be the weakest of the three) finally paired monogamously with another male.

Both of male Y's mates initiated nests within one day of each other and successfully brought off broods, but not all females involved in polygynous relationships bred successfully. One of the females in each of four trios was known to nest successfully, while the second female in three trios was classified as nonbreeding. The behavior of the second female in the fourth trio indicated that she was nesting but neither a nest nor brood were found. The females in this trio nested at least two weeks apart. Neither of male G's mates were known to renest after raising their first brood.

Polygynous males guarded their mates more effectively than most monogamous males; the mean rate of chasing and forced extrapair copulation attempts of their primary mates ($\bar{x} \pm$ SE $= 0.039 \pm .014$, $n = 6$) was significantly lower than the mean rate for females of monogamous pairs which established territories (0.254 ± 0.034, $n = 35$, Mann–Whitney U-test, $U = 191$, $P = 0.001$). Effective mate guarding by the male is probably essential to a successful nesting attempt by the female. Considering only the female's prelaying and laying period, females that abandoned a nesting attempt before starting incubation were subject to a significantly higher rate of chasing and forced extrapair copulation attempts by other males (0.196 frequency/female-h) than females that nested successfully (0.125 frequency/female-h, $G_{adj} = 6.07$, $P < 0.025$). In addition, the time spent feeding by females that abandoned a nesting attempt ($\bar{x} \pm$ SE $= 34.7\% \pm 5.7\%$, $n = 9$) was significantly less than the time spent feeding by females which nested successfully ($49.1\% \pm 3.0\%$, $n = 12$, $U = 82$, $P = 0.047$). Of 90 monogamous pairs, 64 established a territory, and 45 of these 64 pairs initiated a nest; 26 monogamous pairs showed no signs of breeding. In contrast, all six polygynous males held territories, and all six had at least one mate initiate a nest ($G_{adj} = 7.33$, $P < 0.01$).

Pair-bond duration.—Both long-term pair bonds and mate changes occurred (Table 3). Of 37 pairs studied in 1985 and 1986 in which both mates were marked, 10 pair bonds (27%) were still intact in the following year of study, 13 pairs (35%) divorced (both mates were alive in the following year and all had a new mate except one male), one member of 13 pairs (35%) had a new mate in the following year but the other mate was not sighted (the mate changes in these pairs could have been due to the death of the mate), and both members of one pair (3%) were not sighted in the following year. Alternatively,
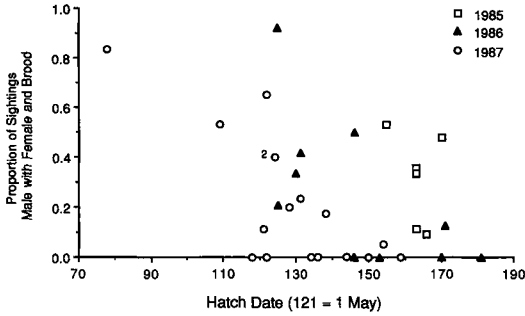
Fig. 5. Effect of hatch date on proportion of time male spent with his mate and brood for first three weeks of brood-rearing. Only females sighted more than five times included. Mean ± SE sightings/female = 14.5 ± 1.2, n = 33 pairs.
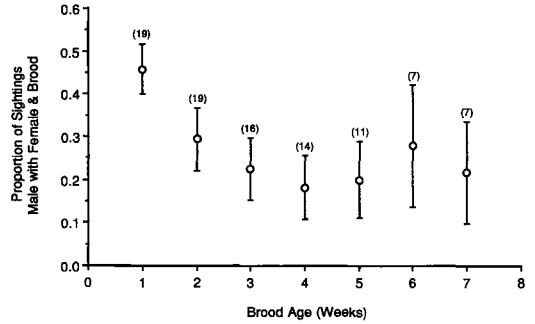

Fig. 6. Effect of duckling age on proportion of time male spent with his mate and brood. Means ± SE of raw data are shown. Sample sizes (number of pairs) in parentheses. Includes only pairs sighted from first week of brood-rearing and for which there was at least one sighting of male with his mate and brood.

43% (10/23) of marked pairs studied in 1985 and 1986 that had the option of maintaining the same pair bond for two years (i.e. their mate was still alive) did so, while 57% (13/23) divorced. The intact pair bonds listed in Table 3 include 11 pairs that remained together for two years and 3 pairs that stayed together for three years. Two cases of re-pairing following a one year separation also were recorded.

Pairs that had been successful in raising ducklings in one year might be expected to stay together for a second breeding season. I found no relationship between breeding success and subsequent mate fidelity. Considering only the 23 pairs in which both mates were marked and alive in the subsequent year, 4 of 11 pairs that bred successfully in the first year were paired again in the following year, while 6 of 12 pairs that did not breed successfully stayed together ($G_{adj} = 0.44, P > 0.2$).

At least some White-cheeked Pintails remained in pairs throughout the year. Pairs were observed during brief visits to the study area in the nonbreeding season. Many pairs (30 of 35 nonbreeding pairs, and 11 of 13 unsuccessful breeding pairs) remained together each year at least until June and July, when most breeding activity (and my field season) was over, although some bonds were not as strong and pair members sometimes spent time apart on different ponds. Most successful pairs eventually separated during brood rearing (see below), but 5 of 14 brood females that were followed to fledging age (7–8 weeks) were known to reunite with their mate shortly after ducklings fledged.

Parental care and male behavior during brood-

rearing period.—Males showed no signs of actively providing care for ducklings. Instead, they appeared interested in maintaining their pair bond; they followed their mates, defended them from courtship attempts and harassment by other males, and performed head-pumps and other pair-bond maintenance displays. Only females brooded ducklings, responded to duckling distress calls, or guarded ducklings from potential predators, other pintails and other bird species using the ponds. Females also spent much more time than males in an alert posture during this period (Sorenson 1990).

Most males associated with their brood-tending mates at least part of the time: 23 of 33 (70%) females and broods that were sighted repeatedly throughout brood rearing were escorted by the female's mate on at least one occasion. Females breeding early in the season were accompanied by their mate more frequently than females breeding late in the season (Fig. 5; partial correlation between male attendance and hatch date controlling for the effect of year, $r = -0.681, P < 0.01$). Male attendance also varied significantly with brood age (Fig. 6; $F = 29.5$, df = 1 and 72, $P < 0.001$). Attendance was greatest during the first week after hatch and then declined with increasing duckling age. Substantial variability also was apparent in the behavior of individual males. A few males (3/33) escorted their mate and brood almost continuously throughout the entire brood-rearing period, while other males (11/33) were never observed with their mate and brood.

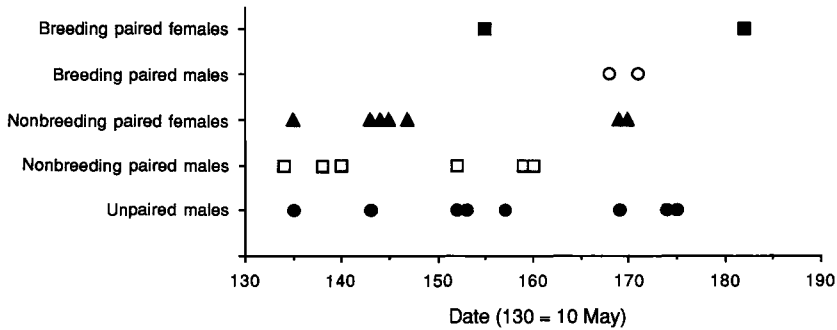Like male attendance, the behavior of males

Fig. 7. Timing of wing molt in relation to pair status and breeding for 25 marked individuals in 1987. Approximate dates of wing-molt initiation plotted. Most breeding birds had not yet initiated wing molt when I left study area on 5 July (=186). Pattern for 1986 was similar, but shifted about one month later.

towards their mate while escorting them was extremely variable. A few males followed their mate closely and provided strong mate defense, while other males were passive and inattentive when associating with their mate, providing little or no defense even when their mate was being harassed.

When not escorting their mate and brood, the activities of males varied. Some were very mobile and active in courtship of other breeding females. Such extrapair courtship was particularly common in the males of pairs breeding early in the season. As the season progressed, male interest in other females appeared to decline; when not associating with their mate and brood, the males of late breeding pairs usually fed or rested, often in close proximity to other males.

Although females showed interest in maintaining the pair bond, most females showed little affiliative behavior towards their mate at this stage (i.e. they did not usually follow or seek out their mate by deliberately swimming toward him if he was some distance away). Thus, the male appeared to be most active in maintaining the pair bond at this stage.

Courtship of brood females.—Females tending broods were preferentially courted by males. The rate of courtship directed at brood females ($\bar{x} \pm$ SE = 0.20 $\pm$ 0.03 males courting/h, n = 21) was twice that directed at nonbreeding females (0.10 $\pm$ 0.02, n = 21, Mann–Whitney U-test, U = 323, P = 0.01). Again, there was a seasonal effect; the mean courtship rate of brood females that bred early (0.26 $\pm$ 0.05, n = 13, hatch date on or before 19 June, 31 May and 30 April in 1985, 1986, and 1987, respectively) was

significantly greater than the courtship rate of brood females that bred late (0.10 $\pm$ 0.03, n = 8, U = 85, P = 0.02). Incubating females also received much attention, but were chased as well as courted.

Incubating and brood-tending females that were courted typically reacted with vigorous aggression (rushes, open-bill-threats) and repulsion displays (Lorenz 1951–1953) and then tried to swim away. If their mate was present, the female swam to his side and incited vigorously. Females were also observed inciting beside their ducklings. These rebuffs did not seem to discourage the courting male(s), which continued attempting to escort and defend the female as if she was his mate. Eventually, some females began to tolerate and accept the presence of a particularly persistent male and, in three cases, a firm pair bond was formed (as indicated by female inciting). Two of these pair bonds were known not to last into the next breeding season (there was no information on the third, since it occurred in 1987, the last field season).

The wing molt.—Although my field seasons ended each year before the majority of my study population had completed the annual wing molt, I was able to document its occurrence in some marked individuals in 1986 and 1987. Unpaired males and nonbreeding pairs began the wing molt earlier in the season than breeding pairs (Fig. 7); a few pairs were still breeding (females still incubating) when both nonbreeding males and females began molting in June and July in 1986 and in May and June in 1987. Only seven birds that had bred had begun the wing molt by the time I left in July 1986 and

1987, so most breeding birds as well as some nonbreeding birds presumably molted in August and September.

Pair bonds did not necessarily break during the wing molt. I recorded six pairs (5 nonbreeding, 1 breeding) that went through the wing molt together. These birds usually remained in close proximity, the male was mildly defensive of his mate, and inciting by the female was recorded many times. In all six pairs, the male began the molt ahead of the female by approximately 5 to 10 days. I recorded wing molt in one member of 10 additional pairs. The male molted first in four of these pairs (2 breeding, 2 nonbreeding), and the female molted first in the remaining six pairs (3 breeding, 3 nonbreeding). In 7 of these 10 pairs, the nonmolting mate was seen with the molting mate at least once, and female inciting and other pair-bond reinforcing displays were observed. The members of 2 of these 10 pairs associated with one another frequently, but the nonmolting mate of the other 8 pairs typically wandered around the Paradise and Rose Island ponds, spending little time with their flightless mate. No flightless adults were recorded escorting broods.

Social courtship involving birds in wing molt was recorded on six occasions. Females in wing molt had down-ups directed to them by their mate and other males. Males in wing molt directed down-ups to their mate, to other females, and to rival males as an aggressive display (McKinney et al. 1990). These courtship bouts were brief and of low intensity (see Fig. 4) compared with courtship that occurred earlier in the season.

There did not appear to be a populationwide molt migration following the breeding season, as is typical for Northern Hemisphere ducks. Most marked birds (including many in wing molt) were still present on the study area at the end of each field season.

DISCUSSION

TIMING OF BREEDING

Breeding in the White-cheeked Pintail appears to be triggered by proximate cues related to the amount and timing of variable winter and spring rains. Breeding also follows rainfall on other islands in the archipelago and Caribbean. For example, ducklings have been noted at Great Inagua (the most southerly Bahama Is-

land) and nearby Grand Turk in February following heavy winter rains (M. Lightbourne, J. Nixon, C. Faanes, P. Maillis, pers. comm.). Nest initiations are also correlated with rainfall in Puerto Rico (E. Rodriguez, pers. comm.). Because rainfall is much more irregular in the extreme southern Bahamas and other islands in the Caribbean (Bahamas Meteorological Department, Nassau, Bahamas), the timing of breeding seasons may be even more variable in these regions. Nesting has been documented in each month from December to June at Great Inagua (McKinney and Bruggers 1983) and from April to November in the Virgin Islands (Norton et al. 1986). Although nest initiations peak in April and July (with a smaller peak in January), nests have been found in every month of the year in Puerto Rico (E. Rodriguez, pers. comm.).

Rainfall appears to be an important proximate cue for breeding in many other tropical/Southern Hemisphere waterfowl. In some of these species, nests have been found in all months of the year, but breeding is generally seasonal and corresponds to the rainy season of the given region (e.g. Pacific Black Duck [*A. superciliosa*], Braithwaite 1976a, Crome 1986; African Yellowbill [*A. undulata*], Siegfried 1974, Johnsgard 1978). In other species or populations, breeding occurs opportunistically in response to irregular rainfall and, in many regions, there is no distinct breeding season (e.g. Grey Teal [*A. gibberifrons*] and Pink-eared Duck [*Malacorhynchus membranaceous*] in Australia, Braithwaite 1976a, b; Red-billed Pintail [*A. erythrorhyncha*] and Cape Teal [*A. capensis*] in Africa, Siegfried 1974, Johnsgard 1978). In general, the breeding seasons of most birds inhabiting tropical and arid environments are extended and determined by rainfall (Marchant 1960, Ricklefs 1969, Kunkel 1974, Wunderle 1982, Halse and Jaensch 1989).

Although variable in timing and apparently triggered by rainfall, breeding in my study population was largely seasonal. Breeding has not been recorded in September and October, the months with the highest average rainfall in the central Bahamas, suggesting that factors other than rainfall also influence the timing of breeding. One likely control is photoperiod (Murton and Kear 1978). Migratory, Northern Hemisphere *Anas* breeding in temperate and subarctic climates show a distinct physiological response to increasing daylength; hormones

associated with breeding (e.g. luteinizing hormone, testosterone) begin to increase as does testes weight and size and, in some species, courtship activity begins (Jallageas and Assenmacher 1980, Bluhm 1988). A similar response has been shown for the seasonally breeding Pacific Black Duck in Australia (Braithwaite 1976b).

The specific proximate cues associated with rainfall to which White-cheeked Pintails respond are not known. In a study on captive Grey Teal, Braithwaite (1976b) suggested that a visual response to rainfall occurred; following a series of thunderstorms, intense social courtship commenced, and the testes began to enlarge. Additional proximate stimuli associated with rainfall, such as fluctuating water levels and increased invertebrate populations may stimulate breeding in White-cheeked Pintails, but abundant food for the nesting female and her ducklings is likely the ultimate factor selecting for breeding in response to rainfall.

MATING SYSTEM

Many aspects of the White-cheeked Pintail's mating system distinguish it from that of migratory Northern Hemisphere dabbling ducks. The sedentary lifestyle (made possible by the subtropical, mild climate) and the potential for variable and extended breeding seasons appear to be the key ecological factors influencing the mating system of this species.

Polygyny.—Despite a sex ratio skewed strongly towards males and intense competition for mates throughout the breeding season, 4 to 9% of paired males were polygynous each year. This is the first study to document the regular occurrence of polygyny in a wild population of ducks.

Two factors relating to the sedentary nature of the population may explain the occurrence of polygyny in White-cheeked Pintails. First, individuals interact with one another year around and year after year, allowing individual recognition and the formation of stable dominance hierarchies. These long-term social relationships may allow females to readily compare and assess the qualities of different males. Second, because most individuals are sedentary, once polygynous pair bonds form, a male can maintain them, because his mates use pond(s) in the same vicinity throughout the breeding season.

This is in direct contrast to the situation in migratory Northern Hemisphere *Anas* in which pair formation takes place in large flocks on the wintering grounds. The fact that males follow their mates back to the female's natal home range precludes the possibility of polygyny in these species. Even if a male was able to pair with two females on the wintering grounds, he could not follow both back to the breeding range. In light of my data, the suggestion that monogamy in Northern Hemisphere species is an unavoidable consequence for males of winter pairing and female philopatry appears accurate (see McKinney 1986, Rohwer and Anderson 1988).

Extended breeding seasons may be another factor influencing the opportunity for polygyny (Emlen and Oring 1977). Asynchrony in the reproductive condition of females may enable males to divide their time between two mates more easily by spending more time with the first female during her prelaying and laying period, and then switching attention to the second female once the first female is occupied with incubation and brood rearing. Such a sequence occurred in four of the polygynous relationships I studied. In one case, however, the two females nested synchronously, indicating that breeding asynchrony is not a prerequisite for polygyny. Within-season serial monogamy may occasionally occur in Northern Hemisphere dabbling ducks as a result of mate switching between renesting attempts (Humberg et al. 1978), but polygyny (the simultaneous maintenance of two pair bonds) has not been recorded in an unmanipulated population (see Ohde et al. 1983).

Emlen and Oring (1977) identified three mechanisms by which males could monopolize more than one mate. In "resource-defense polygyny," males gain access to more than one female indirectly by monopolizing resources critical to reproduction. Although male White-cheeked Pintails defend territories during the breeding season, resource-defense polygyny is not an adequate description of polygynous relationships in this species, because pair formation occurs prior to the establishment of territories and the defense of resources. Female choice, therefore, is based not on territory quality, but on the quality of the male himself.

I propose that polygyny in the White-cheeked Pintail is best thought of as "male-quality polygyny," where polygyny occurs when male quality (as expressed by aggressiveness and attentiveness) is sufficiently variable that some

females receive better mate guarding by pairing polygynously with a high-quality male rather than monogamously with a low-quality male. This idea is analogous to the polygyny-threshold model (Verner and Willson 1966, Orians 1969) with male quality substituted for territory quality. Polygynous male White-cheeked Pintails were particularly effective at establishing territories and guarding their mates during the breeding season, and these qualities were important to female breeding success. As suggested for Northern Hemisphere ducks (McKinney 1986, Rohwer and Anderson 1988), I believe that females determine the mating system of the White-cheeked Pintail; they choose whether to pair polygynously or monogamously, and are not controlled or monopolized by males.

Polygyny has been documented in flight-pen studies of two Southern Hemisphere *Anas*, Cape Teal and Speckled Teal (Stolen and McKinney 1983, McKinney 1985). As suggested here for White-cheeked Pintails, the extended and/or irregular breeding seasons of these two species may provide opportunities for males to obtain two mates. Also, as in the White-cheeked Pintail, some populations of Speckled Teal are sedentary. Cape Teal, however, are highly nomadic, moving irregularly in search of suitable breeding habitat. Siegfried (1974) did note that Cape Teal usually travel in pairs and small flocks. If these flocks represent fairly stable groups of individuals, similar factors (e.g. stable dominance relationships among individuals and their effect on mate choice and the potential for males to simultaneously maintain pair bonds with two females) could also apply to this species.

Pair-bond duration.—A second distinguishing feature of the White-cheeked Pintail mating system is the occurrence of long-term pair bonds. There are several potential advantages for both male and female birds of remaining with the same mate from year to year. Establi. hed pairs may obtain better feeding sites or territories, save time and energy by avoiding courtship, and (through familiarity with patterns of individual behavior) better coordinate activities and movements (Rowley 1983, McKinney 1992). Mate retention is most feasible in species with a nonmigratory lifestyle (Rowley 1983), and the reunion of mates is more likely in sedentary populations of ducks, even when pairs separate during brood rearing, the wing molt, or the nonbreeding season. The absence of a molt migration may be of particular importance; White-

cheeked Pintails in my study population molted on the same complex of ponds in which they live year around, and some pairs molted together. The benefits of desertion for males, therefore, are probably low.

Long-term pair bonds have been documented in several other tropical/Southern Hemisphere *Anas*, including the Laysan Teal (*A. laysanensis*, Moulton and Weller 1984), African Black Duck (McKinney et al. 1978), Grey Teal (Fullager and Davey 1990), and Cape Teal (Siegfried et al. 1976); they are thought to occur in Silver Teal (*A. versicolor*, Weller 1968, McKinney and Brewer 1989) and Chiloe Wigeon (*A. sibilatrix*, Weller 1968, Brewer 1990). The factors influencing pair-bond duration, however, apparently vary among species (Sorenson 1991).

In contrast, long-term pair bonds have not been recorded in migratory Northern Hemisphere dabbling ducks. Males typically desert their mate during incubation and travel to a safe site, where they undergo the wing molt before migration to wintering areas. Pairs do not reunite on the wintering grounds, presumably because of the difficulty or improbability of locating one another. The advantages to the male of proceeding with the wing molt early and in a safe location apparently outweigh advantages that might be gained by maintaining the pair bond (McKinney 1986).

A few cases of mate retention have been documented in several of the migratory Northern Hemisphere sea ducks (tribe Mergini; e.g. Savard 1985, Gauthier 1987) and long-term pair bonds may be common. Both males and females of these species show strong fidelity to wintering sites and tend to winter in relatively small flocks, factors that probably facilitate the reunion of pairs on the wintering grounds.

Although some White-cheeked Pintails remained paired for two or more years, a large proportion changed mates between breeding seasons even though the former mate was still alive. Considering the potential advantages of retaining the same mate, the divorce rate in this population seems high. In other bird species, mate retention may be influenced by breeding success; pairs which remain together have higher breeding success and production of young, while divorce is correlated with reproductive failure in the previous year (e.g. Newton and Marquiss 1982, Coulson and Thomas 1983). Contrary to expectation, however, I found no relationship between breeding success in one year and subsequent mate fidelity; many pairs

that had bred successfully changed mates the following year, while some that had not been successful stayed together. One possible explanation for this pattern is that the social courtship and competition for mates that occurs throughout the year in this species (see below) makes it very difficult for both males and females to keep a good mate from one year to the next.

Although the factors influencing mate retention in the Laysan Teal are unknown, the annual divorce rate in this species was also high; approximately half of all birds changed mates between years (Moulton and Weller 1984). Observations of birds in pairs year around, biparental care, and/or male attendance of brood females in many additional species probably contribute to the long-standing belief that pair bonds in tropical/Southern Hemisphere ducks are permanent (Weller 1968, Kear 1970, Siegfried 1974, Johnsgard 1978). As two studies on sedentary ducks have now shown, however, both long-term pair bonds and mate switching may be frequent in the same species.

Courtship and competition for mates.—Two additional aspects of the White-cheeked Pintail's courtship and pairing behavior contrast with migratory Northern Hemisphere species. First, social courtship and pairing occur year around. Siegfried (1974) suggested that if the onset of conditions suitable for breeding is unpredictable, birds may benefit from remaining in pairs year around so that nesting can begin as soon as conditions permit. Although breeding was seasonal in my study population, the start of the breeding season was quite variable, and breeding is known to be unpredictable and irregular on other islands in the archipelago. Therefore, continued assessment of potential mates through social courtship and maintenance of pair bonds in the nonbreeding season may well be favored. My obervations of (1) birds sometimes associating with a series of mates before a firm pair bond is formed, (2) frequent extrapair courtship, (3) courtship leading to mate switches, and (4) both males and females establishing liaisons outside the pair bond suggest that such assessment is occurring. Because of the male-biased sex ratio, males sometimes lost mates and remained unpaired for the season. Year-around courtship has also been observed in several other tropical/Southern Hemisphere species: Cape Teal, Grey Teal, and Speckled Teal (McKinney 1985). All three species are known to have extended and/or irregular breeding sea-

sons in at least parts of their range, supporting the idea that continuous courtship is associated with unpredictable breeding.

Second, males showed intense interest in females tending broods. Nonbreeding females present at the same time did not attract similar attention. If females vary in "quality" (i.e. some are more fecund or successful), males should prefer to pair with females of the greatest fecundity (Dewsbury 1982). There is some evidence that White-cheeked Pintail females vary in breeding ability; many marked females did not breed each year, while three females bred in all three years of the study (Sorenson 1990). In addition, although occurring rarely, double brooding has been documented in this population (Sorenson et al. 1992). The presence of ducklings may indicate to a male that a female is a proven successful breeder and, by courting her, he may be attempting to establish a pair bond with her for a future breeding attempt, either that season or the next.

Males may occasionally succeed in obtaining a quality mate (for the future) by courting brood females and establishing relationships with them. Courtship of brood-tending females also has been recorded in two South American species, the Red Shoveler (*A. platalea*) and the Chiloe Wigeon (McKinney and Brewer 1989). In Chiloe Wigeon, adult males court not only brood females but also female ducklings, perhaps indicating very intense competition for mates (Brewer 1990). That pair formation can occur during brood rearing indicates that caution must be used in studies involving unmarked birds; one cannot necessarily assume that the male accompanying a female and her brood is her original mate with whom she bred (e.g. McKinney and Brewer 1989).

Year-around courtship, extrapair courtship, courtship during the wing molt, within- and between-season mate switching, the formation of temporary bonds and liaisons, and courtship of brood females may all reflect the intense competition for mates that occurs year around in White-cheeked Pintails. Individuals appear to be constantly assessing one another and maneuvering for breeding opportunities with quality mates, a seemingly favorable strategy in a species in which nonbreeding is common and breeding seasons are variable and extended. A skewed sex ratio forces males to compete for females, and a higher frequency of pairing success in older males suggests that age and ex-

perience influence a male's ability to attract and hold onto a mate.

Male behavior during brood rearing.—In contrast to Northern Hemisphere *Anas*, many male White-cheeked Pintails continued to associate with and defend their mate throughout incubation and for at least part of the brood-rearing period. When accompanying their mate and brood, males were clearly interested in the female and not the ducklings. They did not defend the brood, escort lagging ducklings, or spend time in vigilant postures as has been described for other tropical/Southern Hemisphere *Anas* with male parental care (McKinney and Brewer 1989).

Siegfried (1974) suggested that males may maintain the pair bond during brood rearing in order to make a second breeding attempt after a first brood has fledged. Females in this population only rarely initiate a second nest after successfully fledging a brood (Sorenson et al. 1992), but double-brooding may be more frequent in populations nearer the equator. A second breeding attempt, however, might also be made if the first brood is lost. Overall, patterns of male brood attendance appear to reflect changing probabilities of a second nesting attempt in the same season. Male attendance of brood females declined as the season progressed (Fig. 5), as does the probability that a female will attempt another nest. Male attendance of brood females also declined sharply after the first week of brood rearing. Once beyond this vulnerable age, when total brood loss is most frequent (e.g. Ball et al. 1975, Ringelman and Longcore 1982, Talent et al. 1983), females are very likely to be occupied with brood rearing for weeks to come. Males of two southern African Anatini—the African Yellowbill and the Cape Shoveler (*A. smithii*)—also have been noted associating with females primarily when ducklings were young (Siegfried 1974).

Although some of the variability in male attendance is explained by hatch date and brood age, considerable variation also may result from differences in the behavior of individual males. Many males, whose mates were incubating or tending a brood actively, courted other breeding females, sometimes establishing temporary liaisons or pair bonds. This is consistent with McKinney's (1985) suggestion that males might adopt a bet-hedging strategy, maintaining a pair bond with a brood-tending mate, but switching to another female when an opportunity arises.

Other males, however, showed little interest in extrapair courtship even though opportunities were available. The costs and benefits of pursuing these different tactics probably vary for individual males, perhaps depending on such factors as the condition of the male or quality of the mate. Variable male attendance with females and broods has been reported for a number of other tropical/Southern Hemisphere species (Siegfried 1974, McKinney 1985, McKinney and Brewer 1989), but the factors influencing a male's decision to escort or desert have not been studied in these species.

In summary, the White-cheeked Pintail mating system is more complex and variable than that of migratory, Northern Hemisphere dabbling ducks. Both monogamy and polygyny occur, and there is greater variation in pair-bond duration and male attendance and behavior during brood rearing. Intense competition for quality mates is indicated by my observations of year-around courtship, within- and between-season mate switching, extrapair liaisons, and courtship of brood females. A sedentary lifestyle, the unpredictability in the timing of breeding, and the potential for extended breeding seasons appear to be the most important ecological factors affecting the reproductive strategies of males and females.

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