LONG-TERM PAIR BONDS AND MALE PARENTAL CARE IN SPECKLED TEAL *ANAS FLAVIROSTRIS* IN EASTERN ARGENTINA

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The breeding behaviour of Speckled Teal; hereafter teal, in eastern Argentina, is influenced strongly by their preference for Monk Parakeet nest cavities. I observed a marked population (n = 337) on the Estancia Los Yngleses, province of Buenos Aires, Argentina from August to December between 1991 and 1994. All pair bonds between marked pairs (n = 38) were monogamous and typically lasted at least two breeding seasons and some lasted at least six years (mean = 2.24 ± 1.12, range 1-6). The probability of divorce was 10.6% and five divorces were recorded in a total of 28 pairs observed over four breeding seasons. Most mate changes (71.5%) followed the disappearance of one pair member. Competition among males for mates was intense. Eight of nine males failed to re-pair following mate loss and many males unpaired at the beginning of the study (16 of 21) were thought to remain unpaired during the study. Only females (n = 7) were successful in re-pairing following the loss of a mate. Males were present with the female and brood in all families observed (n = 9) and the absence of male sightings following exodus from the nest area (n = 33) provided circumstantial evidence that males remained with the female and brood throughout the brood-rearing period. Males escorted broods, retrieved ducklings that strayed, shared alert time with females, and performed distraction displays.

Keywords: Pair Bonds, Parental Care, Mating Systems, Argentina, Speckled Teal

The existence of long-term pair bonds in Southern Hemisphere dabbling ducks (genus *Anas)*, suspected for many years (Weller 1968, Kear 1970), has been documented for the African Black Duck *Anas sparsa* (McKinney et *al.* 1978), Laysan Teal *A. laysanensis* (Moulton & Weller 1984), Grey Teal *A. gracilis* (Marchant & Higgins 1990), Cape Teal *A. capensis* (Siegfried et *al.* 1976) and White-cheeked Pintail *A bahamensis* (Sorenson 1991). The occurrence of persistent pair bonds is also suspected in Chiloe Wigeon *A. sibilatrix* (Brewer 1991) and Silver Teal *A. versicolor* (McKinney & Brewer 1989). There is no information, however, on the relative frequency of long-term bonds in wild populations, the duration of pair bonds, or the frequency of divorce in any Southern Hemisphere dabbling duck.

Several factors have been proposed to explain why long-term pair bonds are favoured in some species of waterfowl but not in others. Such factors include: (1) enhanced reproductive success because of mate familiarity eg *Branta leucopsis, Cygnus spp*. (Black et *al.* 1996); (2) mates remaining together to keep an established territory eg *Anas sparsa,* *Hymenolaimus malacorhynchos* (McKinney et *al.* 1978, Veltmann et *al.* 1991); (3) permanent bonds enabling pairs to initiate breeding promptly when unpredictable conditions favourable for breeding occur eg *Malacorhyncos membranaceus, A. gibberifrons* (Braithwaite 1976), and (4) the need for bi-parental care promoting long-term bonding in species using habitats especially hazardous for young eg *A. sibilatrix, A. versicolor, A. specularioides* (McKinney 1991).

The Speckled Teal *A. flavirostris* is a Southern Hemisphere species in which the presence of long-term bonds and the role of the male in brood-care have been uncertain. Several authors have noted that pair bonds are observed after the breeding season in this species (suggesting long-term bonding) (Weller 1968, Johnsgard 1978) and both parents have been seen escorting ducklings (Weller 1968, 1972, McKinney & Brewer 1989). In one study, however, five of 15 broods were escorted only by the female (suggesting that some males desert their mates before or during brood-rearing) and, when males are present, their contributions to duckling care are not well established (McKinney & Brewer 1989). Several criteria can be used to help distinguish between males providing parental care from those mate guarding. Such males would be expected to respond to distressed ducklings, escort separated ducklings back to the brood, remain with the brood during female absence, and perhaps leave the female in favour of ducklings during threats to the brood. Mate guarding males should show little indication of response to distressed or separated ducklings, remain near the female instead of the brood during recess periods, and defend the female when threatened, perhaps at the expense of ducklings.

In this study of marked individuals I document the duration of pair bonds and the behaviour and role of the male during the nesting and brood-rearing period in wild birds in eastern Argentina.

Methods

Study area and natural history

I studied a population of Speckled Teal first described by Gibson (1879) and located on the Estancia Los Yngleses, a private sheep and cattle ranch in east central Buenos Aires province in central Argentina (36°30' S 57°30'W) (**Figure 1**). The ranch is located on the eastern edge of the Argentine 'pampas', an open grassland that extends over 44,400,000 hectares across central Argentina. Temperate in climate, the area receives a seasonal rainfall of 600 to 1,200 mm each year, mostly during spring and autumn months. During the breeding season (August to December), Speckled Teal primarily use small permanent and ephemeral wetlands dispersed across the pampas. Some of the larger permanent wetlands with dense emergent vegetation are used as brood rearing areas later in the breeding season.

Speckled Teal prefer to nest in compound nests of Monk Parakeets *Myiopsitta monachus* as described by Gibson (1920) and Hudson (1920). The large enclosed stick nests, occupied by several parakeet pairs, are located at heights of 5-20 m in trees and provide elevated cavities safe from terrestrial predators and are a potentially re-usable resource (eg Nice 1957, Lack 1968, Martella & Bucher 1993). Cavities within a compound nest are frequently abandoned by parakeets, allowing female Speckled Teal to occupy them during the breeding season. At one time, parakeet nests were located exclusively in the canopy of native Tala *Tala celtis* trees, but since the turn of the century when exotic trees were established in many areas, parakeets have nested almost exclusively in the much taller *Eucalyptus*, providing additional security from predators (Gibson 1880).

My primary study site was a grove of trees (hereafter called grove B) about $^{1}/_{4}$ km in length, consisting of three rows of *Eucalyptus* running parallel to the road leading into the estancia. Approximately 100 m across the grasslands to the east, south and west of the grove a series of wetlands served as primary feeding and roosting areas for teal.

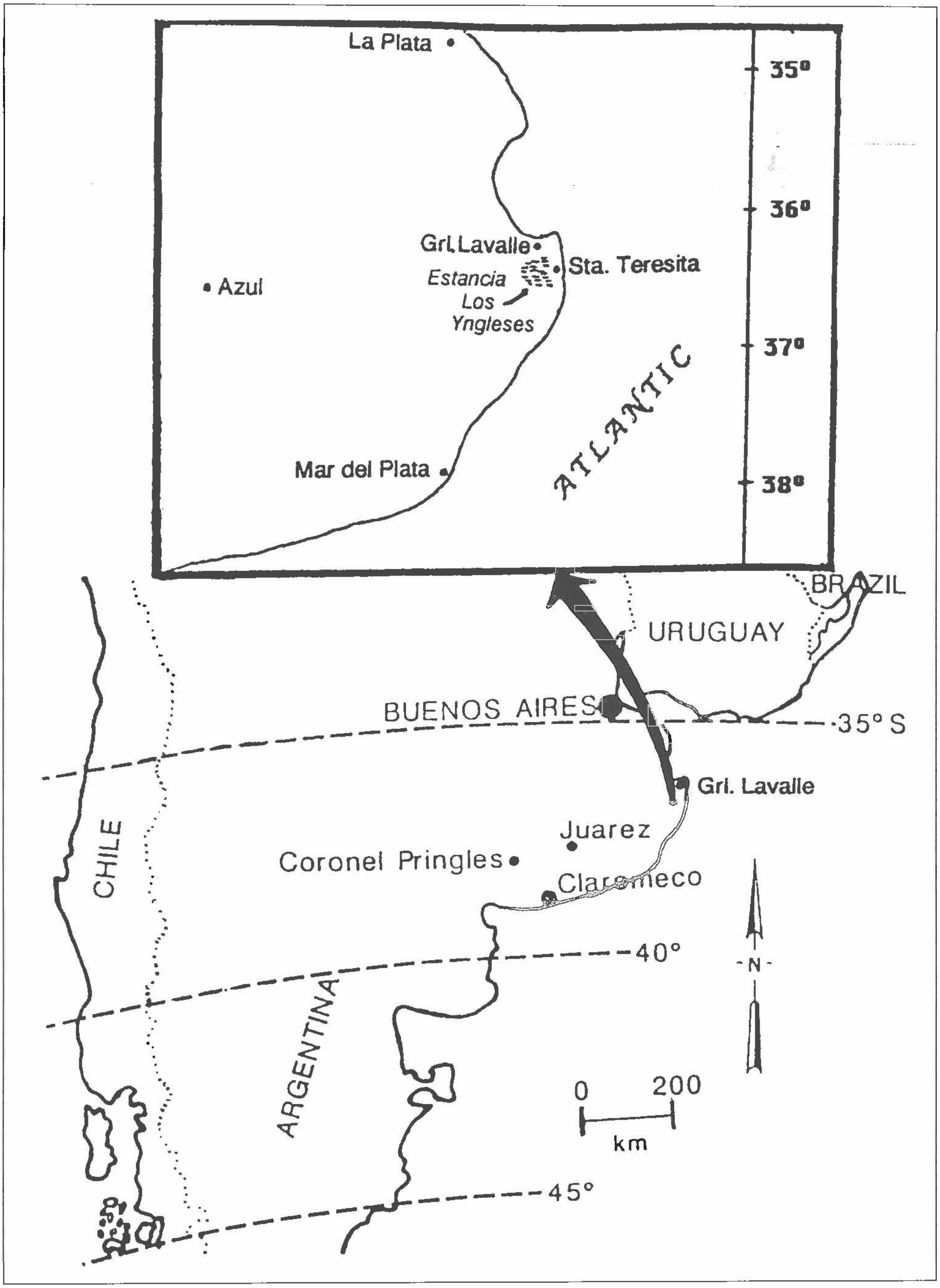

Figure 1. Map of location of Estancia Los Yngleses, Buenos Aires, Argentina. Observations were conducted during the breeding season between 1991 and 1994.

Fieldwork

Fieldwork was conducted between August and December in 1991, 1992 and 1994 and between 10 September and 2 October in 1993. I made observations with binoculars and telescopes from two 4 m tower blinds placed 35 m south of the grove. From 1991 to 1994 marked individuals were followed at the study site for a total of 1249 hrs. Three hundred and thirty seven Speckled Teal (220 males, 117 females) using the site were mist netted and marked with numbered aluminium leg bands and unique combinations of coloured leg bands and nasal markers for identification. Several birds (*n* = 27), marked in 1989 and 1990 by Gwen Brewer, also were observed. Focal subgroup sampling (Altmann 1974) and scanning techniques were used to document pair bond status, courtship behaviour, and time spent by each sex in mate support activities (eg mate guarding, nest defence) and secondary strategies (eg forced extra-pair copulations, brood parasitism).

Ten incubating females (four in 1992, six in 1994) were captured prior to hatch and fitted with radio transmitters attached with backpack harnesses (Dwyer 1972). After ducklings left the nest cavity, females were tracked and, when possible, observed to determine brood movement, duckling survival, male presence with the brood, and parental care behaviour. Broods proved to be difficult to see in dense vegetation, so I used the number of ducklings hatched as an index of reproductive success.

For statistical analysis, parametric tests were used on normally distributed variables; otherwise, non-parametric tests were used. All test results report two-tailed probabilities and tests were carried out using SYSTAT software (Wilkinson 1987).

Terms

I calculated the probability of 'divorce' (Ens et *al.* 1996) in Speckled Teal using only cases in which both members of a pair were known to be alive but not breeding together in a subsequent breeding season. Probability of divorce was calculated by dividing the total number of divorces by the total number of pair-years. Only pairs marked prior to 1994 were used in the calculation of the probability of divorce. 'Mate loss' is used when only one member of the pair was subsequently resighted on the study area. I refer to the emergence and departure of females with broods from cavities within the study site as exodus events. I followed Standen's (1980) terminology for displays.

Results

Incidence of divorce

Although both long-term pair bonds and mate switches occurred (**Table 1**), mate fidelity was high (89.4%) and the probability of divorce was low (10.6%). Prior to 1994, 38 pairs were marked on the study site. Of these pairs, 28 were re-sighted intact in at least one subsequent year (47 pair-years). Ten pairs failed to re-unite in any subsequent year, and in five of these, one or neither of the members were resighted after the first year. Of the remaining five pairs, four divorced between seasons and one case of within-season mate switching was observed. Three of the four between-season divorces occurred in birds paired for a single season following capture.

Mating relationships

Of 76 Speckled Teal, 89.5% had a single mate during the course of the study (mean = 1.13, SD = 0.41). Of the remainder, only 7.9% of marked individuals switched and had two mates and 2.6% (all females) had three mates. Eight of nine males, (88.9%) failed to re-pair following mate loss while all females (*n* = 7) re-paired successfully prior to the next breeding season (X^2 = 12.44, DF = 1, $P < 0.001$).

Sixteen males, unpaired when marked, remained unpaired (mean = 2.6 years unpaired). Five disappeared prior to the end of the study (mean = 2.4 years unpaired) and the remainder were unpaired at the end of the study (mean = 2.7 years unpaired). The

Table 1. Mate retention and mate changes between years among Speckled Teal in South-eastern Argentina

Year	No. Marked pairs observed	No. Pairbonds intact in following year	No. Divorces	One pair member sighted in following year	Neither pair member sighted in following year
1991	11	9	0	0	2
1992	26*	16	4	2	4
1993	26*	14	1**	6	5
1994	28*	-	0	-	-
Total	91	39	5	-	-

* Pairs were followed in several years and are included more than once.
** Divorce occurred mid-season.

difference in years between unpaired males that disappeared from the study site and those that remained is not significant (Mann-Whitney U, $P = 0.225$). None of the males ($n = 11$) that were unpaired at the beginning of the study and remained on the study site obtained mates.

Causes of mate change and divorce

Through 1994, 15 changes in mate status occurred among marked pairs. Most, 66.6% (10), were caused by mate disappearance while 33.4% (five) were caused by divorce. Mate change among pairs partnered for two or more consecutive breeding seasons generally occurred only following the death or disappearance of a mate (seven of eight). One pair together over two breeding seasons subsequently divorced without a nest attempt on the study area.

Courting parties ($n = 661$) were observed throughout the breeding season on the study site, peaking in late September. Parties ranged in size from one to 15 males (median = 2) and consisted of paired and unpaired males courting between one and three females (median = 1).

One divorce was directly observed during a courting party. Over a three-day period (3-5 September, 1992), an unmarked male (C) aggressively chased and courted female A, who was paired to male B at the time. Male C was conspicuously larger than most other males, including male B, and he successfully displayed to the female despite attempts by B to chase him away. Midway through a prolonged and intense courtship bout on day two, the female, who had been inciting beside B, began inciting beside a large unmarked male, probably C observed courting her on day one. Inciting is a display which indicates a female's mate preference and involves threatening toward a rejected male while holding a position beside the mate (McKinney 1975). By the end of this courtship bout, the allegiance of the female had switched completely to C. On the following day, B continued to court the female but she remained paired to C. Throughout the remainder of the breeding season, B was periodically observed following the female, but each time he was aggressively chased away by her new mate. Male B remained unpaired throughout 1992 and 1993 and disappeared prior to the 1994 breeding season.

Four cases of between-season divorce were recorded. In all cases, divorced males remained unpaired during the next breeding season. These switches occurred prior to the start of the breeding season in August, with no observations concerning these events.

Pair bond duration

Most pairs persisted at least two or three breeding seasons after marking (mean = 2.24, SD= 1.12, range 1-6). One pair persisted for six breeding seasons and four pairs remained together for four breeding seasons. An additional eight pairs remained together for three seasons while 16 pairs persisted two years. Some of these pair bonds may have persisted longer because they were intact at the end of my study. In two pairs, dissolution of the pair bond was precipitated by the confirmed death of the female.

Reproductive success and mate change

Of four pairs divorcing between seasons, two hatched a clutch successfully prior to the split and two divorced following a failed attempt. All four females paired to new mates but failed to acquire a nest site in the next breeding season after re-pairing, although one female nested successfully two years after re-pairing.

Seven of 19 (36.8%) pairs that were together two or more breeding seasons nested successfully in the first year they were observed. The remaining 63.2% (n = 12) of pairs failed to nest in their first year on the study site but remained together for a minimum of two breeding seasons. The difference in reproductive success between divorcing and non-divorcing pairs was not significant ($X^2 = 0.236$, DF = 1, NS).

One pair divorced within-season and may have been influenced by breeding failure. Both parents appeared inattentive toward the brood prior to complete loss of the brood. Dissolution of the pair bond was noted three weeks after the disappearance of the ducklings. However, only the female was re-sighted later in the breeding season, paired to an unmarked male.

Male parental care behaviour during exodus

When males were present during exodus (during six of 13 events), they typically attempted to protect their female and brood. Escorting males ran beside or behind the female and brood, maintained alert postures, and pursued other teal that attempted to follow. In one instance, the male returned to retrieve a trailing duckling and accompanied the duckling until they were reunited with the family. On two of four occasions where the safety of the ducklings was threatened by an observer during exodus, males performed distraction displays while the female continued to lead the brood away from the grove. In one instance, the male left the female and brood for the safety of a nearby wetland while the female gave distraction displays.

Males were very interested in ducklings and, on several occasions, were seen to attempt to lead ducklings away or defend ducklings that were not their own offspring (= 'non-offspring ducklings') when their mates behaved aggressively toward the ducklings. Non-breeding females (females in the prospecting phase) were aggressive toward non-offspring ducklings and pecked ducklings that tried to follow them. In such situations of intense social activity, brood females attempted to assemble their ducklings as quickly as possible and lead them away from the nest-site. Occasionally other males attempted to follow unescorted brood females but they generally stopped when the female left the grove. On occasions when males persisted in following the female and brood, the female gave aggressive 'repulsion' behaviour characteristic of incubating or brood females in many dabbling ducks (Lorenz 1971). During one exodus, an unescorted female was defended and accompanied for about 75 m by a male who was not her mate. When joined by her mate, the female gave aggressive repulsion behaviour toward the intruder male and, escorted by her mate, led the brood to the wetland.

Male participation in brood care

Of the ten females equipped with radio transmitters, nine hatched ducklings successfully and were tracked during the brood-rearing period. In all cases, the male remained with the brood and female throughout the brood-rearing period, although poor visibility of broods restricted extended observation in most cases. In seven of nine cases, brood females chose wetlands covered by dense stands of emergent vegetation including bulrush *Scirpus californicus*, cut grass *Senecio bonariensis*, and duraznillo *Solanum melanoxylon*. Pairs and broods foraged and rested within these areas and rarely emerged from cover for more than a few brief moments. For example, over 18 observation periods totalling 1,351 minutes, the pair and brood were visible for 27.8% of the time. In all cases (n = 9), when adults were observed with ducklings, males were present.

Additional evidence that males remained with broods following the 33 exodus events was provided by the absence of male sightings in the grove. On one occasion, however, the marked male was seen on the two days following exodus (when presumably he had not yet found his brood) but not thereafter during the remainder of the season.

Observations on five families (three broods in 1992 and two in 1994) showed that males were responsive to the ducklings and protective of them. For example, one male was observed alone and alert with the ducklings on two occasions when the female left the vicinity to bathe and preen out of sight. Another male escorted his ducklings while the female was chased by a lone male on two occasions. Time spent alert by males was not significantly different from that spent by females (P = 0.771, **Figure 2a**). The day following the loss of the ducklings, both the male and female of family #5 increased the time spent foraging and preening and reduced their combined alert time to less than 7% of the total time (n = 45 minutes). The pair then disappeared from the study area for two weeks before the female returned with a new mate.

The timing and direction of brood movements more frequently was determined by the female (**Figure 2b**). In four families observed, females led the brood an average of 57.9% (95% Conf. Int. 58.7 ± 13.1%) of the time.

Distraction displays performed on six occasions by females (n = 6) and on six occasions by males (n = 4) were observed. One male gave distraction displays on three occasions in response to approaches by observers and another male gave a distraction display in response to a dog chasing birds on the brood-rearing wetland. In addition, two males were seen giving distraction displays in response to broods approached by an observer during exodus. Female displays occurred either following a disturbance at the nest site or approaches by observers during the exodus. The displays involved were similar to those described for other *Anas* species; the bird wing-flapped over the ground or water while vocalising loudly and moving away from ducklings (Johnsgard 1968).

Discussion

Prevalence of long-term bonds in Speckled Teal

Mate selection in most Holarctic dabbling ducks takes place during social courtship, although pair bonds frequently form prior to peak periods of social courtship, apparently forming without periods of complex courtship displays (McKinney 1992). Most dabbling duck populations have male-biased adult sex ratios, and males tend to be the most active sex in courtship. In my study, the intensity of competition among the remaining unpaired males for females late in the breeding season is reflected in the presence of courtship groups, generally consisting of a single female and several (2-15, median = 2) males jockeying for position to perform attention-getting displays toward the female. If the female is paired (as were all females observed in the Los Yngleses population), she rejects courting males with inciting displays and her mate may threaten the courting males as well, resulting in highly visible display groups. Males were largely unsuccessful in obtaining new mates during subsequent breeding seasons. Only one of nine males losing mates re-paired during the study and 16 males were unpaired when marked and remained unpaired for several breeding seasons (mean = 2.6 years unpaired).

Three of four factors that might favour

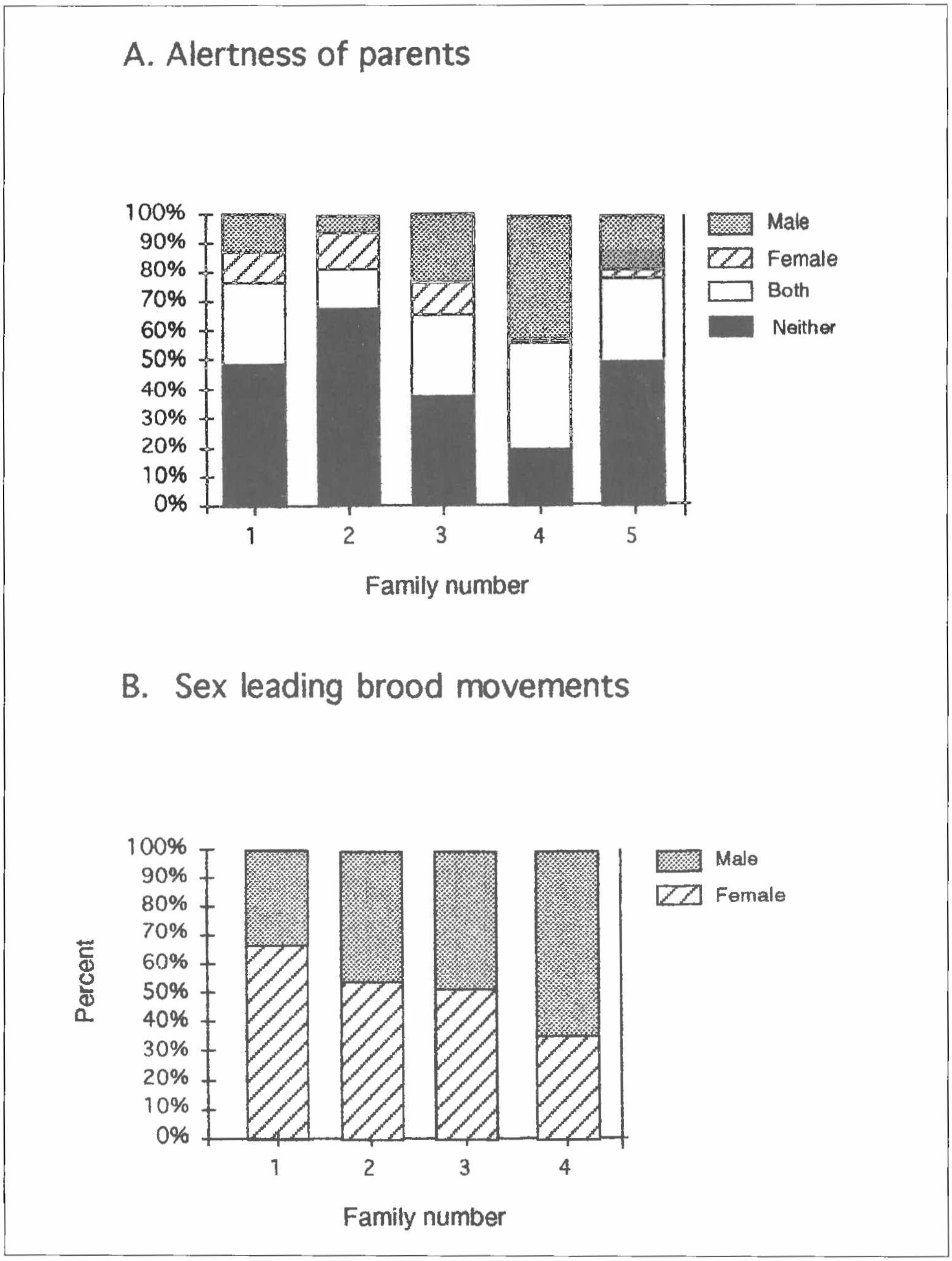

Figure 2. Comparison of time spent alert by each sex during the brood-rearing period for five families. Observations times for families 1-5 were 209, 53, 40, 53 and 21 minutes respectively; point samples taken every 60 s. (A) Percent of times that male and female were in alert position. (B) Percent of time make and female led brood movements.

retention of long-term pair bonds in this population are not supported by the evidence: mate familiarity, territory retention, and unpredictable breeding environments. Although one pair divorced mid-season following reproductive failure, no general relationship was documented between the reproductive success of pairs and the duration of the pair bond. There was no significant difference in success in nest acquisition or number of ducklings hatched between divorcing and faithful pairs. In addition, pairs together two or more years were no more successful than pairs nesting for the first time on the study site.

Retention of an established territory cannot be involved in this species because cavities are utilised only during nesting and no fixed territory is defended after exodus (unpub. data). Reproductive success in this species is not limited by the possession of an all-purpose territory as documented in species such as the African Black Duck or the Blue Duck (McKinney *et al.* 1978, Veltmann *et al.* 1991).

Speckled Teal breeding at the Estancia Los Yngleses have regular annual breeding seasons (Port 1998, Weller 1968). While breeding seasons were extended, clutches typically were initiated in late August and continued into December in all years of the study. No direct linkage to rainfall patterns was detected (Port 1998). Therefore my study does not support the idea that long-term bonds are favoured in response to unpredictable environmental conditions.

Links to biparental care

Male responsiveness to ducklings during exodus and the brood-rearing period suggest the participation of males in parental care in this species. During the exodus period, I observed males perform distraction displays in response to approach by human observers and accompanying ducklings that became separated from the brood, escorting them back to join the female and brood. In addition, two males responded to attacks by females on unrelated ducklings and later gave distraction displays.

The need for bi-parental care may be an important factor favouring long-term bonds in this population. The greatest brood mortality in Speckled Teal occurred within the first twenty-four hours (Port 1998). During the overland journey to a brood-rearing wetland, ducklings face exposure to predators and risk of abandonment if they become separated from the female (or male if present). High mortality during this period is common in many waterfowl species (Afton & Paulus 1992) and may be particularly important in species with nest-sites distant from brood-rearing wetlands.

I found no evidence that some males do not accompany the brood, as suggested by McKinney & Brewer (1989) and Weller (1968) for other populations of Speckled Teal. Males were present with all radio-tagged females, and circumstantial evidence from 33 pairs following hatch suggests that this was the general pattern. Moreover, males showed active parental care by closely accompanying the brood, escorting ducklings that stray, and sharing alert time with the female.

The behaviour documented in my study suggests active male interest and participation in brood-rearing activities and supports the hypothesis that male accompaniment is not solely the result of mate guarding behaviour. However, in order to fully assess the impact of male presence on brood survival, male removal experiments would be necessary. If male presence does increase duckling survival, removal of males should decrease survival among broods.

While male parental care behaviour may be a major factor in the selection for long-term pair bonds, other mate support behaviours probably are important as well. Most males routinely participated in defending the nest cavity from other prospecting females (Port 1998). Males also provided important protection to females from harassment and interference by courting males during laying and incubation. Mate retention may also be favoured by males due to the intense competition for females in this population.

The strong linkage assumed between bi-parental care, and long-term monogamy in birds in general (Mock *et al.*1996) needs to be closely examined in Southern Hemisphere duck species (McKinney 1991). Williams and McKinney (1996) noted that among waterfowl species with long-term pair bonds, species with bi-parental care were less likely to divorce than those with female-only care. Long-term studies of marked individuals are scarce, however, and more such studies are needed to fully identify the factors promoting long-term monogamy and provide a clearer picture of the reasons why some birds divorce.

I thank S. Port, P. Johnson, S. Osborne, N. Rojek, T. Port and A. Sarrias for excellent assistance with the fieldwork. I am also very grateful to the John Boote family for permission to use to the Estancia Los Yngleses to conduct my research and generous access to rainfall records. I thank M. Beade, Fundacion Vida Silvestre Argentina, and the Argentine National Parks Service for logistical support. I thank F. McKinney for support and comments on my many drafts and Gwen Brewer for use of data from 1989-1990. This study was supported by grants from the Dayton Natural History Fund and James W. Wilkie Fund of the James F. Bell Museum of Natural History, Frank M. Chapman Memorial Fund of the American Museum of Natural History, Sigma Xi Society, a University of Minnesota Doctoral Dissertation Improvement Grant, and a grant to F. McKinney from the National Science Foundation (BNS-8820065).

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