SPECIES AND SEX-BIASED PREDATION ON HATCHLING GREEN TURTLES BY FRIGATEBIRDS ON EUROPA ISLAND, WESTERN INDIAN OCEAN[1]

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Abstract. Europa Island is a major breeding place for green turtles (*Chelonia mydas*; 0.7 to 2.4 million juvenile turtles hatch there annually), Great Frigatebirds (*Fregata minor*; 700 to 1100 breeding pairs), and Lesser Frigatebirds (*Fregata ariel*; 1000 to 1200 pairs). By visual observation, we quantified the proportions of males, females, and juveniles of both frigatebird species prospecting over the hatching sites and preying on hatchling turtles. Of 1828 juveniles observed hatching at daytime (35 separate turtle emergences), 1632 were immediately eaten by male Great Frigatebirds. Only 10 hatchlings were preyed upon by female Great Frigatebirds; the remaining 186 were captured by juvenile Great Frigatebirds. Such feeding behavior was not observed in Lesser Frigatebirds. We suggest that the sexual and species differences in hatchling turtle predation are due to size differences between the two species and between male and female Great Frigatebirds.

Key words: feeding ecology, frigatebirds, green turtle, predation, sexual size dimorphism.

Sesgos de Especies y Sexo en la Depredación de Tortugas Verdes por Fragatas en la Isla Europa, Océano Índico Occidental

Resumen. La Isla Europa es un importante lugar de reproducción de tortugas verdes (*Chelonia mydas*; 0.7 a 2.4 millones de tortugas juveniles eclosionan allí anualmente), así como de *Fregata minor* (700 a 1100 parejas reproductivas) y *F. ariel* (1000 a 1200 parejas). Por medio de observaciones visuales, cuantificamos la proporción de machos, hembras y juveniles de ambas especies de fragatas que investigaban los sitios de eclosión y se alimentaban de tortugas juveniles. De un total de 1828 tortugas observadas eclosionando durante el día (35 episodios de eclosión diferentes), 1632 fueron inmediatamente depredadas por machos de *F. minor.* Sólo 10 tortugas fueron consumidas por hembras de *F. minor,* mientras que las 186 restantes fueron capturadas por individuos juveniles de esta especie. Este comportamiento de alimentación no fue observado en *F. ariel.* Sugerimos que la depredación diferencial de tortugas juveniles es consecuencia de las diferencias en tamaño entre las dos especies de fragatas y entre machos y hembras de *F. minor.*

The family Fregatidae includes five closely related tropical seabirds which feed mainly at sea by surface seizing (Nelson 1975). Their main prey are fish (mainly flying fish Exocoetidae) and squid (mainly Ommastrephidae; Nelson 1983, Schreiber and Clapp 1987, Niethammer et al. 1992), although some authors report occasional inland predation on seabird chicks and hatchling turtles (Nelson 1975, Megyesi and Griffin 1996). Frigatebirds are also well known for their piratical habits (Vickery and Brooke 1994).

Frigatebirds exhibit reversed sexual dimorphism (females are larger than males in all five species), that is more or less pronounced according to the species. For example, male body mass is 85% of female body mass in Great Frigatebirds (*Fregata minor*; F. Lagarde, unpubl. data) and 94% in Lesser Frigatebirds (*Fregata ariel*; Nelson 1975). Such reversed sexual size dimorphism is a trait which appears also in raptors (Falconiformes), owls (Strigiformes), skuas and jaegers (Stercorariidae), and boobies (Sulidae) (Andersson and Norberg 1981, Mueller 1990). Different hypotheses have been proposed to explain the evolution of this trait in birds: resource partitioning, sex role partitioning in parental care, and sexual selection (Anderson and Norberg 1981, Mueller 1990). Among these, resource partitioning between members of a given pair assumes differences in feeding behavior, resulting in little overlap in food niches of males and females. Several studies of kleptoparasitism have shown that male and female frigatebirds do not chase the same seabird species. Females generally chase large species, such as boobies and Red-tailed Tropicbirds (*Phaethon rubri-*

cauda), whereas males do not kleptoparasitize or select smaller host species like terns, noddies, or shearwaters (Osorno et al. 1992, Gilardi 1994, Le Corre and Jouventin 1997a).

Although kleptoparasitism is very conspicuous in the vicinity of breeding colonies, it is not the main feeding strategy of frigatebirds (Diamond 1973, Nelson 1975, Vickery and Brooke 1994). Indeed, sexual differences in feeding ecology are still poorly documented among frigatebirds. Megyesi and Griffin (1996) described female-specific predation of Brown Noddy (*Anous stolidus*) and Sooty Tern (*Sterna fuscata*) chicks, suggesting that differences between male and female feeding strategies do not concern only kleptoparasitism. Predation of hatchling turtles on beaches has been reported (Hirth 1971, Nelson 1975, Stancyk 1982) but not in all studies (Diamond 1973, Niethammer et al. 1992), and sexual bias in this behavior has never been examined.

The aim of our study was to examine hatchling turtle predation by frigatebirds at Europa Island, in the Mozambique Channel. In this place, hatchling turtle predation by frigatebirds occurs during daylight (Servan 1976), providing opportunity for a detailed study of this feeding strategy.

METHODS

STUDY AREA

Europa Island (22°20′S, 40°22′E) is one of the best-preserved islands of the Malagasy area. It is a flat, 30-km^2 coral island (for a complete description, see Le Corre and Jouventin 1997b). Between 2000 and 11 000 female green turtles breed annually on its sandy beaches (Le Gall et al. 1986, Le Gall 1988), laying approximately 3 clutches of 110 eggs each, and about 0.7 to 2.4 million juveniles hatch (Le Gall et al. 1985, Miller 1996). Between 700 and 1100 pairs of Great Frigatebirds and 1000 to 1200 pairs of Lesser Frigatebirds breed in the dry forest, dominated by *Euphorbia stenoclada,* that covers the oldest and highest rocky part of the island (Le Corre and Jouventin 1997b). On Europa Island, frigatebirds breed throughout the year (Le Corre, in press), while the main hatching period for green turtles lasts from January to April (Servan 1976).

BEHAVIORAL OBSERVATIONS

Continuous observations of preying sequences on green turtle emergences were conducted at "Baie des Congres" beach, a major hatching place for turtles. Observers used 10 × 42 binoculars or a 25× telescope to watch emergences from a distance of 50 to 250 m. Most emergences occur at night, but at Europa 25% of emergences occur during daylight, mainly during late afternoon and dusk (Servan 1976). Thus, we observed turtle emergences and predation by frigatebirds from 16:00 to 18:40. The study was conducted during two emergence seasons, from 20 March to 10 April 1995 and from 1 March to 14 April 1997, totalling 35 different emergences observed during 4 different days each year.

We determined the apparent sex ratio within the flock of frigatebirds flying over the beach during the afternoon, by counting males, females, and juveniles

of both species (13 counts). We also estimated the apparent sex ratio at the frigatebird colonies by counting all observed birds along a linear transect on 1 March 1997 and 14 April 1997.

When an emergence occurred, we counted the number of depredated hatchlings, and the number, species, age, and sex of frigatebirds preying upon hatchlings. We differentiated males, females, and juveniles of each species using Marchant and Higgins (1990) and Orta (1992).

STATISTICAL ANALYSES

The values reported in the results section are means ± SD and percentages. Differences were considered statistically significant at $P < 0.05$. χ^2 tests for proportion comparisons were performed using Statistica 5.1 (Statsoft 1997).

RESULTS

SPECIES PREYING UPON HATCHLING GREEN TURTLES

Thirty-five turtle emergences were recorded during the course of the study, containing 4 to 147 hatchling green turtles each (mean 52 ± 40). We counted a total of 614 Great Frigatebirds in 13 separate flocks foraging over the beach (not merely crossing the beach). Lesser Frigatebirds were seen flying over the beach only when commuting between the sea and the colonies, and never foraged over the beach. During turtle emergences, all 1828 hatchling turtles that we saw emerge were preyed upon by Great Frigatebirds.

AGE AND SEX RATIO IN FLOCKS OF FRIGATEBIRDS AND IN BREEDING COLONIES

Of the 614 Great Frigatebirds we counted foraging over the beach, 81% were adult males, 19% were juveniles (sex undeterminable in the field), and less than 1% were adult females. Most captures were made by males (1632 of 1828 captures, 89%), whereas female captures were rare (only 10 captures, 0.5%). The remaining 186 were taken by juveniles (10%). There was no difference in the proportion of males and females foraging over the beach compared to those attacking a turtle emergence ($\chi^2_{34} = 29$, $P = 0.7$ for males and $\chi^2_{34} = 31$, $P = 0.6$ for females). On the other hand, there was a greater proportion of juvenile birds foraging in flocks than preying upon hatchling turtles ($\chi^2_{34} = 118$, $P < 0.001$).

In the frigatebird colonies, we found no significant difference between the sex ratio measured in March and April (49 males and 48 females observed in March, versus 69 males and 50 females in April; $\chi^2_1 = 1.2$, $P = 0.2$). Thus the data were pooled, giving a male-biased sex-ratio of 1.2:1. This sex ratio was obviously very different from the one observed in flocks over the beach ($\chi^2_1 = 220$, $P < 0.001$) or from the one observed in frigatebirds preying on turtle emergences ($\chi^2_1 = 699$, $P < 0.001$).

DISCUSSION

IMPORTANCE OF FRIGATEBIRD PREDATION FOR THE PREY

As soon as turtle emergence begins, a few frigatebirds start to prey. But quickly, tens of other birds converge at the emergence point and join the hunt. All turtles

reaching the surface of the sandy beach are immediately snatched (Servan 1976, this study).

Turtle emergence is temperature-dependent (Servan 1976, Miller 1996). On Europa Island, most emergences occur when the temperature is lower than 28.8℃, above which the emergence process is inhibited. Therefore, the majority of emergences begin at the end of the day and last until the end of the night, but on Europa Island, 25% of emergences occur during the day (Servan 1976). Nocturnal frigatebird activity over the beaches was scarce, many birds spent the night at roosting sites, and we never observed night predation on green turtles. By comparison, diurnal emergences seem much more accessible to frigatebirds.

Frigatebird predation on green turtles is not always observed where these species are sympatric. For example, at French Frigate Shoals (Hawaii), Great Frigatebirds were never seen preying upon green turtle hatchlings. This was ascribed to the nocturnal emergence of turtles on this island, making hatchling turtles inaccessible to feeding frigatebirds (Niethammer et al. 1992). Thus, geographical differences in frigatebird feeding strategy on hatching turtles may simply be a reflection of the geographical variation in green turtle emergence patterns.

INTERSPECIFIC DIFFERENCES IN FEEDING ECOLOGY AT EUROPA ISLAND

Frigatebird feeding ecology is still poorly documented. At Aldabra Atoll, Indian ocean, Diamond (1973) found no differences in feeding ecology of Lesser and Great Frigatebirds. Our study and a previous one conducted on kleptoparasitism (Le Corre and Jouventin 1997a) clearly indicates that at Europa, the two species do not feed in the same way. Lesser Frigatebirds were never observed feeding inland, over the beach, or in proximity of the coast, suggesting that this species is a strictly pelagic feeder. Great Frigatebirds were often observed feeding on the beaches (preying upon hatchling turtles) and close to the coast (chasing other seabird species).

FORAGING ECOLOGY OF THE GREAT FRIGATEBIRD AND REVERSED SEXUAL DIMORPHISM: CAUSE OR CONSEQUENCE?

Sexual variation in feeding behavior among frigatebirds has been reported in Great Frigatebirds (Gilardi 1994, Megyesi and Griffin 1996, Le Corre and Jouventin 1997a) and Magnificent Frigatebirds (Osorno et al. 1992). In all these studies but one (Megyesi and Griffin 1996), the feeding behavior involved was kleptoparasitism: females chased larger host species, whereas males chased smaller ones or did not kleptoparasitize. This intraspecific difference of host size in relation to the size of the kleptoparasite is consistent with the general trend observed when considering all kleptoparasite-host interactions in birds. Smaller kleptoparasites select smaller host species to increase their chance of success, and probably to avoid being injured by the host during the chase. On Europa Island, only female Great Frigatebirds were observed kleptoparasitizing Red-footed Boobies (*Sula sula*; Le Corre and Jouventin 1997a). Indeed, while males foraged over the beach, females were awaiting Red-footed Boobies a few hundred meters away, over the water (Le Corre and Jouventin 1997a). Clearly, these females could rapidly have joined the flock and preyed upon hatchling turtles when an emergence occurred but they did not do so. Preying upon hatchling turtles demands a very active flight with numerous passes, close to the ground, and with many competitors. In such a context, small males may be more efficient than females in attacking terrestrial prey, while large females may be more efficient at aerial chases. Therefore, is the niche partitioning a cause or a consequence of sexual size dimorphism in frigatebirds? Because of the strong difference in the degree of parental care between the sexes (Orta 1992), it is problematic to pull apart the respective causes and consequences of sexual size dimorphism, and thus, further studies are needed. Food sampling and satellite telemetry should allow us to investigate more precisely the feeding ecology of frigatebirds and to explore the relative importance of inshore versus offshore feeding strategies in both sexes. A better knowledge of frigatebird mating strategy, breeding biology and feeding ecology could illuminate the complex implications of sexual size dimorphism in these seabirds.

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POST-FLEDGING BROODS OF MIGRATORY HARLEQUIN DUCKS ACCOMPANY FEMALES TO WINTERING AREAS[1]

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Abstract. We describe evidence that Harlequin Duck (*Histrionicus histrionicus*) broods accompany their mothers from breeding streams to coastal molting or wintering areas. Observations indicated that all surviving female-offspring groups left breeding areas together. We later sighted some family members at the coast near each other, suggesting that they had arrived together, then separated. We observed family groups at wintering areas in August and September. Family groups tended to separate quickly, although some family members maintained contact for over five months. To our knowledge the evidence we provide is the first

suggesting that female migratory ducks bring their offspring to wintering areas, a pattern similar to geese and swans. This may be facilitated by an unusual strategy of wing molt, in which Harlequin Ducks molt after migrating to wintering areas. Due to winter pairing and strong philopatry in Harlequin Ducks, migration of families may contribute to genetic differentiation among populations.

Key words: brood abandonment, Harlequin Duck, Histrionicus histrionicus*, migration, parental care, population structure.*

Los Juveniles de *Histrionicus histrionicus* Migratorios Acompañan a las Hembras a las Áreas de Invernada

Resumen. Presentamos evidencia de que los juveniles de *Histrionicus histrionicus* acompañan a sus madres desde los arroyos de reproducción hasta las áreas costeras de muda o invernada. Las observaciones indicaron que todos los grupos sobrevivientes de hembras y crías abandonaron juntos las áreas de reproducción. Más adelante observamos algunos miembros de grupos familiares cerca unos de otros en la costa, sugiriendo que habían llegado juntos y luego se habían separado. Observamos grupos familiares en las áreas de invernada en agosto y septiembre. Los grupos familiares tendieron a separarse rápidamente, aunque algunos miembros mantuvieron contacto por más de cinco meses. A nuestro entender, esta es la primera evidencia de que las hembras de patos migratorios llevan a sus crías a los sitios de invernada, un patrón similar al de los gansos y cisnes. Esto podría ser facilitado por una estrategia poco usual, en la que *H. histrionicus* muda las plumas de las alas después de migrar hacia las áreas de invernada. Debido a la formación de parejas en invierno y a la fuerte filopatría en *H. histrionicus,* la migración de familias podría contribuir a la diferenciación genética entre poblaciones.

The age at which juveniles separate from their parents can be predicted from theories of parent-offspring conflict (Carlisle 1982). Parents should abandon their young when prospects for future fitness through abandonment are greater than fitness gained from attending the present brood. Among waterfowl there are two broad patterns of brood abandonment. In swans and geese (Anserini), which have long-term pair bonds, juveniles generally accompany both parents throughout the first year of life, staying with them during both migratory journeys between breeding and wintering grounds (Prevett and MacInnes 1980). In contrast, in seasonally monogamous ducks (Anatini, Aythyini, Mergini), males of migratory species abandon their mates, usually before young hatch, while females accompany their young for a variable period but typically are thought to leave them prior to fledging (Afton and Paulus 1992, Eadie et al. 1995, Mallory and Metz 1999).

Timing of brood abandonment is presumably an optimization of costs and benefits, which may vary with brood size and age, female condition, and other life history variables. Parental care enhances brood survival, particularly early in the lives of the offspring, through brooding, protection from predators, aiding in competitive interactions, finding suitable habitats, guiding offspring during migration, and helping them locate staging and wintering grounds. Conversely, caring for young may be costly for females because it may reduce their foraging time and they may suffer increased mortality risk while defending the young (Afton and Paulus 1992).

We examined the timing of brood abandonment by Harlequin Ducks (*Histrionicus histrionicus*). They have long-term pair bonds in common with Anserini, and uniparental care in common with the ducks. Some previous studies have suggested that females may abandon their broods prior to fledging (Wallen 1987, Cassirer and Groves 1991, Diamond and Finnegan 1993, Reichel et al. 1997), while others have suggested that they are still with their broods at fledging (Bengtson 1966, Kuchel 1977). There are anecdotal accounts of family groups at great distances from suitable breeding streams (Cooke et al. 2000). Research at both breeding and wintering areas of part of the Pacific population allowed us to investigate the departure of juveniles and family groups from breeding streams and their subsequent arrival and behavior at coastal wintering areas.

METHODS

We conducted the breeding-season portion of this study from May to September, 1996 to 1998, on the Bow, Elbow, Highwood, and Kananaskis Rivers, and Smith-Dorrien Creek, in southwestern Alberta, Canada. We conducted observations at coastal wintering areas from 1997 to 2000 at Hornby Island, the Cape Lazo area of eastern Vancouver Island (between Comox and Campbell River), and White Rock, British Columbia, Canada, and at Birch Bay and Point Roberts, Washington, USA.

On breeding streams we used mist nets to capture Harlequin Duck females with other adults in May and with flightless broods in August and September. We marked each bird with a USFWS tarsal band and a uniquely engraved colored plastic band. In 1997 and 1998, 16 females and their broods received either intra-abdominal transmitters with external whip antennae, or external transmitters, attached mid-dorsally with subdermal wire anchors and sutures. We monitored these families at least once per week until migration or mortality, then made telemetry flights over the Strait of Georgia, British Columbia, using fixed-wing aircraft during winter 1997–1998 and October 1999.

On wintering areas, we surveyed White Rock once per week in 1997, two to three times per week in 1998 and 1999, and opportunistically in 2000. We surveyed Birch Bay and Point Roberts once every two weeks in 1999, Hornby Island from 8 to 13 September 1999 and from 10 to 15 September 2000, and the Cape Lazo area from 14 to 18 September 1999 and from 29 August to 8 September 2000. Many birds were identifiable by unique tarsal bands or nasal disks from previous banding operations. Juveniles were separable from adults by finely vermiculated plumage on the breast, belly, and

vent, mottled yellow and gray legs and feet, dusky faces, and occasionally, notched tail feathers.

On wintering areas, we defined a "family" as an association between one adult female and one or more juveniles in which the adult female had full old primaries, indicating recent arrival, and assumed a leading or vigilant role. To avoid duplicate recording of families, we report separate families only if they were seen concurrently, were separated in time by at least 10 days (this is the average time to the loss of primaries, FC unpubl. data), or if females were identified.

We recorded composition of all Harlequin Duck groups to determine the frequency of family groups and the social choices of juveniles in all locations in 1999 and at Hornby Island and Cape Lazo in 2000. We defined a group as one or more individuals separated from others by at least 10 m. Surveys conducted at the same location on different days may have included juveniles sampled on previous days. We did not attempt to correct for duplicate sightings, but conducted only one survey in any location on any day.

We captured three family groups, one at Cape Lazo in 1999, and one each at Cape Lazo and Hornby Island in 2000 (families had four, four, and two juveniles, respectively) using mist nets and decoys. We marked all individuals with tarsal bands and nasal disks in both years, and with external radio transmitters in 2000. We conducted 10-min to 2-hr behavioral observations on the two families marked at Cape Lazo on four and five occasions in 1999 and 2000, respectively. We observed both juveniles from the family at Hornby Island on three occasions one and two days following capture; both died shortly thereafter. During observations we recorded the relative locations and social interactions of family members.

RESULTS

We were able to monitor the fates of 15 families that were radio-marked at breeding areas. No female abandoned her brood prior to migration from the breeding stream. When both the female and her brood survived (three cases), the entire family departed at the same time. For the remaining females, either the female died (five cases) or the brood died (seven cases).

We observed two cases of at least temporary adoption on the breeding streams. One female added a duckling to her brood of 6 for at least 14 days. One duckling whose mother died joined a female that had lost her brood and appeared to migrate with her, as both disappeared from the stream at the same time. We also observed one case of brood amalgamation and one case of at least temporary brood mixing.

At wintering areas we resighted two families that had been marked at the breeding streams. Family members were sighted in the same general area (within 15 km), but were not observed to associate with each other.

We observed 25 different Harlequin Duck families at wintering areas from 22 August to 26 September in four years. Females were seen with one ($n = 5$), two ($n = 8$), three ($n = 3$), four ($n = 4$), five ($n = 1$), six ($n = 3$), and seven ($n = 1$) juveniles. Four previously banded females were seen in family groups at White Rock, and all were with juveniles when they were first observed at the site that season. We also observed one family-like association that was clearly not a family group: one female with four juveniles was a banded yearling that had been in the area throughout the year.

Most families separated shortly after arrival at wintering areas, but some individuals maintained contact for at least five months. Previously banded females seen with juveniles were without them 9 to 46 days after the initial family sighting. All adult females captured in family groups were resighted with at least some of the juveniles captured with them. Only two juveniles from the family captured in 1999 remained with the adult female one day after capture, one remained after two days, and none remained after a month. The female from the family captured at Cape Lazo in 2000 was 2 km from the juveniles one day after capture, but all family members were together again after 13 days, and all were within 1 km of each other after 42 days. After 73 days, the female and two juveniles were together, the third juvenile was 2 km away, and the fourth had died. Observations of the marked families suggested that the females did not act aggressively toward the juveniles, but interacted with them and defended them from other adults.

We observed juveniles in a variety of group compositions. Of 161 coastal juvenile sightings, juveniles were solitary (21 times), in the company of other juveniles only (24 times), in the company of non-vigilant or newly molted females only (23 times), in the company of adult males only (21 times), with a mix of adult males and females (44 times), and in family groups (28 times).

DISCUSSION

Our study provides evidence that Harlequin Duck broods accompany females from breeding to wintering areas. Three entire families departed from breeding streams after the young fledged, and some family members were subsequently sighted near each other on wintering areas, an observation that would be unlikely if they had migrated independently to the coast. Observations on wintering areas indicated that family-like groupings appeared, then generally separated rapidly; hence most juveniles were not seen in family groups but in a wide range of social associations. Thus, although some juveniles may arrive at the coast alone or in sibling groups without their mothers, the presence of juveniles on the coast without females is not proof that they arrived alone (cf. Robertson and Goudie 1999). Our results suggest that most females accompany their young and that most family groups separate soon after arrival at the coast, although some family members may associate for several months.

Although we cannot be certain that the associations observed at wintering areas were true families, we think that most were for several reasons: (1) no radio-marked female abandoned her brood on the breeding stream, (2) behavior of coastal family-like groups was indistinguishable from that of known post-fledging families in breeding areas, (3) family-like groups that were captured and marked continued to associate afterwards, (4) group size was similar to expected family size, given high juvenile mortality (Smith 2000), and (5) arrival of females with young in wintering areas coincided with the time expected for successful nesters (Smith et al. 2000). Clearly

some family-like groups were unrelated, because we observed one group that could not have been a true family, and adoption and brood amalgamation in breeding areas has been observed in this and in other studies (Bengston 1966, Rodway et al. 1998).

The arrival of entire families at wintering areas has implications for population genetic structure, demographics, and conservation. If juveniles arrive at the molting or wintering area of their mothers, then they may find themselves in the same wintering locations as their siblings from multiple breeding seasons, given high site fidelity of females to molting and wintering sites (Breault and Savard 1999, Robertson et al. 1999). Due to winter pairing in Harlequin Ducks, this could lead to local wintering populations becoming more genetically similar over time, which could lead to genetically differentiated populations, something that is thought to be rare in migratory ducks (Anderson et al. 1992). Additionally, if all recruitment to local wintering populations comes from specific groups of birds, recovery from local population reductions could be slow.

In breeding areas, we observed death of the mother, adoption, brood amalgamation, and brood mixing, all of which could result in juvenile migration from breeding to wintering areas alone or with a female that is not its biological parent. Such juveniles are unlikely to migrate to their mother's molting or wintering location because coastal wintering habitat is extensive and individuals breeding in proximity can migrate to widely separated wintering sites (Regehr et al., unpubl. data). Juveniles departing alone or with an adoptive parent would therefore not be related to the individuals that they wintered and subsequently paired with, and their introduction into local populations would have a homogenizing effect on population structure similar to winter dispersal. Presently there is no genetic evidence for fine scale differentiation in Harlequin Ducks (Brown 1998, Lanctot et al. 1999), but at a broader scale there is (K. Scribner unpubl., in Robertson and Goudie 1999). Research on winter movements of individuals and on frequencies of true versus adoptive families is required to determine the degree to which family migration could lead to population differentiation and to demographically closed populations.

Harlequin Ducks (at least the Pacific population) are unlike most species of ducks in that they often molt and winter in the same location (Breault and Savard 1999, Robertson et al. 1999), and this difference may allow Harlequin Duck juveniles to migrate with their mothers. Molting sites for females are not specific habitats close to breeding areas as they are in some duck species (Hohman et al. 1992), where an extended family bond could represent a fitness cost to both the flightless mother and her young. In Harlequin Ducks, both females and offspring could benefit from family migration because offspring would reach a successful wintering location and females would improve their own fitness if the survival of their offspring were enhanced.

To our knowledge the evidence we provide is the first suggesting that female migratory ducks bring their offspring to wintering areas, a pattern that is well known in geese and swans. Such evidence is extremely difficult to obtain by traditional methods of study. Although there are several studies that provide convincing evidence of brood abandonment prior to fledging (Joyner 1977, Pöysä

et al. 1997), it may be difficult to detect cases where families stay together. For example, permanent abandonment may be confused with temporary absences (Ball et al. 1975) or mortality of the female. Thus in many species the precise time of brood abandonment is not known, and often it is simply assumed to occur at fledging. With the development of satellite technology, it should be possible to investigate this question more thoroughly and in a wider range of species.

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THE SOCIAL ORGANIZATION AND MATING SYSTEM OF THE STRIATED GRASSWREN[1]

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Abstract. This paper summarizes the breeding biology, social organization, and mating system of the Striated Grasswren (*Amytornis striatus*), a member of

one of the least-known genera of Australian passerines, the grasswrens. I studied 18 color-banded groups and 14 nests in South Australia for one breeding season in 1996. Mean territory size was 3.0 ha, and territories consisted of sandy dunes dominated by spinifex (*Triodea irritans*). This apparent dependency on mature spinifex, coupled with poor dispersal ability, suggests that the Striated Grasswren is particularly susceptible

to habitat destruction. Most groups consisted of socially monogamous pairs, mean group size was 2.1 adults, and the adult sex ratio was 0.95 (males:females). The average clutch size was 2.2 ± 0.4 eggs and an average of 1.1 ± 1.1 young fledged per nesting effort. A male and a female provided similar amounts of parental care at a single nest. Cloacal protuberance size and amount of sperm collected did not suggest intense sperm competition among males.

Key words: Amytornis striatus, *breeding biology, conservation, social organization, South Australia, Striated Grasswren.*

Organización Social y Sistema de Apareamiento de *Amytornis striatus*

Resumen. Este trabajo resume la biología reproductiva, organización social, y sistema de apareamiento de *Amytornis striatus,* miembro de uno de los géneros menos conocidos de paserinos de Australia. Durante la estación reproductiva de 1996 estudié, en el sur de Australia, 18 grupos identificados con bandas de colores y 14 nidos. El tamaño promedio de los territorios fue 3.0 ha, siendo los territorios dunas arenosos dominadas por *Triodea irritans.* Esta aparente dependencia de sectores maduros de *T. irritans,* en combinación con una limitada capacidad de dispersión, hacen que *A. striatus* sea particularmente sensible a la destrucción del habitat. La mayoría de los grupos sociales fueron parejas monógamas; el tamaño promedio del grupo fue 2.1 adultos, y el cociente de sexos en adultos fue 0.95 (machos:hembras). El tamaño medio de nidada fue 2.2 ± 0.4 huevos, y un promedio de 1.1 ± 1.1 juveniles por intento de nidificación abandonó exitosamente el nido. Un macho y una hembra proporcionaron esfuerzos similares de cuidado parental en un único nido. El tamaño de la protuberancia cloacal y la cantidad de esperma colectados no sugirieron que exista intensa competencia espermática entre machos.

Grasswrens (Maluridae: *Amytornis,* 8 species) are cryptically colored, terrestrial passerines which inhabit some of Australia's most arid and isolated regions. Although a source of keen interest to Australian ornithologists for well over a century (Schodde 1982, Rowley and Russell 1997), they are among the least known Australian birds. The little that is known suggests they have followed a very different evolutionary trajectory than fairy-wrens (*Malurus*), their close relatives. Whereas fairy-wren males are much brighter than females, grasswrens are dull-colored and exhibit mild reverse sexual dimorphism. Also, while fairy-wrens are extremely sexually promiscuous (Brooker et al. 1990, Mulder et al. 1994), the dull plumage and small testes of grasswrens suggest relatively low levels of sexual promiscuity. Finally, fairy-wrens are common in virtually every terrestrial habitat within Australia, whereas grasswrens are restricted to the arid zone, have narrow habitat preferences, and some species may be threatened with extinction (Rowley and Russell 1997).

The most recent species of grasswren was discovered in 1968 (Favaloro and McEvey 1968), and even the Striated Grasswren *Amytornis striatus,* which has

the largest range in the genus, remains largely unknown. Published accounts of the Striated Grasswren's biology are either anecdotal (Whitlock 1910, Schodde 1982, Howard and Howard 1984) or based solely upon observation of captive birds (Hutton 1991).

I studied a color-banded population of Striated Grasswrens (*A. s. striatus*) in South Australia for one breeding season in 1996. This study was motivated by two objectives. The first was to provide the first quantitative documentation of the social organization, mating system, and habitat use of this little known species. The second was to make available information which might aid in the conservation of this threatened bird species and of the vanishing mallee habitat in which it lives.

STUDY AREA AND METHODS

This study took place at Calperum Biosphere Reserve (34°10′S, 140°45′E), within the UNESCO Bookmark Biosphere Reserve in South Australia. Calperum Reserve, a former pastoral property, is a large (242 800 ha) tract of relatively undisturbed mallee habitat (Lindsay 1995). The 3-km² study area is characterized by sand dunes roughly 20 m in height interspersed with clay-rich swales. Vegetation on the dunes is dominated by spinifex (*Triodea irritans*) and multi-stemmed mallee eucalypts, most commonly red mallee (*Eucalyptus socialis*) and ridge-fruit mallee (*E. incrassata*). In the swales, chenopod shrubs, grey mallee (*E. dumosa*), and red mallee are the most common plants. Similar habitat, known to contain Striated Grasswrens, surrounds the study area. Calperum Reserve averages 259 mm of precipitation annually, varying from less than 88 mm to more than 500 mm per year (Australian Government Bureau of Meteorology, unpubl. data).

Field research was conducted from 16 September–20 December 1996. Birds were captured in mist nets aided by amplified playbacks of tape-recorded male song. I weighed each captured individual and measured tarsus length (from the tibiotarsal notch to the first split scale at the base of the toes), folded-wing length (from the bend of the wrist to the tip of the longest primary), and tail length (the length of the longest rectrices). I also recorded the presence or absence of body molt for all captured birds. As in most malurids, male Striated Grasswrens have a cloacal protuberance (Mulder and Cockburn 1993). I used three measures of the cloacal protuberance: length (L), or the distance from the anterior portion of the cloacal opening to the posterior edge; maximum depth (D); and maximum width (W) to calculate volume as $\pi \times D/2 \times W/2 \times L$ (Mulder and Cockburn 1993, Tuttle et al. 1996). Sperm samples were collected, stored, and counted by E. M. Tuttle following the methods in Tuttle et al. (1996). Finally, I banded each bird with an Australian Bird and Bat Banding Scheme metal identification ring and a unique combination of three colorbands.

Group composition and social behavior were established by repeated monitoring of banded individuals. Habitat selection was determined by observation of banded individuals in the field. Territorial boundaries were mapped by attaching flagging tape to vegetation where males engaged in territorial singing with neighboring males. An enlarged aerial photograph of the

TABLE 1.   Morpholgoical measures of adult male and female Striated Grasswrens at Calperum Biosphere Reserve, South Australia.

| | Males ($n = 30$) | | Females ($n = 18$) | | |
	Mean ± SD	Range	Mean ± SD	Range	P
Mass (g)	20.2 ± 1.0	18.0–22.5	19.1 ± 1.2	17.0–22.0	<0.01
Wing (mm)	59.0 ± 1.2	56.6–61.3	56.5 ± 1.7	53.5–60.4	<0.001
Tarsus (mm)	24.9 ± 1.0	22.8–27.1	24.4 ± 0.8	22.6–25.7	0.10
Tail (mm)	85.8 ± 5.1	71.1–93.2	83.6 ± 4.1[a]	76.7–89.8	0.15

[a] $n = 17$ females.

study site on which individual shrubs were recognizable was used to map the locations of sightings, and straight lines were then drawn between known points. Territory areas were calculated by superimposing a grid of 25-m² squares onto the map and counting the number of squares within each territory. Singing within 15 m of a known nest was considered to be singing around the nest; otherwise it was considered to be territorial song.

Nest width and height were measured using a tape measure. Nest height was measured from the ground to the bottom of the nest's opening. Clutch sizes were determined by counting number of eggs or young present in each active nest. Nests were checked every other day to determine duration of the breeding season and dates of laying, hatching, fledging, and predation. When calculating clutch sizes, I assumed there had been no partial predation of nests. Parental care at a single nest was observed from a hide placed 15 m from the nest. A total of ten 90-min nest watches were conducted between 07:30 and 18:00 over eight days.

All statistical tests were two-tailed, and values reported below are means ± SD. *P*-values < 0.05 are considered significant.

RESULTS

MORPHOLOGY AND MOLT

I captured a total of 69 individuals: 30 adult males, 18 adult females, 4 juveniles, and 17 nestlings or fledglings. Males tended to be larger than females in all measures, significantly so for wing length and mass (Table 1). Body molt in adults was observed throughout the study but was more prevalent in the second half of the study (16 November–16 December) than the first half of the study (16 October–15 November; χ^2_1, $P < 0.05$). There was no difference between the sexes in the timing or intensity of molt. At the time of capture, all but one adult female had a brood patch and all adult males had enlarged cloacal protuberances (see below).

HABITAT SELECTION AND TERRITORIALITY

All territories contained spinifex-covered sand dunes, where most foraging and nesting occurred. Average territory size for 17 contiguous territories was 3.0 ± 1.1 ha (range 0.6–5.2 ha). The density of adults on the study area was 0.5 birds ha⁻¹. The birds were highly territorial and boundaries of territories appeared to change little during the course of the study. Males sang at their territory boundaries for at least one hour each

morning from 1–2-m perches in shrubs, trees, or fences. As many as five males were observed counter-singing within a 1-ha area where several territories adjoined. Males were sometimes joined by females in territorial singing but usually sang alone while the female foraged, preened, or perched nearby. The male member of a pair was engaged in territorial singing in 97% of 60 cases in which the identity of the singer was known. Around the nest, however, females were more vocal (12 of 19 song bouts around the nest were by females). The song of both males and females was long, complex, and much more varied than those of *Malurus* fairy-wrens (for sonograms see Rowley and Russell 1997). The common features of most song types were short, staccato bursts followed by high-pitched notes and whistles.

SOCIAL ORGANIZATION AND BEHAVIOR

I monitored and recorded group composition for 18 groups in which all, or all but one, of the individuals were color banded. Mean group size, excluding juveniles, was 2.1 (range 2–3), and adult sex ratio was 0.95 (males:females). Fifteen groups were simple pairs, but three groups had additional members whose age and sex were not clear from field observations. Three of these additional birds were sexually immature, but a fourth had bright red plumage under the wing, indicating that it was an adult female. This individual was in a group containing a breeding male with an enlarged cloacal protuberance and a breeding female with a brood patch. It is likely that this additional female was an adult helper, though I never found the nest of this group and therefore never saw it feed at the nest.

Family groups spent most of their time foraging together. Dust-bathing and allopreening were other frequent group activities. I also observed the rodent run display (Rowley and Russell 1997) and a threat display similar to that described by Hutton (1991), in which an adult male erected feathers on his crown, nape, and throat to form a ring around his face. This display had a striking effect, as all the streaking around the head formed radiating lines and focused one's vision directly at the face.

BREEDING BIOLOGY

In 1996, the breeding season at Calperum Reserve probably lasted at least five months, from August to January. When I arrived in mid-September, some groups were already feeding young in the nest (implying that nesting had been initiated in late August), and

when I left in December there were still four active nests (three with eggs, one with nestlings). Females whose nests failed in early December were found rebuilding in mid-December, suggesting that the breeding season potentially extended into mid-January. Further, there was no decrease in cloacal protuberance volume in males during the study (see below).

Six of 14 nests (43%) successfully fledged at least one young, three (22%) were depredated, two (14%) were abandoned during incubation, and three (22%) had unknown fates because the female was still incubating when I left. All three predations occurred during the nestling stage. Considering only those nests in which at least one egg was laid and the fate was known, the average clutch size was 2.2 ± 0.4 eggs (range 1–3, n = 6 nests), and an average of 1.1 ± 1.1 young fledged per nesting effort (range 0–3, n = 11 nests).

Incubation did not begin until the last egg was laid, and eggs hatched on the same morning 14 to 19 days after the last egg was laid (n = 2 nests). Females usually incubated eggs; no males had brood patches, but on one occasion I flushed a male off a nest with eggs on it. Males often fed females on and off the nest with insects and seeds. Incubation bouts usually lasted 45–90 min, interspersed with 30–60-min foraging bouts.

I quantified provisioning rates for 937 min over the course of six days (26 November–2 December) at a single nest with two nestlings in it. The nest was tended by one adult male and one adult female. There was no difference between the feeding rate of the male and female (2.0 ± 0.1 feeds hr^{-1} vs. 2.3 ± 1.5 feeds hr^{-1}, P > 0.3) nor the brooding rate of the male and female (3.9 ± 0.7 min hr^{-1} vs. 5.4 min hr^{-1}, P > 0.3). Insects were the most commonly identified food item. At this one nest, the duration of the nestling stage was 14 days, and the two young fledged within 20 min of each other at midday.

Young were completely dependent when they fledged, and remained hidden less than 25 m from the nest in spinifex or some other shrub for the first week after fledging. Although extremely cryptic, recently fledged young were highly vocal, and their high-pitched calls were audible to the human ear from more than 40 m. After one week, although still dependent and largely hidden, the young began to range more widely. By 25 days, the young were seen feeding themselves and were mostly independent, though the female continued to provide some food for another two weeks.

Seventeen nests were located in spinifex, usually in older and larger clumps with an average volume of 0.3 ± 0.02 m^3. Most nests were located on sandy dunes and were cryptic. The mean nest height was 26.2 ± 12.0 cm. The orientation of the nests was random with respect to the cardinal directions.

CLOACAL PROTUBERANCES AND SPERM PRODUCTION

Cloacal protuberances averaged 120.3 ± 48.1 mm^3 (n = 28 males, range 40–197 mm^3). An average of 8.3 ± 9.7 × 10^6 sperm was collected from each male sampled (n = 9 males, range 0.2–30.6 × 10^6), and the average concentration of sperm was 4.5 ± 6.0 × 10^6 per μl (n = 9 males, range 1.0–14.9 × 10^6).

There was no relationship between cloacal protuberance volume and time of day (r^2 = 0.004, P > 0.7) or the date the measure was taken (r^2 = 0.001, P = 0.6). Nor was there a relationship between male body mass and volume of the cloacal protuberance, or between body mass and concentration or volume of sperm collected. There also was no relationship between volume of cloacal protuberance and concentration or total volume of sperm gathered. Finally, there was no relationship between the total volume of sperm and concentration of sperm for each male (all P > 0.2).

DISCUSSION

SOCIAL ORGANIZATION AND BREEDING BIOLOGY

This study provides the first account of the mating system and social organization of the Striated Grasswren. In the population I studied, grasswrens formed simple breeding pairs and adult helpers were rare. Only one of 18 groups had more than two confirmed adults and I never witnessed more than two adults feeding nestlings or fledglings. Likewise, previous reports of the Striated Grasswren mention only pairs of adults, with no evidence of adult helpers (Izzard et al. 1973, Miller 1973). In most species in the family Maluridae, however, three or more adults have been seen provisioning a single nest (Rowley and Russell 1997), including the two other species of grasswren which have been studied in any detail, the White-throated Grasswren (*A. woodwardi*) and the Thick-billed Grasswren (*A. textilis*). The White-throated Grasswren was observed mainly in pairs during the breeding season, but a small number of larger groups were recorded and three adults were seen feeding at one nest (Noske 1992). Similarly, most groups of a color-banded population of Thick-billed Grasswrens were simple pairs, but in one group three adults were observed feeding at a single nest (Brooker 1988). In general, helping behavior appears to be present in low levels in grasswren species studied to date.

The 1996 breeding season probably extended into January despite previous reports that breeding in South Australia is usually completed in November (Schodde 1982, Rowley and Russell 1997). Annual rainfall in 1996 (251 mm), however, was slightly below the yearly average (259 mm). Further, rainfall totals in the months of October (23 mm), November (13 mm) and December (3 mm) were well below average (28, 21, and 18 mm, respectively) (Australian Government Bureau of Meteorology, unpubl. data). Because grasswrens are thought to breed in relation to rainfall (Rowley and Russell 1997), the probable extension of nesting into January despite relatively low rainfall levels indicates that the breeding season may normally extend later than has previously been thought.

The feeding rate I recorded at a single nest with two nestlings (male and female combined averaged 4.3 feeds per hr) is low compared to other malurids with similar-aged nestlings (8–14 days; Pruett-Jones, unpubl. data; Karubian, unpubl. data). However, observation of a single Striated Grasswren nest in New South Wales with two 10-day-old nestlings revealed a similar rate of 3–4 feeds per hr (Howard and Howard 1984).

Song is highly elaborated in Striated Grasswrens.

Both males and females have surprisingly variable vocal repertoires, and males spend considerable amounts of time singing from territory boundaries each day. Both Schodde (1982) and Rowley and Russell (1997) have discussed the range of grasswren vocalizations, and I also was struck by their vocal lability. Fairywrens, conversely, have relatively stereotyped song with little variation within or among individuals. It may be that song has evolved as the most important display for Striated Grasswrens, perhaps in response to the open environment in which grasswrens live, in which conspicuous plumage could incur a predation risk (Rowley and Russell 1997).

TERRITORIALITY, HABITAT USE, AND CONSERVATION

Striated Grasswrens were highly territorial, and song was the main territorial display. The density I recorded (0.5 birds ha^{-1}) lies between those recorded for other grasswren species. In the Northern Territory, Noske (1992) recorded a density of 0.08 White-throated Grasswrens per hectare, with an average territory size of 10 ha and a smallest territory of 7 ha. In Western Australia, Brooker (1988) reported 2.2–2.8 Thick-billed Grasswrens per hectare.

Birds showed a marked preference for sandy soil with high densities of spinifex. Individuals used spinifex as a food source (both seeds and insects), for shelter, and as a nesting substrate, and every territory contained some area with sandy soil and spinifex where the birds spent most of their time. Other reports of the Striated Grasswren invariably mention the presence of mature spinifex (e.g., Izzard 1973, Schodde 1982, Rowley and Russell 1997), and it appears that spinifex is a habitat requirement for the Striated Grasswren. The White-throated Grasswren (Noske 1992) shows a similar dependence on spinifex, although the Thick-billed Grasswren (Brooker 1988) does not. Spinifex-dominated habitat is still widespread across Australia but is threatened by clearing, burning, and livestock.

The preference Striated Grasswrens display for spinifex is coupled with a highly terrestrial lifestyle. I rarely saw an individual fly more than a few meters at a time, and all the birds I caught in mist nets were caught within a few centimeters of the ground. Even when ascending to a perch a few meters off the ground, birds usually hopped from branch to branch rather than flying up. This apparent unwillingness to fly makes it difficult to imagine an individual dispersing over areas of unsuitable habitat larger than a few km.

The combination of relatively specific habitat preferences and probably poor dispersal ability indicate that habitat fragmentation is a serious threat to the conservation of the Striated Grasswren. Although it has the largest range of any grasswren species, it is fragmented into isolated populations, and two of its subspecies are potentially threatened (Rowley and Russell 1997). Habitat loss and fragmentation is a threat of varying severity to most *Amytornis* species (Noske 1992, Rowley and Russell 1997).

SPERM COMPETITION

Sperm competition occurs whenever females mate with more than one male during the span of a single breeding attempt. Because sperm production is tightly correlated with levels of sexual promiscuity in birds (Birkhead et al. 1993, Møller and Briskie 1995), it can be used as a general indicator of the level of promiscuity exhibited by a particular species. The Striated Grasswren produces very little sperm compared to other Maluridae for which data are available. Three species of fairy-wren (*Malurus splendens, M. lamberti,* and *M. leucopterus*), each of which weighs roughly one-half as much as the Striated Grasswren, produced on average three to four orders of magnitude more sperm per ejaculate sample than did Striated Grasswrens sampled by the same investigator using identical methods (Tuttle et al. 1996).

Cloacal protuberance size is also positively correlated with intensity of sperm competition (Birkhead 1993). Although the presence of a cloacal protuberance does imply some low level of sperm competition, the Striated Grasswren has a relatively small cloacal protuberance. In two surveys of 80 species (Birkhead et al. 1993, Briskie 1993), only 17 species (21%) had cloacal protuberances smaller than that of the Striated Grasswren. All 17 of these species weighed less than the Striated Grasswren. The small cloacal protuberances and low volumes and concentrations of sperm produced by the Striated Grasswren suggest relatively little sexual promiscuity.

Based on this study, the Striated Grasswren appears to be a socially monogamous species with low levels of cooperative breeding. The social monogamy seems to be complemented by low levels of sexual promiscuity, as inferred from common indices which indicate very low sperm competition between males. The breeding season extended longer than was previously believed. Density of adults was intermediate for that reported for other grasswren species and territories were restricted to areas containing spinifex. This dependency on a particular habitat type, in conjunction with seemingly poor dispersal ability, makes the Striated Grasswren especially vulnerable to habitat loss.

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