Observations on the Mating System and Breeding Success of Marsh Harriers* in Coastal South-eastern Australia

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Marsh Harriers *Circus aeruginosus* bred at a density of one pair per 67 ha and all pairs were monogynous. Clutch sizes averaged 3.6 eggs and 2.0 young were fledged per successful nest, or 1.3 young per nest site. The mean fledging date was 6 January.

Several species of harrier, including the Marsh Harrier, have been found to be polygynous (Schipper 1978, Balfour and Cadbury 1979, Cramp and Simmons 1980, Baker-Gabb 1981a). With this in mind, one breeding season (1979-80) was spent studying the mating system, breeding density and nesting success of the harriers at Reedy Lake, Victoria (38°15′S., 144°28′E.). Some additional data were collected during four visits in 1980-81. Data were also collected from four nests near the Werribee River (37°57′S., 144°40′E.) during the 1979-80 and 1980-81 seasons.

Study Area

Reedy Lake is situated on the Bellarine Peninsula which has been described by Jenkin (1976). The peninsula is mostly open farmland but contains an extensive tract of salt marsh and reed swamp which includes Lake Connewarre and Reedy Lake. These lakes are fed by the Barwon River and together comprise the 3 240 ha Lake Connewarre Game Reserve which is managed as a feeding ground for migratory waterfowl.

Above Reedy Lake's flood water mark about 10% of the vegetation consists of low shrubland including *Arthrocnemum* spp. and Tangled Lignum *Muelenbeckia cunninghamii* (Specht *et al.* 1974). A further 10% consists of herb land and rushes such as *Stipa teretifolia* and *Juncus* spp. and the rest has been largely converted to introduced pasture grasses or crops. Below the flood water level about half of Reedy Lake is filled with extensive reed beds of *Phragmites australis* and *Typha orientalis*. The other half of the 1 000 ha lake is open water.

The extensive reed beds are the main feature that distinguishes Reedy Lake from the second study area: the Werribee River and the adjacent Melbourne and Metropolitan Board of Works Farm. Both areas have similar climates (Bureau of Meteorology 1979), both support large numbers of waterfowl and in the surrounding farmland introduced mammals such as Rabbits *Oryctolagus cuniculus* and House Mice *Mus musculus* are abundant.

Breeding Density

In 1979-80 there were 18 pairs of harriers that bred in 1 200 ha of Reedy Lake and its surrounds or one pair per 67 ha (Figure 1). All birds were monogynous. Nest sites were 525 m apart on average (range = 275-800 m). Males usually hunted within 3 km of their nest sites.

The density of breeding harriers at Reedy Lake was almost twice as high as it was at Pukepuke Lagoon in New Zealand (Baker-Gabb 1981a), but the minimum distance between nest sites was similar (275 and 300 m). The higher breeding density at Reedy Lake was most likely due to there being a greater area of suitable nesting habitat there.

Nesting Habitat

On the Australian mainland, harriers usually restrict their nesting activities to extensive reedbeds of *Typha* and *Phragmites* near or in water.

* The author follows Amadon (1978) and Mayr and Cottrell (1979) who recognised the representative of the Marsh Harrier complex in Australia as being the Swamp Harrier *Circus approximans*, which is monotypic (Baker-Gabb 1979) and one of the five component species of a Marsh Harrier superspecies.

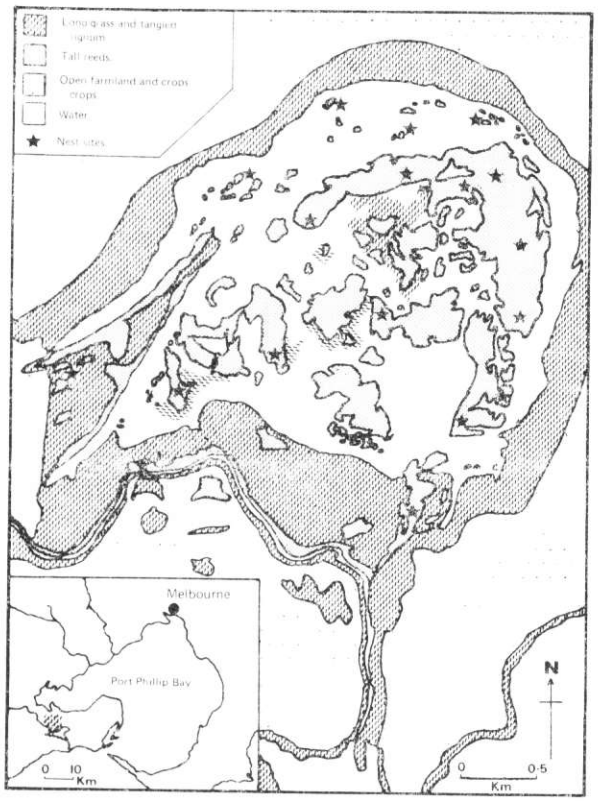

Figure 1. *Map of study area showing vegetation distribution and nest sites.*

Of the nests I located, 17 (68%) were in *Phragmites*, seven (28%) were in *Typha* and one (4%) was in *Juncus* above water 1.5 m deep. Occasionally tall grain and hay crops, or rushes are used (Readers Digest 1976, Pizzey 1980, RAOU nest record cards), but I think that such nests tend to be found and recorded far in excess of their proportion in the population because they are more accessible, and in Australia hay and grain crops are nearly always harvested before the young harriers fledge.

The favoured Australian nesting vegetation, *Phragmites*, does not occur in New Zealand (Salmon 1963). At Pukepuke Lagoon eight nests were in *Typha* reeds and 11 were in rushes that grew in dune hollows which contained shallow temporary ponds during winter only (Baker-Gabb 1981a). Nests are also found in crops, Bracken *Pteridium esculentum* and long grass (Stead 1932, Soper 1958, Falla *et al.* 1981). This shift to include a greater amount of non-reed and dry land vegetation as nesting habitat has probably evolved because nest sites are sometimes a resource limiting breeding density (Baker-Gabb 1981a), and because in New Zealand there are no snakes and, until recently, no mammalian predators of ground-nesting birds and their progeny.

This suggestion is supported by the observation that in Australia, harrier nests are kept relatively free of food remains and pellets which might attract mammalian predators. At ten Australian nests I found only one pellet and no food remains, whereas at five nests in New Zealand there were a total of 89 pellets (range = 8-32) and the remains of 20 prey (Baker-Gabb 1978). Pellets and food remains might also attract ants to a nest. Ants are widespread and abundant scavengers in Australian ecosystems (Brown and Taylor 1970), but not in more temperate regions like New Zealand. Cupper and Cupper (1981) blamed ants for the deaths of a few raptor nestlings and I witnessed attacks by ants that killed one nestling and would almost certainly have resulted in the death of three other broods of tree-nesting raptors had I not intervened (Baker-Gabb 1982a).

Clutch Size

Because Marsh Harriers readily desert their eggs if disturbed by man (Stead 1932, Soper 1958), during the incubation period only five nests close to the lake shore were visited. These could be inspected in the time that the females were feeding away from their nests. These nests contained 18 eggs, an average clutch size of 3.6 eggs (range = 3-4). Three (17%) eggs failed to hatch.

Marsh Harrier clutch sizes are significantly larger ($t = 2.72$, $p < 0.01$) in New Zealand than in Australia (Baker-Gabb 1981a), and the data from this study and Tasmania support that conclusion (Table 1).

TABLE 1

Marsh Harrier clutch sizes in Australia and New Zealand.

Reference	Mean	Range	Number of nests
Reedy Lake	3.6	3-4	5
RAOU nest record scheme	3.7	3-5	11
N. Mooney, Tasmania	3.8	2-7	9
OSNZ nest record scheme	4.6	2-7	25

TABLE 2

Marsh Harrier fledging success in Australia and New Zealand.

Reference	Young fledged per nest				Mean fledged per successful nest	Mean fledged per nest site
	0	1	2	3		
Reedy Lake 1979-80	6	3	6	3	2.0	1.3
Werribee and Reedy Lake 1980-81	1	1	3	2	2.1	1.8
RAOU nest record scheme	5	2	8	4	2.1	1.6
N. Mooney, Tasmania	3	3	5	5	2.1	1.7
OSNZ nest record scheme	7	2	8	3	2.1	1.3
Pukepuke Lagoon, New Zealand	8	4	5	2	1.8	1.1

These differences may be due to geographical influences because an increase in clutch size with latitude has been well documented for most orders (Moreau 1944), but the evidence is less convincing for the Falconiformes (Cody 1966). The application of Moreau's argument is weakened by the knowledge that about two-thirds of New Zealand's land mass lies in the same latitudes as southern Australia and Tasmania.

Cody (1966) has also argued that birds in stable environments like tropical areas or oceanic islands with few predators have smaller clutches than their congeners in less stable temperate and mainland areas. This view is supported by Clouet's (1978) data on the Marsh Harrier of Reunion Island which lays 2-3 eggs compared with other members of the Marsh Harrier complex which in similar latitudes lay 3-5 eggs on the large island of Malagasay and mainland Africa. Add to this the evidence that the Marsh Harrier in New Zealand is less restricted to breeding in swamps which are rich food sources that should promote higher productivity (Orians 1969), and the New Zealand clutch size data seems to be at odds with established trends.

There is a substantial body of evidence demonstrating that clutch size varies with available food supply (Lack 1954, Klomp 1970). During late winter and spring when pair formation, courtship feeding and egg laying by harriers occurs in New Zealand, sheep carrion from the lambing season is abundant and comprises about one-fifth of the number and one-third of the biomass of animals in the diet (Baker-Gabb 1981b, 1982a). By summer, comparatively few sheep carcases are available and sheep then comprises less than 4% of the number of animals in the diet. Perhaps this temporary annual food abundance provides the resource for larger clutches in New Zealand. A similar resource does not seem to be available in Australia and the carrion that is available is keenly competed for (Baker-Gabb 1982a). Although harriers in New Zealand lay 4.6 eggs per clutch on average and have never been known to fledge more than three young, larger clutches might still be favoured if the resources for their manufacture are abundant and readily available and they are not subsequently wasted. For example, if most eggs hatch and any excess younger nestlings are killed and eaten by their older siblings during critical periods of food shortage, more young of greater fitness may be fledged per nest than might otherwise have been the case. Fratricidal behaviour may play an important role in the demise of younger nestlings of members of the Marsh Harrier complex (Weis 1923, Buxton 1933, Redhead 1969, Cupper and Cupper 1981, Baker-Gabb 1982b).

Fledging Success

At five closely-studied nests at Reedy Lake, 15 nestlings hatched and ten of them fledged during 1979-80. Nestlings from seven other nests were also banded* and wing-tagged. An accurate count of all birds that fledged during 1979-80 was easily obtained because the siblings from each nest site initially perched together in exposed positions while waiting for their parents' return with food. Twenty-four young fledged

* Bands used were provided by the Australian Bird-banding Scheme, Division of Wildlife and Rangelands Research, CSIRO.

from 12 of the 18 nests giving an average fledging success of 2.0 young per successful nest, or 1.3 young per nest site. When the data from seven nests from Werribee and the 1980-81 breeding season were included the figures were: 37 young fledged from 18 of 25 nests, giving the same average fledging success per successful nest and 1.5 young per nest site. Fewer unsuccessful nests were located away from Reedy Lake and in 1980-81 as I did not attempt to find every territory-owning pair after the 1979-80 breeding season.

The mean fledging date recorded over two breeding seasons was 6 January (range = 6 December-17 January). Two male nestlings fledged in about 43 days and two females in 45 and 46 days respectively.

The studies from Pukepuke Lagoon and Reedy Lake in 1979-80 (Table 2) can be most legitimately compared because in these I included both non-breeding territorial pairs and pairs that laid eggs but failed to fledge any young as unsuccessful breeders (Postupalsky 1974), whereas birds were only included in the nest record schemes and the other data sources if they laid eggs. Fledging success was marginally higher at Reedy Lake and the mean fledging date was about ten days earlier.

Breeding Behaviour and Displays

Most of the displays of the harriers that bred at Reedy Lake and Werribee were the same as those recorded for the species in New Zealand (Baker-Gabb 1981a). However, I had not previously observed multiple diving displays as recorded by Sharland (1932). Early in the breeding season at Reedy Lake I saw on four occasions diving displays involving as many as eight males at the same time. Two points that may be noted were that the displays performed in the company of other birds were similar to those described for birds displaying alone (Baker-Gabb 1981a), and that each bird from a widely-dispersed group ended its display diving over its own territory, and not some communal area, whether it initially displayed in the company of others or not.

I did not see multiple diving displays at Werribee nor at Pukepuke Lagoon in New Zealand, possibly because in these areas nesting density was lower and physical features like dune ridges or pine plantations rather than adjacent neighbours delineated most of the length of territory boundaries. Marsh Harriers usually display dive above potential nest sites (Baker-Gabb 1981a). Where there are large areas of suitable nesting habitat as at Reedy Lake (Figure 1) and a dense population of breeding birds, then some harriers may occasionally be stimulated to display by rival neighbours. Some multiple displays may be the result of fortuitous synchrony in the times of display.

Multiple diving displays have not been recorded often, yet Fox (1978) reported "Although I interpreted this (talon-grappling) as a territorial conflict the question of polygamy in this species has yet to be clarified. On 15 October 1977 I observed copulation by the harriers on this adjacent territory and throughout the proceedings a second adult male was perched only 200 m from the birds in full view. This leads me to believe that the pair bond may be a rather flexible feature in this species, especially as multiple courtship displays are common". I can see no valid reason for Fox's inference concerning polygamy based on the observations provided because, firstly, nest sites as close as 300 m apart are strongly defended from all intruders (Baker-Gabb 1981a) and secondly, in my experience, multiple courtship (diving) displays are rare compared with diving displays by pairs or solitary harriers. Fox (1978) may have overemphasised the courtship function of diving displays at the expense of their territorial function (see Harmata 1982), but perhaps he was thinking of the multiple diving display being analagous to those of lek species? However each of the male harriers that I saw involved in multiple diving displays eventually landed at widely-dispersed individual locations, and not some communal area.

Polygyny

Although Marsh Harriers are often monogynous (Stead 1932, Soper 1958), two (12%) were polygynous at Pukepuke Lagoon (Baker-Gabb 1981a) where males defended all of the available nesting habitat. This resource had a patchy distribution and it seemed to limit the breeding density of birds ("resource defence polygyny" of Emlen and Oring 1977). Despite the breeding density being almost twice as high at Reedy Lake, nesting habitat was not in short supply as it was at Pukepuke Lagoon. Given that harriers will nest as close as 275 m apart there was room for another four or five years (Figure 1). This surplus of available nest sites probably lowered

the likelihood of polygyny because, as Verner and Willson (1966) pointed out, population density must be sufficiently high to force some males into poor marginal sites or monogyny will persist, even in a habitat with an extraordinarily rich food supply.

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