

BREEDING BIOLOGY OF THE DUSKY MOORHEN IN A SUBURBAN PARK

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The breeding biology of a Dusky Moorhen *Gallinula tenebrosa* population in Jells Park, Melbourne was studied from 1991 to 1996. Data were supplemented by records from the Birds Australia Nest Record Scheme for the period 1963–1995. The breeding season at Jells Park lasted from August to March. Mean individual clutch size was 6 eggs at Jells Park and 7 eggs in Nest Record Scheme. For breeding groups at Jells Park with only one laying female, clutch size was negatively correlated with laying date. The eggs comprising a clutch were usually laid daily, egg mass was about 7 per cent of adult mass and the mean incubation period was 23 days. Egg mass and incubation period conformed to allometric predictions based on adult mass, but clutch mass exceeded prediction simply because of the significant incidence of communal clutches. Clutch success was 61 per cent at Jells Park and 72 per cent in the Nest Record Scheme. Predation was the main nesting mortality agent. Survival of chicks from fledging to independence was 40–50 per cent at Jells Park. Females in the park contributed eggs to a similar extent to single-female or communal clutches, but Nest Record Scheme females contributed about one more egg to communal than single-female clutches. All communal group members participated in nest building and feeding chicks. Both members of pairs incubated substantially, but relative involvement in incubation in communal groups for which we had quantitative records ranged from 9 to 44 per cent among males and 15 to 67 per cent among females. Results are compared with data for other Australian Dusky Moorhen populations and for the cosmopolitan Common Moorhen *G. chloropus*. Their contribution to the debate about divergence in life history strategies of Australian and Northern Hemisphere birds is evaluated.

INTRODUCTION

The breeding biology of Australian birds is still relatively poorly documented (Magrath *et al.* 2000), but available data indicate that Australian 'old endemic' passerines differ from their Northern Hemisphere counterparts in several life history traits. In particular, they tend to have greater longevity, smaller and less variable clutch sizes, longer incubation and nestling periods, longer breeding seasons, a higher incidence of multiple broods and co-operative breeding and perhaps lower reproductive success (Woinarski 1985; Yom-Tov 1987; Ford 1989; Major 1991; Rowley *et al.* 1991; Magrath *et al.* 2000; Berry 2001). Additionally, the latitudinal gradients in life history traits such as clutch size apparent for Northern Hemisphere passerines seem to be lacking or less pronounced in Australian species (Ford 1989).

We have inadequate data for Australian non-passerines to test whether they exhibit a similar contrast in life history traits. However, in general, the Australian waterbirds appear to have a similar breeding ecology to that of waterbirds elsewhere, except that they are more flexible in the timing and duration of breeding episodes than their Northern Hemisphere counterparts. Timing and success of breeding in this group are linked to food availability, which in turn is a function of rainfall and associated flooding (Kingsford and Norman 2002).

The Dusky Moorhen *Gallinula tenebrosa* (Rallidae) inhabits wetlands over a 29 degree range in latitude in eastern Australia and also occurs in south-west Australia, Indonesia and Papua New Guinea. It breeds in territorial

groups of between two and eight birds and often a communal clutch includes the contributions of multiple females. Populations have 'mixed' mating systems (Pywell 1999; Buchan 2000). Communal nesting is rare in birds, but is often accompanied by suppression of individual clutch size or destruction of subordinates' eggs (Mumme *et al.* 1983; Gibbons 1986; Koford *et al.* 1990; McRae and Burke 1996). Apart from significant investigations in the Australian Capital Territory (35°S, 149°E) (Garnett 1978, 1980) and Brisbane (27°S, 153°E) (Buchan 2000; Putland and Goldizen 2001), this widespread species' breeding biology has not been described extensively.

This study documents key features of the breeding biology of Dusky Moorhens in a suburban Melbourne park. The findings are supplemented by data from the Birds Australia Nest Record Scheme. The main aim was to broaden the fairly restricted body of information on the species' breeding biology by adding data for a population at a different location (about 3 degrees and 11 degrees further south, respectively) to those studied previously (Garnett 1978, 1980; Buchan 2000; Putland and Goldizen 2001). The results are potentially relevant to the debate about the 'special' nature of Australian avian life histories (Ford 1989) and extend current knowledge of the dynamics of communal nesting in birds.

METHODS

The 1991–1996 study was conducted at Jells Park (37°54'S, 145°12'E) in suburban Melbourne, which contains a 14 hectare artificial lake, with an associated system of wetlands, small ponds and creeks on which the moorhens bred. Emergent macrophytes of the genera

Typha, *Phragmites* and *Eleocharis* grew in isolated, small patches in the wetlands. *Kunzea* and *Salix* spp. lined parts of the lake's shoreline and extensive grassy areas adjoined other stretches of it. Many ponds contained patches of *Myriophyllum* spp. The area contained about 20 moorhen territories in 1991 but the number declined later in the investigation.

From early September to mid-January each year, we monitored the reproductive performance of the various moorhen groups almost daily. Most nests were found before or during laying and were checked frequently, especially at predicted laying and hatching times. Eggs in some clutches were marked with a non-toxic marking pen on the day that they were laid to facilitate recording of laying sequences and incubation periods. Fresh eggs in some clutches were weighed (± 0.5 g). Additionally, we examined 418 records of moorhen breeding in the Nest Record Scheme for the period 1963–1995, which were obtained from throughout the species' range, except north of latitude 25°S.

The variables recorded were: type of nest site and nest materials, seasonality and timing of breeding, clutch size, egg mass, laying behaviour and incubation period. Laying usually occurred daily, so a clutch was deemed to be complete when the same number of eggs was present on successive days. Clutch initiation date was either recorded directly or calculated from clutch size and hatching date of the last egg laid. The incubation period was calculated as the time from laying to hatching of the last egg laid.

For Jells Park, reproductive success was assessed in terms of clutch success (percentage of clutches in which some eggs hatched), egg success (percentage of eggs that hatched) and percentage chick survival from fledging to independence. For Nest Record Scheme data, we estimated reproductive success from the daily probability of survival using the method of Bart and Robson (1982). With nests from this data set that had no estimated hatching date and were found to be empty at a particular inspection, we restricted the calculation of daily survival probability to the period prior to the penultimate nest inspection. This was necessary because the semi-precocial chicks cannot be detected reliably in the nest vicinity due to their cryptic behaviour.

All instances of nest building and provisioning chicks were routinely noted, but quantitative recording of the relative involvement of group members was not attempted. However, the proportional contribution of group members to incubation was measured quantitatively in a 'coarse-grained' way by recording, at intervals of at least 30 minutes at various times of day throughout the incubation period, which member of a breeding group was incubating.

We used Kolmogorov-Smirnov (KS) and Mann-Whitney (MW) tests to compare two independent samples and chi square tests to determine whether contributions of group members to incubation differed from random. Least squares linear regression was employed to examine the relationship between clutch size and date of clutch initiation.

RESULTS

Nest sites and nest building

Nests at Jells Park were constructed from pieces of soft, aquatic vegetation or occasionally woody material and lined with grass or twigs. They were surrounded by water and often partly or totally concealed in reed-beds or low, overhanging tree branches. In territories lacking a low vegetation cover, nests were built on substrates such as logs, mud islands and thick growths of non-emergent macrophytes. The nest base was commonly on or within 30 centimetres of the water surface, but the floor was above the waterline and usually dry.

Nest construction usually took four to five days. A rise in the water level stimulated adult birds to raise the floor level by adding more material, but flooded nests were abandoned. Nests were generally completed between 1 and 14 days pre-laying and new material was added throughout the incubation period. Breeding groups generally built one

or two, but occasionally three or four nests simultaneously or serially, before laying in one of them. Group members spent much time sitting or displaying in these nests pre-laying. In ten groups of differing composition in which nest building was observed regularly, all members contributed, sometimes passing the collected material to another individual to deliver and use for construction. Chicks vacated the nest between one and three days post-hatching, but often returned to it or to specially constructed brood nests to be brooded by adults. Re-use of previous breeding nests within a season was rare.

Breeding seasonality

The Jells Park breeding season extended from August to January (Fig. 1). The earliest clutch was initiated on 22 August and the latest on 24 January, but 85 per cent of clutches were initiated between mid-September and early December. Most first clutches were initiated in the first eight to nine weeks of the breeding season; more than 50 per cent of clutches produced after that period were the product of re-nesting. Nest Record Scheme data revealed a fairly similar breeding season duration and an indistinguishable pattern of within-season clutch initiation ($D_{98, 41} = 0.171$, $P > 0.05$, KS test) (Fig. 1).

Clutch size

The mean and modal clutch sizes were six at Jells Park and seven in data from the Nest Record Scheme. Figure 1 shows the frequency distributions of clutch size at Jells Park and in Nest Record Scheme data; these data include clutches to which two females contributed in unknown proportions. The largest clutch definitely attributable to a single female at both Jells Park and from the Nest Record Scheme, comprised eight eggs. Seven definite two-female clutches at Jells Park and four such clutches recorded in the Nest Record Scheme contained nine or more eggs, although a few of the nine-egg clutches in this latter group could have been laid by single females. However, the frequency distributions for clutch size differed significantly between those from Jells Park and those from the Nest Record Scheme data, whether all clutches or just those with eight or fewer eggs (i.e. almost certainly laid by single females) were considered ($D_{117, 34} = 0.383$ and $D_{80, 27} = 0.441$, P in both cases < 0.001 , KS test).

At Jells Park, females made a similar mean individual contribution to two-female and single-female clutches (5.6 ± 1.0 and 5.7 ± 1.4 eggs, respectively; $U = 99$, $n = 34$, $P > 0.05$, MW test). In contrast, the data from the Nest Record Scheme showed a significant mean discrepancy of about one egg in individual contributions to two-female (5.3 ± 1.0) and single-female (6.6 ± 1.2) clutches ($U = 2378.5$, $n = 117$, $P < 0.001$, MW test). For Jells Park breeding groups with only one laying female, clutch size was significantly, but weakly, negatively correlated with laying date ($r^2 = 0.18$, $n = 80$, $P < 0.001$) (Fig. 2); all small (i.e. = 6 or fewer eggs) clutches were laid after November.

Laying behaviour

Mean egg mass at Jells Park was 33.3 ± 1.9 grams ($n = 48$ from ten communal and single-female clutches) or 6.7 per cent of mean adult female mass. Fresh eggs added

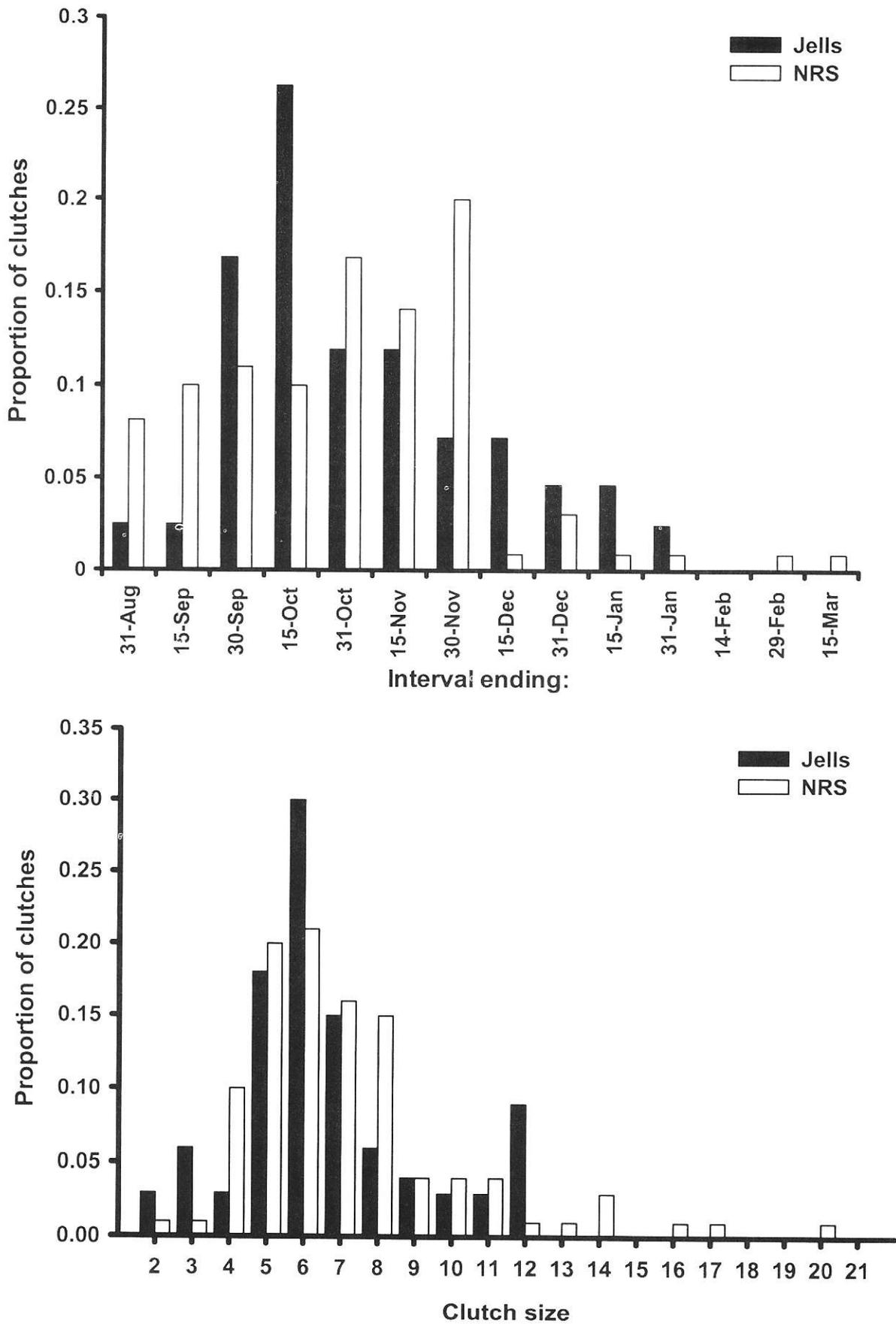


Figure 1. Proportions of moorhen clutches initiated in each half-month of the breeding season (upper graph) and of different sizes (lower graph). Black bars indicate Jells Park and white bars Nest Record Scheme data. N = 41 (Jells) and 98 (Nest Record Scheme) for initiation date and 34 (Jells) and 117 (Nest Record Scheme) for clutch size.

incubation was 44 per cent and collective male contributions ranged from 33 to 85 per cent. Individual females in communally nesting groups performed 15 to 67 per cent of incubation.

Reproductive success

For the 46 clutches laid at Jells Park during the study, clutch success was 61 per cent; clutch failures were due to predation (26%), flooding (6.5%) and unidentified causes (6.5%). None of the 28 successful clutches contained any infertile eggs. Partial clutch loss was recorded only three times, predation being involved in one case. Thus at Jells Park, egg success and clutch success were almost identical. Identified egg predators were the Purple Swamphen *Porphyrio porphyrio* and Australian Raven *Corvus coronoides*. The daily survival rate of Nest Record Scheme clutches was 0.986 (95% confidence limits 0.980–0.990). Assuming the incubation period = 23 days, this translates into a clutch success rate of 72 per cent (95% confidence limits 63–80%). Causes of nesting failure were not commonly recorded in Nest Record Scheme records, but predation and flooding were common and desertion was noted. Unlike the Jells Park records, Nest Record Scheme data contained several records of a single infertile egg in a clutch.

It was difficult to determine the survival rate of fledglings due to their cryptic behaviour. About 40–45 per cent of 150 chicks that hatched from 24 Jells Park clutches survived at least until independence at eight weeks post-hatching. Chick mortality occurred mainly in the first four weeks, but the agents were hard to determine. Predation by a Purple Swamphen was observed once but entire broods often disappeared rapidly when the chicks were apparently in good condition. Females commonly re-nested after clutch or brood loss, some up to four times in a season. Re-nesting also occurred after 26 per cent of the 19 instances in which young were successfully reared to independence and a few of these re-nesting events were successful too.

All members fed the young in ten breeding groups in which provisioning of chicks was regularly observed but we did not quantify their contributions. In the few groups that successfully reared two broods in a season, juveniles from the first brood fed chicks in the second, but not at high frequencies; however, they did not incubate eggs or brood young.

DISCUSSION

Comparisons with other Australian Dusky Moorhen populations

Reliable breeding data for the Dusky Moorhen are few and better information from a spread of locations across its large geographic range is needed.

BREEDING SEASONALITY

Nest sites and material at Jells Park conformed with Beruldsen's (1980) descriptions. The breeding season lasted seven months, from late August to early March. Reported breeding seasons at six other Australian localities at increasing latitudes are: August–January, six months,

northern Queensland (Bravery 1970); September–February, seven months, south-eastern Queensland (Czechura 1983); September–March, seven months, coastal northern New South Wales (Gosper 1981); October–January, four months, south-western Western Australia (Masters and Milhinch 1974); August–December, five months, south-western Western Australia (Halse and Jaensch 1986); September–February, six months, coastal eastern Victoria (Bedgood 1980). Beruldsen (1980) notes that breeding activity is less seasonally restricted in tropical northern Australia, but nonetheless occurs mainly in a seven-month period from December/January to May/June. Apart from this, no systematic latitudinal variation in breeding season length or timing is evident within Australia.

EGG AND CLUTCH SIZE

As in our study, Garnett (1978) found that female moorhens in the Australian Capital Territory laid one egg on successive nights or early mornings until their clutch was complete and the females contributing to a communal clutch started laying within three days of one another. Mean egg mass at Jells Park was very similar to that in some other southern Victorian localities (Lill 1990), but 10 per cent less than the value we calculated (using Hoyt's 1979 formula) from measurements reported by Beruldsen (1980) for a variety of Australian locations. The mean clutch sizes of individual females at Jells Park (6), in the Australian Capital Territory (6.1–6.7; Garnett 1980) and in south-western Western Australia (5; Masters and Milhinch 1974) were similar. The Nest Record Scheme data revealed no gradient in the clutch size of individual females over 15 degrees of latitude ($r^2 < 0.05$, $n = 117$, $P > 0.05$). There are few reliable incubation period estimates for the species, but the mean for Jells Park (23.2 days) was within the 19–24 day range reported for the Australian Capital Territory (Garnett 1978).

REPRODUCTIVE SUCCESS

Clutch success at Jells Park (61%) and from Nest Record Scheme data (72%) was much lower than in early breeding attempts (86.6%), but comparable to that in late attempts (61.5%), in Garnett's (1980) study. Conversely, the latter investigation reported much poorer survival rates of hatchlings to independence (25.2% and 7% from early and late attempts, respectively) than observed at Jells Park (40–45%). However, these contrasting embryo and chick survival rates resulted in fairly similar survival rates to independence for Jells Park (22%) and early (26%), but not late (4%), Australian Capital Territory young. Twenty-five per cent of Jells Park groups were multi-brooded, whereas no Australian Capital Territory group raised more than one brood per season.

In general, the Dusky Moorhen's breeding biology at Jells Park resembled that reported for other Australian localities. This is an interesting finding, because the Jells Park wetlands are artificial and could theoretically vary in a number of ecological parameters from natural wetlands. Whilst components of reproductive success do vary substantially among the few Australian Dusky Moorhen populations that have been studied, there is little evidence of a latitudinal gradient in any breeding variable.

Comparison with the cosmopolitan Common Moorhen

The well-studied, smaller Common Moorhen *G. chloropus* inhabits all continents except Australasia and therefore occurs over a wide range in latitude. A comparison of the breeding biology of the two species thus has relevance to the question of whether Australian non-passerines exhibit the same life history divergence from their Northern Hemisphere counterparts as do passerines.

In the Northern Hemisphere, the Common Moorhen's breeding season appears, on average, to be about 1.5 months shorter than that of Australian Dusky Moorhens (Wood 1974; Huxley and Wood 1976; Cramp 1980; Helm *et al.* 1987; Brazil 1991). However, in South Africa, at similar latitudes to Australia, its breeding season lasts as long as, or longer than, that of Australian Dusky Moorhens (Siegfried and Frost 1975). This is consistent with Wyndham's (1986) conclusion that the breeding seasons of Australian and southern African birds are about 1.5 months longer than those of their Northern Hemisphere counterparts.

Common Moorhen females, like Dusky Moorhens, lay daily, but in the evening (McRae 1996). At differing latitudes in southern Africa and India they have a similar clutch size to Australian Dusky Moorhens. At higher latitudes in the Northern Hemisphere their clutch size is more variable (Lack 1947; Wood 1974; Siegfried and Frost 1975; Huxley and Wood 1976; Gibbons 1986; McRae and Burke 1996), but not, on average, significantly different from that of the Dusky Moorhen in Australia. The clutch size of the Common Moorhen declines during the breeding season in Britain (Huxley and Wood 1976; Gibbons 1989), as it did in the Dusky Moorhen population at Jells Park, although the underlying reasons are unknown in both cases. When scaled allometrically, egg mass, clutch mass and incubation period are very similar in Dusky and Common Moorhens (Table 2). In both species, egg mass and incubation period are also very close to the allometric predictions from body mass; in contrast, clutch mass is about 60 per cent greater than predicted, but this simply stems from the fact that many clutches in both species are communal.

TABLE 2

Ratio of observed to allometrically predicted values for breeding variables in moorhens. M_E = egg mass, M_B = adult female body mass, M_C = clutch mass and IP = incubation period. Values used in calculations were: Dusky Moorhen M_B = 500g (S. Pywell unpublished data; Marchant and Higgins 1993), M_E = 33.4g (Lill 1990), clutch size = 6 and IP = 23 days (this study); Common Moorhen M_B = 350g (Anderson 1975; Gibbons 1989), M_E = 24.9g (Wood 1974), clutch size = 6 (Wood 1974; McRae 1996), IP = 22 days (Huxley and Wood 1976). Equation for M_E for Gruiformes from Rahn *et al.* (1975) and other equations for all birds from Western and Ssemakula (1982).

| Allometric equation | Ratio predicted: observed values | |
|--------------------------------|----------------------------------|----------------|
| | Dusky Moorhen | Common Moorhen |
| M_E (g) = $0.697M_B^{0.634}$ | 1.07 | 1.13 |
| IP (days) = $12.03M_E^{0.217}$ | 1.12 | 1.09 |
| IP (days) = $9.33M_B^{0.16}$ | 1.1 | 1.08 |
| M_C (g) = $1.35M_B^{0.72}$ | 0.59 | 0.61 |

Three nesting success estimates for the Common Moorhen are 56 per cent (U.K., Relton 1972), 21 per cent (U.K., Wood 1974) and 63 per cent (U.S.A., Helm *et al.* 1987). Petrie (1984), considering only the pairs in a United

Kingdom population, also reported that 52 per cent had some hatching success in a season, although only 29 per cent of first attempts were successful. Survival of hatchlings to independence was over 90 per cent in the Relton (1972) and Wood (1974) studies. The nesting success rates in the Relton (1972) and Helm *et al.* (1987) investigations were comparable with those of Dusky Moorhens in Nest Record Scheme data, at Jells Park and of early breeders in Garnett's (1980) study. However, hatchling survival to independence was much greater than in Garnett's (1980) and the present study of Dusky Moorhens. Petrie (1983) recorded much higher nest depredation rates for Common Moorhens in Britain (69%) than we observed in Dusky Moorhens at Jells Park.

This interspecific comparison thus yields mixed evidence on whether Australian moorhens exhibit the same life history divergence from their Northern Hemisphere 'counterparts' as do endemic passerines. Certainly, Common Moorhens breeding in the North Temperate Zone seem to have a shorter breeding season and a more variable clutch size than Australian Dusky Moorhens, but the two species are similar in mean clutch size, the frequency of re-nesting, within-season clutch size decline and probably nesting success. A comparison of just two congeneric species clearly has limited resolution with respect to the life history divergence issue and further detailed life history studies of some of the other Australian *Gallinula* rails would be useful.

Distribution of reproductive effort in communally breeding groups

In communally-nesting Avorn Woodpecker *Melanerpes formicivorus* and Groove-Billed Ani *Crotophaga sulcirostris* groups, eggs of the female initiating laying are removed by the second female until she is ready to commence laying. Consequently, the second female makes a disproportionate contribution to the communal clutch (Mumme *et al.* 1983; Koford *et al.* 1990). In contrast, in communal Common Moorhen groups, females usually commence laying synchronously and within-group egg destruction is relatively rare (Gibbons 1986; McRae 1995, 1996). Egg destruction also appeared to be rare in Dusky Moorhens, despite a less synchronized initiation of laying.

Nonetheless, the number of eggs contributed to the communal clutch by the various females in a Common Moorhen group is usually unequal; the female who initiates laying makes a contribution equal to that of paired females, but the secondary females lay fewer eggs (Gibbons 1986; McRae 1996). Consequently, the mean contribution of females to a communal clutch is less than the clutch size of paired females. Data from the Nest Record Scheme show a similar trend for Dusky Moorhens but this is not supported by Garnett's (1980) study or that at Jells Park. Gibbons (1986) found that, as in our study population, one of the females in some Common Moorhen communal groups did not contribute to the clutch, yet all females nonetheless incubated the clutch and fed the brood. Males also incubated, performing more than 70 per cent of incubation in a southern African population (Siegfried and Frost 1975), which is comparable with the contribution of males in some Jells Park Dusky Moorhen groups. There

was no evidence of intra-specific brood parasitism in Dusky Moorhens at Jells Park. Female Common Moorhens, however, often dump up to six eggs in neighbours' nests, which can stimulate egg removal by the host birds (Gibbons 1986; McRae 1995; McRae and Burke 1996).

Juvenile Dusky Moorhens have been reported feeding chicks produced later in the season by their natal group in Melbourne's Botanic Gardens (Fleming 1972), Canberra (Lenz 1990) and Brisbane (Putland and Goldizen 2001). Unlike Jells Park juveniles, however, those in Brisbane contributed up to 33 per cent of the chicks' food in some groups and sometimes brooded chicks in nursery nests. This disparity may stem from differences in food availability, because the extent of helping by juvenile Common Moorhens is influenced by food abundance in the breeding territory (Eden 1983). Juvenile helping behaviour also occurs in the Tasmanian Native Hen *G. mortierii* (Ridpath 1972).

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