SIMULTANEOUS POLYANDRY IN THE PURPLE SWAMPHEN

Breeding by the Purple Swamphen (or Pukeko) *Porphyrio porphyrio melanotus* normally involves pairs or communal groups of 3 to 6 adults with immature 'helpers' often aiding the reproductive effort (Craig 1979). While adult sex ratios are generally equal in stable communal groups, Craig (1980) observed one group where the males outnumbered the females (5 males and 2 females) early in the breeding season with one female later disappearing. This can be interpreted as an instance of 'simultaneous polyandry' (Jenni 1974).

Polyandry is 'the acquisition by a female of more than one male as a mate' (Wilson 1975: 592). Few species of bird are known to utilise this mating system (Lack 1968; Jenni 1974). 'Simultaneous polyandry', where the female mates and associates with more than one male concurrently, is rarer than 'sequential polyandry' where there is no long term association with a male and where more than one male is mated in succession (Jenni 1974). Frequent simultaneous polyandry has been described in the American Jacana *Jacana spinosa* and the Tasmania Native-hen *Gallinula morterii* by Jenni & Collier (1972) and Ridpath (1972), respectively; although the details of the arrangements are different for each species (see Jenni 1979). Sporadic instances of polyandry have been observed in other bird species (Jenni 1974).

When polyandry occurs in the Tasmanian Native-hen the males (usually two brothers) copulate and maintain a continuous bond with one female who lays a clutch which is cared for by all. To date this is a unique situation amongst birds (Jenni 1974); it is explained in evolutionary terms by Maynard Smith & Ridpath (1972). Ridpath (1972) also reported breeding 'trios' in the Purple Swamphen. Although he implied that such groups may be polyandrous, no sex ratios were determined.

I observed a small population of Swamphens (fifteen to twenty birds) from May 1975 to May 1977 at Longneck Lagoon, near Pitt Town, N.S.W. Several birds were trapped, banded, and patagial tagged for identification. Sexing followed the guidelines of Craig *et al.* (1981) and was confirmed by copulatory behaviour.

The location of existing or incipient breeding groups at Longneck was established by observation before and during the 1976–77 breeding season. All observed copulatory attempts were recorded and categorized as to their location, identity of the participants, and the stage of copulation reached. Three copulatory stages were recognised: (i) 'Following', where the female walks in front of a male(s) who follows one to 5 metres directly behind, one male behind the first when two males are involved. The distance covered during 'following' was variable. (ii) 'Hunching to mounting', which occurs after 'following', consists of the female adopting a 'precopulatory hunch' (Craig 1977) and the male stepping upon her back. (iii) 'Complete copulation' is characterized by cloacal contact, and is reached after the preceding stages. The copulatory sequence can terminate at any point.

RESULTS AND DISCUSSION

Of the birds studied, four came under scrutiny because of their polyandrous mating arrangement. Three of these were patagial colour-tagged and sexed, RY - female, RO - male, and RP - male. A fourth bird (UC - male, sexed by behaviour) was never trapped but was consistently with the other three birds. During the winter of 1976 three tagged birds were commonly associated with some untagged birds in one area of the lagoon. On 26 August an 'incomplete copulation' was observed between RY and RP with RO 5 metres away. Two days earlier these three birds were observed in a territorial boundary dispute (see Craig 1977 for the relevant behavioural postures) with the untagged birds in the area where the aborted copulation occurred. These observations, in association with later events, suggest that this group of birds was formed from a 'flock' of birds and were attempting to establish a territory.

On 25 September RY, RP and UC were observed in an area uninhabited by Swamphens since the previous autumn. They, plus RO, resided in and defended this area ('Channel Territory') for the remainder of the study (until June 1977). Also on 25 September RY and UC had an 'incomplete copulation' which was interrupted by RP. Later on 25 September RY and RP successfully copulated. UC was close by but did not participate. Throughout the spring similar instances occurred with the males' copulatory performance summarized in Table I. Few 'complete copulations' were achieved (17%, Table I) and most consisted of 'following'. This was a much greater proportion of unconsumated matings than was observed in the other two breeding groups at Longneck, with the group in 'Tree' territory achieving 60% and 100% 'complete copulation' during 1975 and 1976 respectively (Wettin unpubl.). Craig's (1980) polyandrous group achieved 10% complete copulation compared with greater than 75% for other groups.

Table I further reveals a differential participation in copulation by each male. RO rarely took part in mating and then only in 'following' with RP and UC also

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present. On 36 occasions 'following' involved two males (RP and UC); RP was the only male to 'follow' RY alone (11 times). RP had more 'complete copulations' (7) than UC (4) though this difference was not significant (Binomial test, p = 0.32; Siegel 1956). The combined copulation and mounting success of RP was also not significantly greater than that of UC (Fisher's exact test, p = 0.68; Siegel 1956). RP took part in every 'following' event and furthermore was the male directly behind RY, with UC behind RP. On the two occasions when RY copulated with RP and UC in succession, RP was first. Only RP copulated alone with RY. This trend suggests RP was sexually dominant to UC and RO.

TABLE I

Copulatory performance of males in "Channel" territory observed during 1976. Data indicate the stage at which the sequence terminated. Numbers in brackets are the percentage of the total.

MALE	STAGE OF COPULATION REACHED		
	"Following"	"Cloaking – mounting"	"Complete copulation"
RO	7	0	0
UC	36	3	4
RP	47	5	7
TOTAL	47 (71%)	8 (12%)	11 (17%)

The multiple participation of males in copulation is common in Swamphens and probably serves to stimulate and synchronise the female(s) sexually (Craig 1980). Craig (unpubl.) also found that in groups dominant males attempted more copulations than subordinate males and dominants interfered with copulatory attempts by subordinates. My results confirm these findings. However, in his polyandrous group Craig (unpubl.) noted no differential male copulatory success. Similarly, Ridpath (1972) found no significantly greater copulatory success by dominant males in the polyandrous groups of *T. morterii* though indications were that one male interacted sexually more often with the female.

The copulatory behaviour of UC, and particularly RP, is perplexing. RP seemed intent on preventing UC from copulating with RY yet he allowed it on a few occasions. The overall effect of this competition for copulation was highly disruptive. For example, on 3 November RP and UC 'followed' RY almost continuously for four hours and while this was the most extreme instance observed, it was not an isolated event. As a result RY must have been greatly affected, especially in her ability to collect food (Swamphens are herbivores and spend most of the day procuring food - Wettin unpubl.). Perhaps it is not surprising that she laid only one egg (on 10 December) and it was either abandoned or lost and incubation was not observed. Two clutches from other females at Longneck during the same breeding season consisted of 3 and 5 eggs, which hatched successfully (Wettin unpubl.). Craig's (1980) polyandrous group produced eggs and chicks but no surviving offspring.

Therefore, the 'Channel' males' courtship behaviour appears maladaptive in terms of energy expended and reproductive success. Craig (unpubl.) also believed this to be the case for his polyandrous group. Thus the existence of polyandrous groups in Swamphens poses some questions. Perhaps they reflect a shortage of females amongst those birds not in established territories ('flock' birds). Hence 'flock' males may have a greater chance of reproductive success by sharing a 'flock' female with another 'flock' male(s) than if he attempted to establish a paired relationship that is likely to be energetically expensive to defend and maintain. Or the polyandrous mating may be transient, with successful reproduction in subsequent years when male dominance and the territory is well established and perhaps another female added to the group. It is perhaps significant that both of the recorded polyandrous groups were formed from 'flock' birds without long term bonds or territory establishment. Finally, the 'Channel' groups' mating system could reflect an unreasonable expectation (by biologists) that all individuals in a population are perfectly adapted. We should expect some aberrant, maladaptive situations to arise, as suggested by Gadgil & Bossert (1970). From the existing evidence of Swamphen breeding it would seem that polyandry may be an unusual, and perhaps aberrant, situation. However, it is interesting to note its occurrence in both areas where the species' social behaviour has been studied in Australiasia. As has been suggested (M.G. Ridpath pers. comm.), a detailed study of the primary and secondary sex ratios of wild populations in differing ecological situations would do much to answer these questions.

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INTERSPECIFIC AGGRESSION WITHIN THE GENUS *MANORINA*

Local populations of miners (genus *Manorina*) typically exclude most other avian species from their territory (Dow, 1977; Smith & Robertson, 1978). Here I report an aggressive interaction between populations of two congeneric species, the Bell Miner *Manorina melanophrys* and the Noisy Miner *Manorina melanocephala*. Populations of these two species occupied abutting territories in 2 ha of dry layered woodland lining a small gully running into the Plenty River at the Janefield Training Centre, Bundoora, 16 km north-north-east of Melbourne. The site is described in detail as Region II by Smith & Robertson (1978).

During the study thirty-two Bell Miners were colour banded to facilitate recognition of individuals. Detailed estimates of the size of the Bell Miner population were obtained on average 2.5 times per week during observation periods lasting 60 to 180 min between September 1981 and February 1983, by taking a census of the banded and unbanded birds present in the study site. During these observation periods any other avian species present were noted.

The study site was marked with a 20 m grid pattern by white stakes so that birds' positions and sites of territorial boundary conflicts could be plotted on a map. The Noisy Miners initially occupied open woodland surrounding the gully and were not present in the study site.

RESULTS AND DISCUSSION

Between September 1981 and June 1982 the study site was occupied by Bell Miners and three other avian species (Table I). All other avian species were excluded from the site by the Bell Miners. The Bell Miner population appeared to be divided into two social groups. The southern group consisted of a mated pair and up to eleven non-breeding individuals while the northern group consisted of four mated pairs and up to twelve non-breeding individuals (Fig. 1a).

There were twenty-five individuals in the Bell Miner population when the first of four birds was seen to be suffering from a sickness which caused the swelling of the middle anterior phalanx of one foot on 18th May 1982. The sick birds were unable to perch properly and were often seen trying to feed while hanging from one foot. This appeared to be a severe handicap and a gradual deterioration in the appearance of their plumage was observed. Between 18th May 1982, and 8th June 1982, approximately eight birds disappeared from the southern group area. One was known to have been shot; the others may have dispersed or died. An inspection of neighbouring Bell Miner populations within 3 km of the study site failed to locate any of the individuals which had disappeared.

On 8th June 1982, fifteen or more Noisy Miners were seen fighting with Bell Miners 20 m inside the southern group area (Fig. 1b). The next day Bell Miners from the northern group were also seen harassing Noisy Miners in the southern group area. From this time on the boundary between the southern and northern group areas became less distinct (Fig. 1 b-h). In such fighting a group of six or more Noisy Miners flew high above a section of Bell Miner territory calling loudly; they would then descend into a particular tree and attempt to feed while being attacked by resident Bell Miners. After the fighting the Noisy Miners usually continued to occupy

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