

Breeding Success of a Communal Gallinule

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Summary. 1. The breeding success of the pukeko or swamphen, *Porphyrio porphyrio melanotus*, was studied for three seasons in two different habitats in the Manawatu, New Zealand.

2. There was a direct relationship between clutch size and the number of birds in a territory. In groups the dominant female was at a reproductive advantage, laying more eggs overall, but especially in the first and more successful clutch. Dominant females in groups were still at a disadvantage compared with females breeding in a pair.

3. Overall reproductive success was greater for pairs than for groups, although much of this difference could be attributed to habitat variables and membership stability.

4. Attempts to measure the 'helping effect' of non-reproductive helpers were inconclusive. The advantages and disadvantages to individuals are discussed, and it is concluded that breeding success is of limited value in explaining the communal habit of pukeko.

Introduction

This paper is one of a series on the biology of two populations of a communally living gallinule, the pukeko or swamphen. These were studied for three years in two different habitats within the Manawatu district, New Zealand. The general aim of this paper is to outline differences in the reproductive output of individuals in differently sized social units and to relate these to behavioural and ecological variables.

Communal breeding systems are a relatively recent area of research (Brown, 1978; Emlen, 1978). As suggested by Brown (1978), they are a critical test

for some aspects of sociobiological theory, especially Hamilton's (1964) ideas about inclusive fitness, altruism and kin selection. A number of studies on communal social systems have been explained at least in part by using kin selection theory (e.g. Maynard-Smith and Ridpath, 1972; Brown, 1974), whereas others (e.g. Zahavi, 1974, 1976; Woolfenden, 1976) have attempted to emphasize selfish benefits. Thus some controversy has arisen over the selective advantage of communal breeding and especially over whether non-reproductive helpers really help or hinder. Overall there is a lack of empirical data, and only one other published study (Vehrencamp, 1977) has data from more than one habitat to enable evaluation of ecological determinants of communal breeding systems.

Pukeko have an extremely varied social system (Craig, 1979) and hence show a wide range of helping situations: (1) pairs alone, (2) groups of promiscuously breeding adults, (3) groups with non-breeding yearlings, (4) pairs and groups assisted by juveniles from earlier clutches in the same season.

This paper aims to describe the reproductive success of these varied social units and to determine which factors were responsible for the observed differences.

Other relevant aspects of pukeko communal biology published elsewhere include: social organization (Craig, 1979) and the degree of participation in breeding (Craig, in press).

Materials and Methods

Study Areas

Pukeko (*Porphyrio porphyrio melanotus*) were studied in two swamp areas: Pukepuke Game Management Reserve (a dune lake under the control of New Zealand Wildlife Service) and Linton (a complex of stream valleys running through pasture). Detailed

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Table 1. Mean 'overall' clutch size. Linear correlation of clutch and group size significant at: * $P < 0.05$; ** $P < 0.01$

	No. of birds in territory and no. of laying females					All pairs and groups
	2 1♀	3 1♀	4 2♀♀	5 2♀♀	6 2♀♀	
1970-1971 *	4.5 (n=2)	5 (2)	5.7 (7)	5.0 (1)	—	5.3 ± 0.5 (se)
1971-1972 **	5.3 (6)	—	6.0 (6)	7.1 (7)	—	6.2 ± 0.4
1972-1973 **	5.2 (5)	4 (1)	5.5 (2)	—	7.4 (7)	6.2 ± 0.6
						(excluding pairs)
First clutch	5.6 (7)	—	5.0 (9)	7.0 (4)	5.5 (5)	5.5 ± 0.4
Subsequent clutches	5.2 (5)	—	6.2 (6)	7.5 (4)	9.5 (2)	7.3 ± 0.6
All clutches **	5.4 ± 0.3 (n=12)	4.7 ± 0.9 (3)	5.8 ± 0.5 (15)	6.9 ± 0.7 (8)	7.4 ± 0.9 (7)	6.0 ± 0.3 (n=46)

descriptions of these are given elsewhere (Craig, 1979). The major difference between the two areas as related to breeding success was water level. At Linton, levels were relatively constant throughout the year, being maintained by an open spring, whereas at Pukepuke they fluctuated widely (during two summers, the lake bed became dry in the study area).

Methods

General methods are presented elsewhere (Craig, 1979 and in press). Where possible, study nests were visited at one- or two-day intervals during laying and hatching and twice weekly during incubation. Eggs were numbered as they were laid. With few exceptions, nests were located before the laying of the first egg.

In two-hen clutches, the egg colour of each female was determined in order to calculate the number laid by each. This was done in three ways: (1) By observing which female was on the nest when an egg was laid. To pinpoint exact arrival time of eggs, nests were checked immediately before dawn and again after a female left the nest. The presence of a female on the nest was observed directly or, where this was not possible, was deduced from the fact that all other territory members were in view. (2) By comparing egg colours between years when previously only one of the females had been present. This circumstance applied in two territories only. (3) By feeding dyes to females to stain yolk and shell. In 1972, the females of one group were trapped as regularly as possible and force-fed with gelatine capsules containing lipid dyes of different colours. The dyes used were Sudan III and Sudan black, which stain the yolk. Rhodamine B, which is recorded to stain egg shell (Romanoff and Romanoff, 1949) was also fed to the bird given Sudan III.

As more than one female laid in some nests, it is necessary to distinguish two different clutch sizes. *Individual clutch size* was taken as the maximum number of eggs an individual female contributed to a nest, while *overall clutch size* was the sum of these and was the maximum number of eggs in a nest.

Hatching success was measured by the percentage of eggs laid in the nests which subsequently hatched, reproductive success by the percentage of eggs laid which produced young surviving for at least four months. Predation by harriers was observed directly and was presumed to have occurred where claw and beak damage could be seen on the discarded shell fragments. Mustelid predation was presumed when the whole egg was removed from the nest and nesting material was disturbed.

Results

Clutch Size

In group territories, more than one female copulated and each laid in the same nest, usually at the same time. All such nests contained eggs of clearly differing colours, there being a regular difference in size between eggs of different colours. Analysis of variance within and between sizes of eggs of two colours in the same nest showed the size of the differently coloured eggs to be significantly different (Northern Territory $F_{1,25} = 9.59$, $P < 0.01$; Southern Territory $F_{1,32} = 41.77$, $P < 0.001$). Egg size and colour in pair territories was consistent from nest to nest, and egg shells from most territories, kept for comparison, showed that colour within a territory was also consistent from year to year. Colour differences were less apparent in the Hide Territory where females were related (mother and daughter) in all years, but there were manifest differences in size.

Most pairs and groups laid two clutches but, if clutches were lost, up to three replacement layings could occur.

Overall clutch size (Table 1) varied directly with the number of birds in a territory. This correlation partly stems from the number of laying females although comparison of clutch size of groups with four to six shows an increase, albeit none had more than two laying females. Because there were more larger groups in the second and third seasons, overall clutch size was greater in these years than in the first. In pair territories, first clutches were similar to later ones ($z = 0.37$, 10 *df*, NS), while in all group territories, first clutches with one exception were smaller than subsequent ones. This difference is significant ($t = -2.69$, 30 *df*, $P < 0.05$).

Among the adult females in group territories, the dominant female laid slightly larger individual clutches than the subordinate (4.1 ± 0.3 , $n=16$; 3.6 ± 0.5 , $n=11$), although this difference is not significant ($t=0.83$). Age was a complication in that the older subordinate laid more eggs than the dominant in three nests. The relative ages of most females were not known, so the effects of age and status could not be evaluated separately.

The dominant female laid in all clutches, whereas in almost a third of all nests the subordinate adult female made no contribution. Thus when considering all group nests, the dominant female made a significantly greater contribution than the subordinate adult female (4.1 ± 0.3 ; 2.5 ± 0.6 ; $t=2.5$, 30 *df*, $P < 0.05$). This skew in laying was especially significant when considering the more successful first clutches, as the subordinate adult female did not lay in 44% of these. Except in groups which had lost an adult female and had elevated a yearling to breeding status, subordinate yearling females made no contribution to any clutch.

The average individual clutch size for females in groups (3.9 ± 0.3 , $n=27$) was significantly smaller than that of females in pair territories (5.4 ± 0.3 , $n=12$) ($t=-3.1$, 38 *df*, $P < 0.01$). This held for both the dominant ($t=-2.9$, 26 *df*, $P < 0.01$) and the subordinate females ($t=-2.9$, 21 *df*, $P < 0.001$).

Reproductive Success

Of 91 eggs known to be lost before hatching, predation was the greatest (38%) factor although desertion (22%), especially of last eggs, and ejection (16%) were common. Australasian harriers (*Circus approximans*), the main predators, most often took eggs from nests exposed in the crown of *Carex* tussocks. Eggs suspected to have been taken by mustelids were in nests close to ground level and surrounded by less than 0.3 m of water. Harriers were rarely seen at Linton, mustelids never.

Chick loss was high in the first two months, even more so in the first few days. When a few chicks hatched well in advance of the majority of the clutch, they frequently died in the nest – presumably of starvation. Less frequently, the last eggs were deserted and the hatched chicks were led to food. Dead chicks were frequently found in territories within the first fortnight after hatching, and chicks continued to disappear until 2–3 months old.

Hatching success and survival rate varied markedly between territories (Table 2) and also from year to year. Survival rates were very low at Pukepuke. In the 1970–71 season, only two chicks survived from

all broods, and in all years early clutches were more successful than later clutches (Table 3). This difference between the success of first and subsequent clutches is especially marked for groups. As most groups were found at Pukepuke, the difference may relate to lower water levels at the time of second nesting. Water levels were high under most Linton nests and for early nests at Pukepuke, but drying of the lake at Pukepuke each summer meant that water levels around later nests were low. To investigate the effect of water level around the nest on overall reproductive success, the results for all nests are pooled. Where the water depth under the nest was greater than 0.3 m, 28% of eggs ($n=189$) produced surviving offspring, but for water depths less than this, only 4% of eggs laid ($n=80$) produced surviving offspring. This difference is significant ($\chi^2=20.1$, 3 *df*, $P < 0.0001$).

For those territories with less than 600 m² of emergent cover, no chicks survived. This suggests a relationship between overall breeding success and the amount of cover. However, these territories also had low water levels and in all cases were held by groups recently established by flock birds.

Overall breeding success in both habitats showed that pairs were more successful than groups. This trend is maintained when comparison is made within each study area although sample sizes are small. At Pukepuke, groups of five and six were slightly, but not significantly, more successful than groups of three and four.

From results so far, it appears that a number of factors affect reproductive success. Therefore if a realistic comparison is to be made of the relative output of pairs and groups, an attempt must be made to reduce the effects of the other variables. (a) Membership stability: Pair and group territories at Linton were relatively stable in membership, whereas some of the groups at Pukepuke were unstable through their recent formation from flock birds. When results only of stable pairs and stable groups (i.e. those resident in the study area for at least two successive breeding seasons and with relatively constant membership) are compared, Linton still had a higher overall breeding success than Pukepuke and pairs were more successful in rearing young than were groups. Unstable groups at Pukepuke were totally unsuccessful (Table 2). (b) Cover: As all stable pairs and groups had more than 600 m² of cover, comparison of only stable units removes much of the influence of this factor. (c) Water depth around the nest: Because this was more variable at Pukepuke than at Linton, it affected the success of groups more than pairs. When the effects of water levels are factored out, and the overall breeding success of stable groups at Pukepuke

Table 2. Reproductive output of pairs and groups at Linton and Pukepuke. Where appropriate, data were reorganized into 2 × 2 contingency tables for χ^2 test

	All pairs	All groups	Linton		Pukepuke			Stable				Unstable Groups	Over all total
			Pairs	Groups	Pair	Groups		Linton	Pukepuke groups		Pairs		
						3&4	5&6		All nests	Water >0.3 m			
No. of territories	7	21	6	4	1	8	9	8	9	9	5	4	28
No. of nests	14	37	13	7	1	14	16	18	17	11	12	8	51
No. of eggs	70	206	64	36	6	77	93	90	109	65	60	30	276
No. hatched	48	158	42	34	6	58	66	66	88	57	38	17	206
Hatching success	69%	74%	66%	94%	100%	75%	71%	73%	81%	88%	63%	57%	75%
	NS		$P < 0.01$		NS		NS	$P < 0.01$		$P < 0.05$			
No. of chicks surviving to 4 months	28	31	26	11	2	6	14	34	17	16	24	0	59
Overall breeding success	40%	14%	41%	31%	33%	8%	15%	38%	16%	25%	40%	0%	21%
	$P < 0.001$		$P < 0.05$		$P < 0.01$		NS	$P < 0.001$		NS			
% No. hatched surviving	58%	20%	62%	32%	33%	10%	21%	52%	19%	28%	63%	0%	29%
	$P < 0.001$		NS		NS		$P < 0.001$		$P < 0.01$				
								$P < 0.001$					
Mean no. of chicks surviving/territory/season	4	1.4	4.3	2.8	2	0.8	1.6	4.2	1.9	—	4.8	0	2.1
Mean no. of chicks surviving/bird/season	2	0.3	2.2	0.6	1.0	0.2	0.3	1.6	0.4	—	2.4	0	0.5

Table 3. Breeding success for first and second clutches of stable pairs and groups. Using χ^2 contingency tables (testing the number of eggs that produced surviving chicks against the number of eggs that did not), significant differences in survival were shown between (a) first and second clutches of groups ($P < 0.05$); (b) first and second clutches of pairs and groups combined ($P < 0.01$); (c) second clutches of pairs and groups ($P < 0.05$). For first clutches of pairs and groups $0.1 > P > 0.05$; differences between first and second clutches of pairs were not significant

	No. of territories	First clutch			Second clutch		
		No. of eggs	No. of 4-month-old chicks	% Survival	No. of eggs	No. of 4-month-old chicks	% Survival
Pairs	5	27	17	63	28	9	32
Groups	9	49	13	27	64	4	6
Total	14	76	30	39	92	13	14

is revised to include only nests surrounded by a water depth of greater than 0.3 m, results (Table 2) are closer to the value for pairs at Linton where water depths were greater than 0.3 m for all nests. Thus using only nests from stable groups and pairs sur-

rounded by comparable water levels, 25% of eggs laid by Pukepuke groups produced surviving offspring. While lower than the 40% for Linton pairs, this difference is no longer significant (Table 2).

A series of linear models were fitted to the data

Table 4. Comparison of reproductive output of (a) early clutches in pair territories with later clutches when chicks of the first brood were available to help, and (b) groups with and without yearling helpers (probability calculated with χ^2 contingency tables)

	a)		b)	
	Juvenile helpers		Yearling helpers	
	Absent	Present	Absent	Present
No. of nests	9	5	7	5
No. of eggs laid	44	26	46	39
No. of eggs hatched	35	13	29	30
Hatching success	80%	50%	63%	77%
	$P < 0.05$		$P = 0.25$	
No. of surviving chicks	21	7	6	9
Reproductive success	48%	27%	13%	23%
	$0.2 > P > 0.1$		NS	
Chicks hatched surviving	60%	54%	21%	30%
	NS		NS	

in an attempt to extricate the effects of all these variables on overall reproductive success. Two factors and two covariates and suitable interaction terms were included. These models were fitted and residuals calculated using the statistical computer package GLIM (Nelder, 1975). The factors were (a) S: stability (two levels – stable and unstable membership), and (b) W: water level (three levels – <0.3 m, $0.3-0.6$ m, >0.6 m); and the two covariates were (a) B: number of birds in a territory, and (b) C: amount of emergent cover in the territory. The results and significance must be regarded with caution, but the probabilities given below are suggestive and serve to confirm earlier comments. Results suggest the following:

1) The number of birds in a territory significantly affected overall reproductive success, but this effect was different for the two stability levels. Water level did not have any detectable effect on this relationship (H_0 = all slopes of B are same for all levels of S and B, $F_{5,37} = 2.75$, $P = 0.03$; H_0 = slopes of B are same for different levels of S, $F_{1,41} = 7.91$, $P = 0.008$; H_0 = slopes of B are same for different levels of W, $F_{2,40} = 1.77$, $P = 0.18$).

2) Membership stability (in association with B) also had a significant effect on overall reproductive success (see above $F_{1,41} = 7.91$, $P = 0.008$).

3) Cover had no significant effect, though the low probability suggests such an effect may exist (H_0 = slopes of C equal, $F_{4,38} = 2.43$, $P = 0.06$), but when pooled (H_0 = single slope of C = O, $F_{1,42} = 0.05$, $P = 0.83$).

4) Water level surrounding the nest was shown

to affect overall reproductive success after correction was made for effects due to S and (H_0 = no effect due to W. After correction by S B, $F_{2,44} = 5.3$, $P = 0.009$).

As well as the comparison of overall reproductive success of pairs versus groups, results may be used to investigate whether helpers really help (Zahavi, 1974). The 'helping value' of chicks of earlier broods in pair territories can be assessed by comparing hatching and overall reproductive success from first and subsequent nests (Table 4a). For second nests when chicks were present, hatching success was lower than for first nests, the difference being significant. However, these differences may be attributed to reduced time available for incubation when the pair was also caring for the first brood. Also, as the help available from the chicks is only in feeding and leading and not in incubation, a comparison of the proportion of hatched chicks surviving would be more meaningful. Such results are similar for both classes of nest.

An estimate of the 'helping value' of yearlings in group territories can be obtained by comparing reproductive success for stable groups without yearlings with the same stable groups the following season when yearlings were present (Table 4b). When yearlings were present, hatching success and overall reproductive success were higher, but sample sizes are small and none of these differences is significant.

Discussion

The correlation between overall clutch size and the number of birds in group territories could partly reflect the increasing age of females through the study. However, some females in groups of five and six were known to be only one and two years old, so at least part of this increase in clutch size may reflect increased food intake for females in groups with more helpers. This could have come about because helpers do release these females, at least partially, from other duties such as defence and chick care (see Craig, 1979 and in press). This argument would explain why the increase in clutch size is more apparent in second clutches. Ridpath (1972) made a similar suggestion to explain the increased clutch size of trios (predominantly 2 ♂♂ and 1 ♀) over pairs.

In order to discuss the possible advantages to the individuals, it is necessary to have some gauge of reproductive output. Among females there appeared a direct relationship between status and reproductive success. Not only did the dominant adult female lay more eggs, but she also laid more in the productive clutches. The subordinate yearling females were prevented from copulating or visiting the nest (Craig,

in press) and so had zero reproductive success. Adult subordinate females were intermediate. No similar relationship can be argued for adult males although subordinate yearling males were similar to the same class of female. In general then, subordinates can be considered at a reproductive disadvantage compared with dominants.

As the greater part of the variation in the success of adult females related to the lower success of second clutches, it is assumed that in non-drought years survival from both clutches will be high and in these years the dominant's advantage over the subordinate adult female will be reduced. Even dominant females in group territories were reproductively disadvantaged when compared with females in pair territories which had a larger clutch and raised more surviving offspring. These differences may be a reflection of age, however, as there is some evidence (Craig, 1979) to suggest that monogamous females may be older and hence more experienced. Similarly, males in groups appear at a marked reproductive disadvantage compared with males from pair territories.

Some measure of the effectiveness of the helping situations found in pukeko can be gained by assessing differences in reproductive success. In light of other studies on cooperative and communal breeders (e.g. Brown, 1978), the lower reproductive success of group territories in comparison with pairs is one of the more unexpected results of the study. My results cannot be compared with the only other published study on a communal rail (Ridpath, 1972), as Ridpath used a calendar month for assessing chick survival and hence counted chicks of widely varying ages. Comparison of the two study areas and the analysis of covariance implies that much of the difference in overall breeding success between pairs and groups may be related to habitat, especially the physical qualities of breeding territory, and to the stability of pair or group bonds.

For successful breeding in any territory, regardless of the number of birds involved, a minimum area of cover seems necessary in relation to aerial predators, and a minimum water depth of about 0.3 m is required to deter ground predators. Territories lacking these requirements are termed suboptimal; they were held by unstable units formed from the flock and these were unsuccessful in rearing young. This suggests that the number of optimal territories (i.e. containing requisites for successful breeding) is severely limited and in order to retain these permanent residence is necessary.

Evaluation of the advantages to all individuals in the different helping situations and the effectiveness of this helping is difficult. Attempts to measure any helping effect by chicks of earlier broods in pair terri-

ories were inconclusive. The slightly lower proportion of hatched chicks surviving may have been caused solely by seasonal differences in habitat. The chicks did undertake much of the care of later chicks and some also helped with territorial defence, but a fuller evaluation of the effectiveness of this help will have to await manipulation experiments. The failure to obtain a significantly greater hatching success and overall breeding success of groups with yearling helpers when compared with those without may have been due to the small sample size. If the difference is real, the increased success may have been the result of direct assistance with feeding and leading chicks and/or may have been caused by the freeing of adults for other activities such as territorial defence and egg production for subsequent clutches.

Such attempts to resolve the problems of whether helpers help or hinder are as inconclusive as those of other workers (see Zahavi, 1974; Brown, 1975, 1978). A major reason for this may be the methods of analysis which treat all helpers' interests as being similar. While this is generally true in terms of gains in inclusive fitness, as all are helping to raise kin, possible future losses in competition for a breeding place vary indirectly with status (cf. Emlen, 1978). Thus it is possible to argue that dominant helpers should contribute the most, and hence the merging of the results of all helpers may obscure any individual helping effects. An experimental evaluation of this is planned.

In conclusion, the results presented above on the breeding biology are on their own of limited value for determining the factors which produce the communal habit of pukeko as has been suggested by Brown (1974) (see also Craig, 1979). Breeding success, per se, appears to be determined by the quality of the habitat within each territory.

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