

Breeding of an Island-endemic Bird: the New Zealand Whitehead *Mohoua albigilla*; Pachycephalinae

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Received 20 September 1987, accepted 12 March 1988

Summary

McLean, I.G. & Gill B.J. (1988). Breeding of an island-endemic bird: the New Zealand Whitehead *Mohoua albigilla*; Pachycephalinae. *Emu* **88**, 177-182.

We document breeding behaviour, timing of breeding, details of the nest site, clutch size, the incubation and nestling periods, numbers of breeding attempts, and seasonal breeding success, for individually marked Whiteheads on Little Barrier Island, New Zealand. Whiteheads bred in groups ranging in size from 2 to 8. Incubation was initiated from late September until late December. Productivity of groups was low (1.38 and 0.73 chicks were fledged per group per season in two years). Few groups laid two clutches in a season. Parental care was extended until the end of winter (8-9 months). Whiteheads exhibited typical characteristics of island-endemic bird species, and also of birds that are constrained to breed co-operatively. Comparisons are drawn with related species.

Introduction

The breeding characteristics exhibited by island-endemic bird species include low fecundity, high breeding densities, delayed reproduction, and extended parental care (Macarthur & Wilson 1967). These characteristics are also exhibited by co-operative breeders (Emlen 1984; Woolfenden & Fitzpatrick 1984), presumably because the constraints acting on both kinds of bird are similar. Here, we describe the breeding biology of an island-endemic species that is also a co-operative breeder, as a first step towards teasing apart the factors that underlie the breeding systems of these two kinds of bird.

The tribe Mohouini of the Pachycephalinae (Sibley & Ahlquist 1987) is a little-studied group of foliage-gleaning passerines endemic to New Zealand. The Whitehead *Mohoua albigilla* occurs in central and southern North Island forests and on two offshore islands (Bull *et al.* 1985). The Yellowhead *M. ochrocephala* occurs primarily in beech *Nothofagus* forests in South Island (Gaze 1985; Elliott 1986). The Brown Creeper *Mohoua novaeseelandiae* (formerly *Finschia novaeseelandiae*) occurs in scrublands and mature forest in South Island, and on offshore islands.

Whiteheads build small cup nests in dense foliage (Oliver 1955). They often breed in groups comprising a primary pair and 0-6 secondary individuals (McLean *et al.* 1986; McLean 1987a,b; terminology after Dow 1980). Occasionally two males in a group appear to have similar status, although it is not known if both copulate. Secondary birds may or may not help at the nest.

We document breeding by individually marked Whiteheads on an offshore island, and make comparisons with the Yellowhead and Brown Creeper.

Methods

Whiteheads were studied below 75 m altitude on the south-west portion of Little Barrier Island (36° 13'S, 175° 3'E). All birds lived in mature Kanuka *Kunzia ericoides* forest, with understorey of either grasses (areas of flat land that were grazed in the recent past) or a mixture of shrubs and trees typical of coastal flora in northern New Zealand (the lower slopes within 0.5 km of the ranger's house). Periods of study were from 6-23 October 1983, 20 October 1984 to 19 January 1985, and 22 October 1985 to 6 January 1986.

Most Whiteheads under study were colour-banded with individual combinations. Sex was determined using plumage and behaviour (details in Gill & McLean 1986; McLean 1987a).

We refer to breeding units as 'groups' in the text for convenience. Groups consisted of pairs, primary pairs with secondary individuals, or polyandrous females with or without secondary individuals.

In October 1984 we selected 21 focal groups for intensive monitoring of breeding. During the 1984/5 summer we realised that a few groups contained two breeding pairs. We do not yet understand the dynamics of Whitehead group structure and, for this analysis, we have treated each primary female as an autonomous unit. However, we suspect that interactions within groups containing more than one primary female, including direct interference at nests, may result in decreased success for one female (McLean *et al.* 1986), and may explain some of the nest failures reported here.

Fifteen focal groups were studied in 1985/6. Only one was known from banding records to include the same primary pair as in 1984/5, but three primary pairs consisting of a banded and an unbanded bird may have remained the same. Apart from the banded pair, one banded primary female and four banded primary males were studied in both years.

Results on nesting phenology and the timing of nest initiation are from all nests found, including groups other than the focal study groups. For each nest we recorded heights of the nest, the tree in which it was built and the immediately surrounding canopy. Tree species was noted. Concealment of the nest was measured by estimating exposure using a five-point scale (0-20% cover = exposed = 0; 80-100% = completely concealed = 4). For cover-from-above we estimated how exposed the nest was to a hawk flying just above the canopy. For cover-from-the-side we envisaged a circle drawn at a 2 m radius at the height of the nest and estimated how exposed the nest would be to a predator climbing in trees immediately outside this circle. The two cover estimates were added together for analyses of nest success in relation to cover to give values ranging from 0 (very exposed) to 8 (concealed).

Initiation of incubation was calculated by backdating from known events (e.g. hatching, fledging, chicks aged using developmental state) using incubation and nestling periods reported here. Initiation of nest-building was determined either by subtracting 10 days from the start of incubation (3 days laying + 7 days for building), or by subtracting between one and four days for birds found nest-building, depending on how complete the nest was when found. Nests were used only if the required date could be calculated with reasonable accuracy (± 3 days); e.g. a nest was not used if it was found during incubation and failed before hatching. Our nest finding effort was fairly constant throughout the breeding season with two exceptions: i) a few early nests may have failed before our arrival on the island, and ii) we were absent from the island for the last 10 days of December in both years (hence we would not have located any short-lived nests initiated in this period).

A nest was 'successful' if at least one chick fledged. Some known nests were never located but chicks were easily found once they left the nest because of their loud and persistent begging. Thus, number of successful nesting attempts for each focal group in each season was always determined. Our data on number of nests initiated are less reliable. However, incubating females behaved in characteristic ways (McLean 1987a) and we are confident that we either located or knew of most nests in which incubation lasted for more than a few days for all focal groups.

Two analyses on characteristics of the nest site were conducted. First, we compared characteristics of nests in which no eggs were laid with characteristics of all nests in which eggs were known to be laid, even if the nest was not found until later in the nesting cycle (e.g. after hatching), using χ^2 tests on the frequency of each measurement.

Second, for nests in which eggs were known to be laid, we used the Mayfield method (Mayfield 1961, 1975; Johnson 1979; Harris *et al.* unpubl.) to compare nests that succeeded with nests that failed.

Results

A total of 72 nests was found in 1984/5 and 1985/6, and evidence (usually fledged chicks) indicating the existence

of 13 more was gathered. Chicks fledged from 21; eggs were laid in at least 50; no activity was seen at 8, and two were abandoned due to our activities.

Density of birds in the study area was approximately 1.6 primary pairs/ha or 6.4 birds/ha assuming an equal number of non-breeders. These densities were considerably higher than is usually observed for Whiteheads on mainland New Zealand.

Division of labour in the breeding system

The primary female built the nest and did all incubation and brooding. The primary male fed the primary female during courtship, laying, and incubation. Most feeds given during incubation were when the female was off the nest; it was rare for any bird other than the female to approach the nest before eggs hatched. Primary males accompanied ('guarded') the female during the nest building and egg-laying periods, spent long periods singing from song posts, and were occasionally involved in interactions with neighbours.

Secondary birds accompanied the primary female when she was off the nest, occasionally fed her, were involved in interactions with neighbours, and gave some song. The role of secondary Whiteheads was highly variable, ranging from association with the flock and alarm calling (McLean 1987b), to doing most feeding of chicks (allowing the primary female to renest), or taking over the role of the primary male if he was injured (observed in one group for several weeks). One secondary male was seen copulating with an unidentified female. This copulation was broken up by the primary male of his group, suggesting that within-group competition for copulations occurs.

We made 21 nest watches (>1 h) where all birds feeding chicks were identified. At nests with no secondary individuals (9 watches at 6 nests), females made $46 \pm s.d. 13.3\%$ and males $53 \pm 13.2\%$ of feeding visits. At nests with 1-4 secondaries (12 watches at 8 nests) the primary female made $43 \pm 18.1\%$, the primary male made $37 \pm 17.7\%$, and secondaries made $20 \pm 18.5\%$ of feeding visits.

Because the extent to which secondary birds associated with breeding pairs was highly variable and in many cases was never determined (if eggs did not hatch we never knew which birds would feed the chicks), we have not presented analyses in relation to group size here. Instead, we make comments below where appropriate as suggestions for further research.

Timing of breeding

The earliest nest was initiated about 14 September (Fig. 1). In 1984/5 there was a progressive increase in nest initiations from this time, reaching a peak in early November.

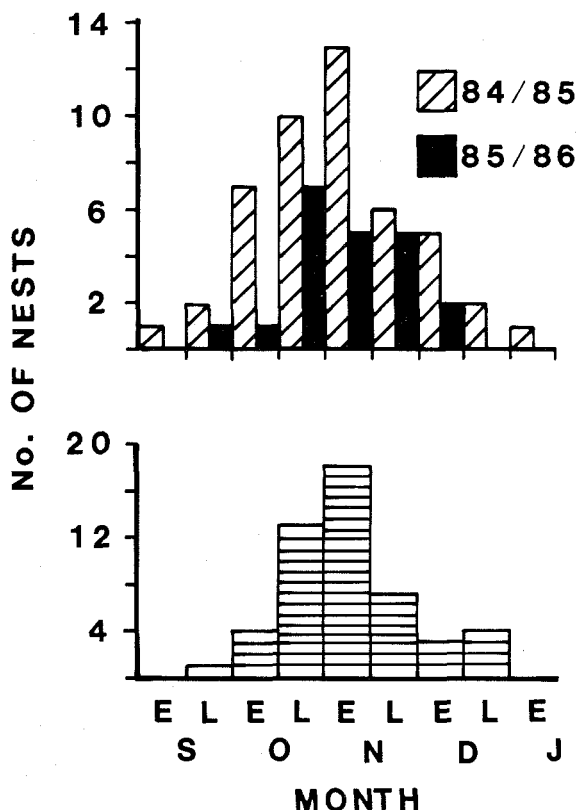


FIGURE 1 Timing of nest initiation in two study years (above), and of initiation of incubation (below), for Whiteheads on Little Barrier Island. Data from both years were combined in the incubation graph. E = early (first half of month); L = late (second half of month).

Nests begun in late November and early December 1984/5 were primarily re-nestings. The last nest was initiated on 5 January. In 1985/6 few nests were initiated before late October and there was no clear build-up as in 1984/5; rather, nests were begun at about equal rates during late October and November, and no nests were begun after 10 December. Few groups re-nested in 1985/6 (see below) so that most initiations represent first attempts.

Incubation was begun primarily between mid-October and mid-November, with a peak in early November (Fig. 1).

Characteristics of the nest site

Most Whitehead nests were built in the canopy where vegetation was locally dense (nests were difficult to see even when the exact location was known). Nests were supported by intermeshing twigs and small branches, and were manufactured from locally available materials such

as tree-fern fibre, dried grasses, dead wood fibre, and spider web. The cup was deep enough for a female to sit completely within it even when on a clutch of eggs; high nests (>15 m) swayed through an arc of up to 3 m in strong winds and the high-sided nest may prevent eggs from being thrown out when the female is away feeding.

Of the 72 nests found in 1984/5 and 1985/6, most (69%) were built in Kanuka, which was the dominant canopy species in the study area. All species used were common in the area in which the nest was found.

No significant differences were found between nests in which eggs were laid ($n = 45$), and nests that were abandoned before laying ($n = 14$) (χ^2 tests on height of nest, ratio of nest height/canopy height, exposure). Thus these data were combined for presentation, and data from nests where egg laying was not confirmed were included. Nests ranged from 2 to 30 m above ground, and were most likely to occur in the canopy (modal nest height/canopy height ratio = 0.9-1). Most nests were well concealed (modal exposure index = 5-6 on an 8 point scale), primarily because the growth form of Kanuka offers small dense clumps of vegetation.

No significant differences were found for any characteristic of successful nests ($n = 20$) when compared with unsuccessful nests in which incubation began ($n = 22$), using the Mayfield method. The sample of 42 is three less than the 45 above because two nests were abandoned due to our activities, and another was destroyed by a predator on the day it was found.

In summary, there was no relationship between any measured characteristic of the nest site and whether the nest was used, or whether it was successful.

Clutch size and egg characteristics

Mean clutch size was $2.82 \pm s.d. 0.53$ ($n = 17$). There was one clutch of 4, 12 clutches of 3, and 4 clutches of 2. Most clutch sizes (including all 2-egg clutches) were determined 2 to 4 days after incubation had begun, and it is unlikely that there was any loss of eggs between laying and inspection. However, one egg was lost from each of two nests between laying and hatching, and the overall clutch size of 2.82 may slightly underestimate actual number of eggs laid.

Egg colour was variable between females but eggs in a clutch were similar. Colour ranged from a white base with a few orange/brown spots, through being well spotted, to a solid orange/brown base with no spots. The small clutch size and lack of within-clutch variation suggested that only one female laid in a nest.

Mean size of eggs was: length, 20.13 mm (range 19.8-

20.6, $n = 4$); breadth, 14.73 mm (range 14.5-14.9, $n = 4$). Five eggs close to hatching weighed 2.18 g (range 2.1-2.3).

Length of each stage of breeding

The length of early stages of breeding was highly variable between groups and impossible to measure precisely because of the difficulty of detecting the first stages of nest building. Courtship behaviour, involving the primary male remaining close to the primary female and occasionally chasing her, often lasted for several weeks before nest-building began. Some pairs courted intensively at some times and less so at others, but never completed a nest or laid a clutch, especially in 1985/6.

Nests were built in 4-7 days. If more than about 10 days elapsed between completion of a nest and the initiation of laying, the nest was abandoned and either a new nest was built or the birds did not breed that year. In a few cases laying appeared to start immediately on completion of the nest but more usually a few days elapsed. Whiteheads appeared to need good weather for the pre-laying period. Rain squalls passed across the island every week or so in 1985/6 and all completed nests that had not been laid in at the time of a squall were abandoned.

Copulation began several days before the first egg was laid, and involved continuous chasing of the female by the male through large parts of the usual range of the birds concerned. One or two other birds sometimes followed, usually 1-3 m behind the chasing pair. The act of copulation took a few seconds only, but chasing lasted for up to several hours during which the pair copulated several times. This chasing behaviour is obviously different from any other behaviour exhibited by Whiteheads, and can be used to determine the pair's stage of breeding even if copulation is not seen.

Eggs were laid one per day (3 nests). We did not determine if there was any delay in completing the only 4-egg clutch.

The incubation period was 18.0 days (range 17-19, $n = 5$); the nestling period was 17.4 days (range 16-19, $n = 5$).

Fledglings could barely fly when they left the nest but gained dexterity quickly. After about ten days they were distinguishable from adults only by plumage differences and begging behaviour. Fledglings began feeding themselves after about ten days but were still often fed by the parents at 4-6 weeks. Whiteheads continued to feed juveniles occasionally throughout the winter and we have seen adults feeding banded juveniles in August, when they are 8 to 9 mo old.

Adult behaviour varied after a nest failed or was successful and may have depended on the size of the group.

The extreme case was a female (assisted by her mate and four secondaries) that completed building a second nest before the chicks left the first nest. Her second nest failed but she laid again in the first nest (the chicks had left about 2 weeks before) and was one of only two females who successfully raised two broods in one season during the study. Three other females initiated new nests while other birds fed their fledglings. However, many females did not re-nest even if they were with a large group, particularly in 1985/6.

Whole season breeding success and differences between years of study

Breeding success and differences between the two years for all focal groups are in Table 1, presented on a per pair basis and on a per nest basis. The data sets cannot be analysed statistically, as many of the same nests were used in calculating each value. None of the 1984/5 values was significantly higher than the equivalent 1985/6 value when analysed separately (t -tests, $P > 0.05$), although 1984/5 was clearly a better breeding season overall.

Breeding success was not high in either year with 1.38 and 0.73 chicks being fledged/group. Three chicks fledged from only one nest in each of the two years, and both families lost one chick within a few days. Thus, no group raised three chicks to independence from one nest and the most chicks fledged by one group in a season was four (from two nests).

TABLE 1 Whole season breeding success for focal groups of Whiteheads on Little Barrier Island in two years.

	1984/5 (21 groups)	1985/6 (15 groups)
Total no. nests	31	20
No. nests/group	1.48	1.33
Total no. clutches	25	15
Proportion of nests with clutches	0.81	0.75
No. clutches/group	1.19	1.00
Clutch size	3.0 ($n = 10$)	2.5 ($n = 6$)
No. successful* nests	16	6
Proportion of nests successful	0.52	0.30
No. successful/group	0.76	0.40
No. fledglings	29+	11
No. fledglings/group	1.38+	0.73
Proportion of groups: laid 2 clutches	0.29	0.13
2 successful nests	0.10	0.0

* A successful nest produced at least one fledgling.

+ No. of fledglings was not determined for one successful nest in 1984/5, so one was assumed for calculation of these values.

Details of known cases of predation and other causes of nest failure have been published elsewhere (McLean *et al.* 1986).

Effect of group size

All pairs that were obviously associated with one or more secondary individuals laid a clutch during both study years, and one pair with four secondaries fledged four chicks from two nests. Three pairs that did not appear to have secondaries did not lay and one of these apparently did not build a nest. These three pairs were monitored in the poor breeding year and it is possible that they were associated with neighbouring groups whose breeding failed, so that no co-operative behaviour was exhibited. In contrast, one pair without secondaries fledged four chicks from two nests in 1984/5. These preliminary data suggest that a relationship between group size and breeding success may exist but large sample sizes will be needed to demonstrate it.

One male who bred successfully in 1984/5 lost his mate during the winter and remained unmated for the 1985/6 summer, although he associated with two birds who were probably his progeny from 1984/5.

Discussion

The main characteristic of Whitehead nesting was cryptic. Most nests were well hidden and located high in the canopy. Females approached the nest quietly and alone (McLean 1987b), even though Whiteheads are usually extremely vocal and social. The only obvious breeding-related behaviours were song-post singing by males and chasing during copulation, and neither of these indicated the location of the nest site. Well concealed nests placed in the forest canopy, and cryptic behaviour near nests, may explain the continued success of Whiteheads on the New Zealand mainland in the presence of many introduced mammalian predators.

We suggest that the chasing behaviour that made copulation obvious operates as a signal among these group-living birds, ensuring that all members of the group (and possibly neighbouring groups) know that a pair is initiating breeding. The behaviour may further ensure the dominant status of the copulating male because other members of the group must be aware of who is inseminating the female. This hypothesis is suggested because copulation is usually a relatively quick and inconspicuous event in passerines (Birkhead *et al.* 1987; pers. obs.). Whiteheads are difficult birds to see because they feed in dense vegetation high in the canopy. It seems unlikely that copulation would be so conspicuous an event if the associated behaviour did not perform some function related to group dynamics.

Weather appeared to influence breeding success because nests were abandoned after rain squalls and weather was

more stormy in the poorer breeding year. However, even in the year of better weather breeding success was low — many groups made only one breeding attempt and 1.38 chicks were fledged/group. Comparisons with mainland populations of Whiteheads will need to be drawn before it can be determined if the characteristics documented here are typical of the species as a whole (which is island-endemic, being restricted to North Island) or if they are specifically tied to the co-operative breeding observed on Little Barrier Island.

Studies of the breeding biology of all three species of *Mohoua* are now either completed or underway. The following summary is taken from this study for Whiteheads (also see Gill & McLean 1986; McLean *et al.* 1987a); Cunningham (1985), McLean, *et al.* (1987b), and IGM (pers. obs.) for Brown Creepers; and Soper (1976), Elliott (1986) and Read (1987) for Yellowheads. All species occur in small flocks during the breeding season, and form larger flocks, often in association with other forest bird species, outside the breeding season. Whiteheads and Yellowheads are co-operative breeders, but Brown Creepers are not (although see McLean *et al.* 1987b). Co-operative breeding usually involves a pair with secondary birds, although more information is needed on who copulates with the primary female. Male Whiteheads and Brown Creepers guard their mates during building and laying. Most nests are built high in the canopy and are well hidden (Yellowheads are cavity nesters). The clutch size is 2-4 and many groups raise only one brood in a season. Thus, fecundity is low, particularly as each group may represent up to eight adult birds. All three species continue feeding juveniles for up to nine months.

Despite the relative prevalence of co-operative breeding among Australian birds, co-operative breeding is rare in the Pachycephalinae (Dow 1980; Howe & Noske 1980). Its prevalence in the Mohouini may be a response to New Zealand environmental conditions, or may reflect population densities achieved in New Zealand that are not found in Australian populations.

It is not yet known if *Mohoua* respond to low population densities with increased fecundity. Preliminary data on a low density population of Yellowheads in the Arthur's Pass region (Read 1987) suggest that they do not. If this result is substantiated in other populations, then population sizes may need to be large for long-term conservation of these species.

Acknowledgements

We thank L.P. Curthoys for field assistance, and A. & M. Dobbins for logistic support on Little Barrier Island. C.R. Veitch and co-workers caught and banded many Whiteheads. J.L. Craig, H.A. Ford, C.M. Miskelly, P.M. Sagar, and J.R. Waas, made many useful comments on the manuscript. This study was conducted under

permit from the Hauraki Gulf Maritime Park Board and the New Zealand Wildlife Service. Funding was provided by the New Zealand Lottery Board, the University Grants Committee, and the Auckland Institute and Museum.

References

- Birkhead, T.R., Atkin, L. & Lundberg, A. (1987). Copulation behaviour of birds. *Behaviour* **101**, 101-38.
- Bull, P.C., Gaze, P.D. & Robertson, C.J.R. (1985). *The Atlas of bird Distribution in New Zealand*. Government Printer, Wellington.
- Cunningham, J.B. (1985). *Breeding Ecology, social Organization and communicatory Behaviour of the Brown Creeper (Finschia novaeseelandiae)*. Unpubl. Ph.D. thesis, University of Canterbury, Christchurch.
- Dow, D.D. (1980). Communally breeding Australian birds with an analysis of distributional and environmental factors. *Emu* **80**, 121-40.
- Elliott, G. (1986). Mohua, a declining species. *Forest & Bird* **17**(3), 26-8.
- Emlen, S.T. (1984). Co-operative breeding in birds and mammals. In: *Behavioural Ecology, an Evolutionary Approach* (eds J.R. Krebs & N.B. Davies) pp. 305-39. Blackwell, Oxford.
- Gaze, P.D. (1985). Distribution of Yellowheads (*Mohoua ochrocephala*) in New Zealand. *Notornis* **32**, 261-70.
- Gill, B.J. & McLean, I.G. (1986). Morphometrics of the Whitehead *Mohoua albigilla* on Little Barrier Island, New Zealand. *N.Z. J. Zool.* **13**, 267-71.
- Howe, R.W. & Noske, R.A. (1980). Cooperative feeding of fledglings by Crested Shrike-tits. *Emu* **80**, 40.
- Johnson, D.H. (1979). Estimating nest success: the Mayfield method and an alternative. *Auk* **96**, 651-61.
- Macarthur, R.H. & Wilson, E.O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton.
- McLean, I.G. (1987a). Working with Whiteheads (*Mohoua albigilla*) and their nests. *Mauri Ora* **14**, 71-6.
- McLean, I.G. (1987b). Response to a dangerous enemy: should a brood parasite be mobbed? *Ethology* **75**, 235-45.
- McLean, I.G., Gill, B.J. & Curthoys, L.P. (1986). Mortality, interference, and injury at Whitehead nests. *Notornis* **33**, 266-68.
- McLean, I.G., Wells, M.S., Brown, R., Creswell, P., McKenzie, J., & Musgrove, R. (1987a). Mixed-species flocking of forest birds on Little Barrier Island. *N.Z. J. Zool.* **14**, 143-47.
- McLean, I.G., Dean, S. & de Hamel, R.J.B. (1987b). Co-operative breeding in Brown Creeper? *Notornis* **34**, 223-24.
- Mayfield, H.F. (1961). Nesting success calculated from exposure. *Wilson Bull.* **73**, 255-61.
- Mayfield, H.F. (1975). Suggestions for calculating nest success. *Wilson Bull.* **87**, 456-66.
- Oliver, W.R.B. (1955) *New Zealand Birds*. Reed, Wellington.
- Read, A.F. (1987). The breeding and flocking behaviour of Yellowheads at Arthur's Pass National Park. *Notornis* **34**, 11-8.
- Sibley, C.A. & Ahlquist, J.E. (1987). The relationships of four species of New Zealand passerine birds. *Emu* **87**, 63-6.
- Soper, M.F. (1976). *New Zealand birds*. Whitcoulls, Christchurch.
- Woelfenden, G.E. & Fitzpatrick, J.W. (1984). *The Florida Scrub Jay; Demography of a cooperative-breeding Bird*. Princeton University Press, Princeton.