

DISPERSAL FROM NATAL TERRITORIES AND THE ORIGIN OF COOPERATIVELY POLYANDROUS BREEDING GROUPS IN THE BROWN SKUA¹

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Abstract. A study of the natal dispersal and first breeding of banded fledglings was carried out on a small population (~235 birds) of cooperatively polyandrous Brown Skua (*Catharacta lonnbergi*) on the Chatham Islands in order to determine the relatedness of the members of breeding groups. Since 1977, all fledglings on Mangere and Rangitira islands have been banded each year and their parents and natal territory recorded. One hundred and one chicks were later documented breeding, 92 of which had full natal history. Mean age at first breeding was 8.03 years and is similar to other skua species. Mean age of first breeding for males was 8.30 years and females 7.74 years. Fledglings dispersed for breeding throughout the Chatham Islands; none has been recorded breeding on other island groups in the New Zealand region. Young birds when first breeding joined established breeding units (53% of birds) or formed entirely new breeding units (47% of birds). Seventy-seven began breeding in pairs compared with 24 in cooperative groups. Only 6 of the 92 known-identity birds settled on their natal territories when first breeding, and just 1 joined a parent in a cooperative group. One pair comprised siblings. I conclude that Brown Skua cooperatively breeding groups do not comprise close relatives. This cooperative system stands in contrast to the more usual ones involving family members.

Key words: *Brown Skua*, *Catharacta lonnbergi*, *Chatham Islands*, *cooperative breeding*, *natal dispersal*, *philopatry*, *polyandry*.

INTRODUCTION

Great Skuas (Stercorariidae) breed at high latitudes in both the Northern and Southern hemispheres. In nearly all of this range, they are apparently monogamous, but on New Zealand, Australian, and Indian Ocean islands, cooperatively breeding Brown Skuas (*Catharacta lonnbergi*) are relatively common with two or more cobreeding males sharing a single female.

The earlier intense debate on the evolution of cooperative breeding polarized into two broad hypotheses in which selection for cooperative breeding was thought to be favored through either constraints to breeding independently or the benefits of philopatry. Because of constraints to breeding independently, such as absence of breeding habitat or shortage of mates, birds staying on the natal territory and helping to rear kin are selectively advantaged (Emlen 1982). In contrast, the "benefits of philopatry" hypothesis (Stacey and Ligon 1987, 1991) suggests that there are intrinsic benefits in remaining on the

natal territory, in gaining experience or knowledge of the habitat, and in the prospect of obtaining a local quality territory, that outweigh the benefits of dispersing with its uncertainties and risks. Recently these competing models have been reconciled within a delayed-dispersal threshold model incorporating both intrinsic benefits and extrinsic constraints (Koenig et al. 1992, Emlen 1994).

These models, with their emphasis on delayed dispersal from the natal territory, do not apply to Brown Skuas. All young skuas disperse and "float" for some years before breeding (Furness 1990, Klomp and Furness 1992, E. C. Young, unpubl. data) so that the formation of a cooperatively breeding family unit (Emlen 1994) through delayed dispersal, which is central to these models, does not occur.

Explanations for cooperative breeding need to take into account the dichotomy that exists among cooperative species between those in which the social units are close kin, typically parents and offspring, and those in which the members are unrelated. In the first case, kin selection incorporating both descendent and non-descendent kin (Brown 1987) may be postulated as a factor in the evolution of cooperative breed-

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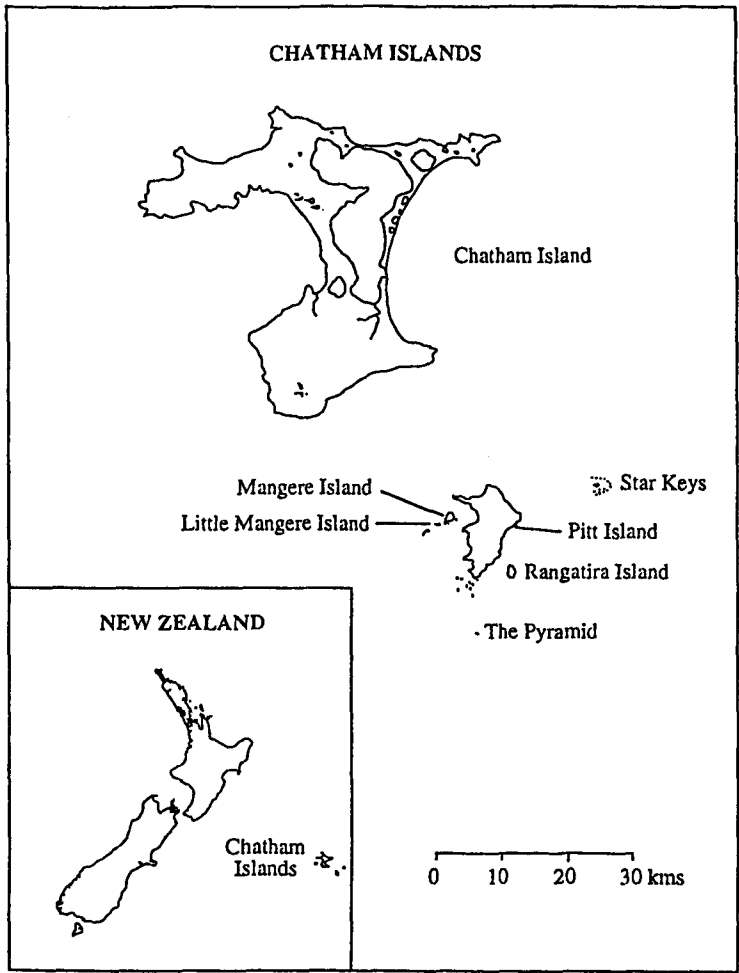


FIGURE 1. The location of the main islands with breeding skuas within the Chathams archipelago. Rangatira and Mangere islands, lying to the east and west of Pitt Island, respectively, contained the main study populations.

ing. In the second case, where close kin relationships do not exist in the groups, evolutionary advantage needs to be sought through classical direct selection. Thus, information on natal dispersal and recruitment into breeding groups is crucial for indicating the degree of relatedness of the members of the cooperatives.

Brown Skuas breed on all of the smaller islands of the Chatham archipelago (44°S, 176°W) (Fig. 1). Most occur on Mangere Island (~25 breeding units) and Rangatira Island (also known as South East Island) (~45 breeding units). About 12 (17%) breeding units are cooperatively breeding groups. Most groups are trios, with two males and a single female (Millar et al. 1992), but there have been two groups of

four adults with three males and a female, one of five adults, with a female and four males, and one of seven adults, with again a single female. Cooperatively breeding groups are very stable with some persisting unchanged since banding commenced in 1977. Most pairs and groups produce two eggs and many raise both chicks. Because the adults may survive over many years, each chick usually has several full and half siblings in the population. In general, the per capita success of males is lower in groups than in pairs (Hemmings 1989a, Young 1994).

All birds in cooperative groups carry out territorial defense, forage for the group, and participate in breeding. In addition, in cooperative groups with two chicks, the young may be fa-

thered by one of the males alone or by two of them in any year, and parentage may change from year to year for an individual group (Millar et al. 1994). During the breeding season these skuas feed almost exclusively on burrowing petrels. Some territories contain all the food needed, others lack food entirely (Young et al. 1988).

The cooperative breeding system of skuas on these islands is nonetheless unusual. It occurs together with the alternative strategy of floating. None of the young birds stay on the natal territory beyond the first season and the territories are largely abandoned over winter (Hemmings 1989b). Cooperative groups occur equally on territories with and without food, so that the incidence of cooperative breeding is independent of this important measure of habitat quality.

The main objective of the present study was to determine the identity and kin relationship of birds in breeding pairs and cooperative groups by following the movement to breeding status of young birds banded on the natal territory. If cooperative groups comprise close kin, this should be evident in the recruitment of offspring and siblings into breeding groups. Young skuas must exhibit very precise natal philopatry to the parental territory, rather than merely to the general natal area, in order that kin groups can form through philopatry. Moreover, for cooperative groups to develop comprising parents and grown offspring, the parents need to survive on the natal territory for at least five to eight years to allow the offspring to mature and return to the territory. Kin groups also might occur among siblings, not necessarily involving natal-territory philopatry. In either case, tracking the recruitment of known-identity skuas into the breeding population should establish the probability of occurrence of cooperative groups of close kin.

A second aim was to determine whether the skuas on the Chatham Islands exist as a single interbreeding population or as localized sub-populations on different islands in order that the extent of inbreeding might be appreciated. Because it is now possible to sex skuas accurately (Millar et al. 1992), it has been possible to compare the dispersal behavior of males and females, with implications both for understanding the population structure on the individual islands and the composition of each breeding unit. Finally, age when first breeding was determined. These statistics, when compared with those of other skua populations, could be expected to in-

dicate to what extent the Chatham birds were delayed in breeding. Significant difference in the ages of each sex when first breeding could well be the consequence of a biased sex ratio among the young birds.

METHODS

The skuas on Mangere and Rangatira islands have been studied since 1974 (Young 1978, 1994). Large-scale banding of adults and chicks began in the 1977–1978 season. In total, 837 chicks have been banded on Rangatira Island and 394 on Mangere Island to the end of the 1995–1996 breeding season. Apart from two seasons (1977–1978 and 1978–1979) in which 53 chicks were banded by others, all chicks each year have been unambiguously identified with their natal territory and parents.

In each year at least one visit was made to the islands when all the chicks of the season were banded and measured. Skuas are such large birds and their nests so well advertised that the surveys were easily done. Few if any breeding birds were missed in surveys. In these isolated, small-island habitats the problems of long distance detectability of dispersal reviewed by Koenig et al. (1996) are largely negated. Virtually all dispersal was recorded. Most visits were made during December, coinciding with the time the first of the chicks fledged. Adults were caught by hand net when flying at the intruder, by radio controlled clap-net set out on the territory, by cannon net, or by spot-lighting at night. The majority of birds in established breeding units can be sexed using morphometrics—females are usually larger and heavier than males—but the size ranges overlap significantly so that discrimination from measurements and weights alone is impossible in a fair proportion of breeding units. It was not until the precise sexing of both chicks and adults was achieved through the discovery of sex-specific markers within the DNA minisatellite profiles of these birds (Millar et al. 1992) that the sexes of all birds in groups could be established. This method for sexing these skuas has been used routinely since the 1987–1988 breeding season.

The analysis of natal dispersal and recruitment is based upon the records of 102 adult skuas which were banded as fledglings and were later recorded as breeding. Seventy-three of these adults were raised on Rangatira Island and 28 on Mangere Island. The remaining skua was

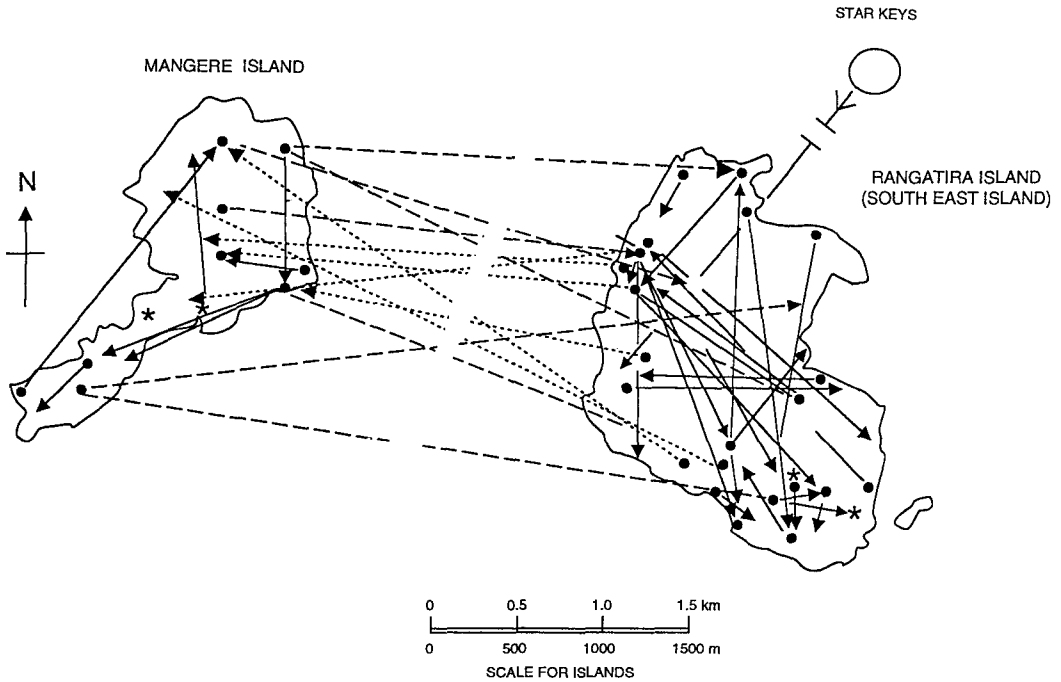


FIGURE 2. Natal dispersal of skuas from territories on Mangere and Rangatira islands. Records of 51 skuas up to the 1992–1993 breeding season. The tracks of dispersing birds are shown as arrows running from the natal to the breeding territory. Tracks of birds dispersing within islands are shown as complete lines; those changing islands as broken lines. Birds settling on natal territories are shown as asterisks (*).

banded as a fledgling on Star Keys but bred on Rangatira. For 93 skuas the natal history of breeding season, territory, and parents was precisely known; for the remaining 9 skuas only breeding season and natal island was known. The records of this latter group are included within the data on breeding age and recruitment into breeding groups but not on dispersal. Statistical analyses were undertaken using Statview 512+. Means are reported \pm SE.

RESULTS

DISPERSAL FROM THE NATAL TERRITORY

There are three possible dispersal paths for these skuas: to other island groups, to different islands within the Chatham Islands, and within the natal island. To date no skua banded on the Chatham Islands has been reported from any other island group. The Antipodes Islands, over 650 km distant, are the closest major breeding area, but two recent expeditions there failed to record any banded skuas among the breeding birds. Of the 73 skuas fledged on Rangatira, 58 (79.6%) first bred there, showing island philopatry, and 15

first bred on Mangere Island. Of the 28 skuas raised on Mangere Island, 21 (75%) first bred there and 7 dispersed to Rangatira. Thus, 22 birds (22% of those breeding) changed islands to breed. The proportions of fledglings raised on Mangere or Rangatira islands and dispersing to the other island to breed were not significantly different (for all chicks $\chi^2_1 = 0.2$, $P > 0.5$, $n = 101$). Dispersal from the natal territory to the breeding territory is illustrated in Figure 2 for 51 skuas up to the 1992–1993 season.

Natal dispersal, graphed as the number of territories moved between the natal and breeding territories along the direct flight path, is shown in Figure 3. On Mangere Island, the territories essentially occupy the whole area of the island and boundaries adjoin so that movement can be recorded by counting territories along a direct line joining them. On Rangatira Island, however, the territories are largely confined to the coastal perimeter so that it is possible to record distances moved in two ways: as distance and numbers of territories around the coast, or as distance and number of territories by direct flight line track-

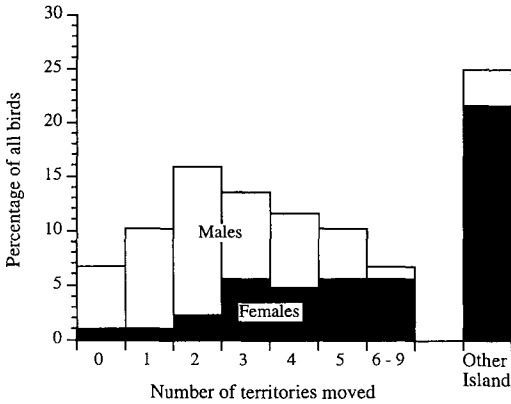


FIGURE 3. Natal dispersal measured as number of territories moved along the shortest flight path between the natal and breeding territories. Percentage of birds in each category ($n = 88$).

ing across the central forest. For most birds these different tracks gave very different measures of dispersal with the direct flight tracks across the forested interior traversing appreciably fewer territories. However, the maximum number of territories on direct flight lines is similar: eight on Mangere, nine on Rangatira.

The figure shows that about 20% of birds settled in the natal territory or its immediate neighboring territory and that 60% settled within four territories distant. This result, however, is biased by the records of skuas moving across Rangatira Island, which, although movement was to a neighboring territory on this strict definition, was usually to an entirely different habitat and to a separate breeding cluster of territories. The apparently strong natal-area philopatry shown in Figure 2 is not as evident when philopatry is judged instead by rates of return to each of the eight clusters of territories, isolated by forest or empty coastline, that occur on these islands. Only 30 of 92 (32.6%) skuas returned to their natal cluster, a much lower level of area philopatry than indicated in the figure.

Six of 92 birds (6.5%) settled within the natal territory or in its expanded area since they fledged. On average there were 65 territories available. From the binomial distribution the expected random probability of 6 or more chicks of 92 settling by chance on their natal territories is 0.0006, indicating significant departure from random. However, the observed probability of 0.065 (95% confidence interval = 0.024 to 0.137) shows that this is not a strong trend and

only a small proportion of birds (between 2.4% and 13.7%) would be expected to settle there.

Overall, females settled farther away from the natal territory than males. Most birds (18 of 21) recorded changing islands for breeding were female. The difference between the two sexes in dispersal distance is significant (Mann-Whitney *U*-test for dispersal measured by direct flight path, $Z = 5.1$, $P < 0.01$, $n = 46$ males, 41 females) and remains significant even if the movement between the islands, with its extreme female bias, is omitted and analysis is confined to the dispersal of each sex within islands (Mann-Whitney *U*-test, $Z = 3.4$, $P < 0.01$, $n = 43$ males, 23 females).

THE RECRUITMENT OF KNOWN IDENTITY BIRDS INTO BREEDING UNITS

Almost equal numbers began breeding in established breeding units (53 birds of 101), replacing or augmenting breeders already there, and in entirely new breeding units (48 birds), either through the replacement of all the original breeders or through claiming new territories. Seventy-seven of the 101 birds began breeding in pairs and only 24 began in cooperative groups.

To establish cooperative groups on the natal territory comprising parents and offspring, the parents have to survive during the several years the offspring are maturing as floaters. Survival of parents to the time breeding began was determined for 86 fledglings. There was only a moderate survival of parents across this interval. For only 27 (31%) of these skuas were both parents (for pairs) or three parents (for trios) still present on the natal territory when breeding began. None of the parents had survived for 21 (24%) skuas and only one parent had survived for the remaining 38 (44%). Taken together with the low incidence of natal territory philopatry, it is not surprising that there were few records of these skuas breeding with close relatives. Only five of these skuas were documented as doing so. Three were in pairs with a surviving parent and one was in a short-lived cooperative group after joining one of the parents which had already remated. None of these skuas joined with siblings to form cooperative coalitions, but there was a single pairing formed between full siblings from different years.

The role of pairs and coalitions of adults in claiming territories can be examined by focusing

upon new breeding units. During the study 16 new territories were established. Ten of these were established by pairs of birds and six by coalitions of three or four birds. Over the same period, 12 long-established territories (all with pairs) had a complete change of occupying birds; the birds of one season replaced by an entirely new set of birds in the following season. Eight of these territories were taken over by pairs and four by coalitions of three to five birds. In total, of 28 new breeding units established throughout this population during the study, 18 were by pairs and 10 by cooperative groups. The proportion of new breeding units established by groups is significantly greater than their representation among the breeding population as a whole ($\chi^2_1 = 3.96, P < 0.05$).

AGE WHEN FIRST RECORDED BREEDING

There were 96 birds whose age of first breeding was precisely known and for which sex was determined from morphometrics, sex-linked bands on DNA profiles, or association with others unequivocally sexed. The youngest birds found on established territories were 4 years old, but the youngest birds found participating in breeding were 5 years old. The oldest bird recorded as a first breeder was 14 years old. The mean age of these birds when first recorded breeding was 8.03 ± 0.21 years, $n = 96$. Within this sample, females on average bred earlier than males: females 7.74 ± 0.32 years, $n = 46$; males 8.30 ± 0.27 years, $n = 50$. This difference is not significant ($t_{94} = 1.36, P = 0.18$).

DISCUSSION

DISPERSAL

There are two important results from this analysis of natal dispersal. First, the Chatham's skuas form a single interbreeding population. Second, although a fair proportion of birds showed local area philopatry, only a very small number settled within the natal territory itself. The majority of birds moved widely within the limited distance available to them on these small islands, or changed islands for breeding. In judging the extent of this dispersal it needs to be remembered that the maximum distance the skuas could disperse for breeding on each island is no more than 2 km, covered by nine territories on a directly measured path. Moreover, the results are biased towards natal area philopatry because on Rangatira Island, where the territories are

confined to the coastal fringe, movements from one side to the other, although measuring over a kilometer, were recorded as dispersal to a neighboring territory.

The overall pattern of distance moved for breeding conforms much more closely to that portrayed by Zack (1990) for singular breeding species than for cooperatively breeding ones. This difference from other cooperative species is not unexpected, taking into account the fact that these skuas have been away from their natal territory for a number of years before breeding. More surprising is the finding that although the birds float for some years, and might well pair within the nonbreeders' club, i.e., an aggregation of nonbreeders which use traditional resting areas on the two islands (Furness 1987), females appear to have settled farther away from the natal territory for breeding than males. The strongest measure of this difference is in the preponderance of females among the birds changing islands for breeding. Eighteen of the 21 birds recorded moving between Rangatira and Mangere islands for breeding were female. But even within islands, females settled farther away than males. Although female-biased dispersal is well documented in birds (Greenwood 1980, Greenwood and Harvey 1982, Russell and Rowley 1993), it was not expected in this population where the young skuas claim breeding territories from the "neutral" location of the club site rather than from their natal territory.

THE WAYS YOUNG BIRDS BEGAN BREEDING

This study has documented the variety of ways that young birds were recruited into the breeding population. Equal numbers began breeding by joining established breeding units as through establishing new territories. New territories were claimed by individuals and pairs more commonly than by cooperative groups of skuas, indicating that cooperative coalitions were not needed to claim breeding areas as hypothesized for the Galápagos Hawk (*Buteo galapagoensis*) (Faaborg 1986, Faaborg and Bednarz 1990) or Acorn Woodpecker (*Melanerpes formicivorus*) (Koenig and Mumme 1987). However, the disproportionately high frequency of cooperative coalitions among new territory holders compared to their number in the population as a whole does suggest that coalitions have an advantage over pairs when gaining territories.

AGE WHEN FIRST BREEDING

The significance of these data is for assessing the degree that breeding is delayed as an indirect measure of habitat saturation or other breeding constraints in this population. Unfortunately, there are no data on the age of first breeding for Brown Skuas in other populations, with or without cooperative groups, with which comparison can be made. However, the mean age determined for this population is almost identical to that found for the Great Skua (*C. skua*) (7.9 years, $n = 18$; Klomp and Furness 1991) and within the range given for the South Polar Skua (*C. mac Cormicki*) by Ainley et al. (1990), who found median ages for three seasons of 8, 8, and 7 years, respectively. Neither of these skuas breeds cooperatively. The similarity in breeding age in all three species suggests that the Chatham Island skuas have not had their breeding deferred more than is common for the genus, but to be conclusive, comparison should be of conspecific populations, preferably living within the same environmental conditions. However, there is on this basis no evidence that the Chatham Island skuas have atypically delayed breeding.

SIGNIFICANCE OF THE RESULTS ON NATAL DISPERSAL FOR EXPLANATIONS OF COOPERATIVE BREEDING IN THIS POPULATION

The most important conclusion from the research on Brown Skua dispersal is that the birds in the cooperative breeding groups are unlikely to be closely related. Only 1 of 23 birds (for which there were complete natal records) that joined a cooperative group was an offspring or sibling of other birds in the group. Moreover, in this single case the pairing lasted for only one season.

At first sight the sample of known-identity birds followed in this study seems too small to define relationships within cooperative groups conclusively, but these records in fact pertain to a high proportion of the groups established during the research period. Twenty cooperatively breeding groups formed between the 1983–1984 season, the first year that banded chicks would have been old enough to breed, and the 1995–1996 season. The 23 known-identity skuas joining cooperative groups were associated with 14 (70%) of these groups. At least for this high proportion of new cooperative groups, only one of them contained close relatives.

Brown Skua cooperative breeding provides a further example of cooperation among nonkin. Together with Dunnocks (*Prunella modularis*) (Davies 1986, Davies and Houston 1986) and Galápagos Hawks (Faaborg and Patterson 1981, DeLay et al. 1996), they represent a special category of cooperative systems in which the cooperative groups originate independently of the natal territory or parents, and neither philopatry nor delayed dispersal occur. These are, however, rather simple breeding systems. In more complex ones, such as Acorn Woodpeckers, there is both cobreeding among relatives and nonrelatives and helping from immatures (Koenig and Stacey 1990).

Although there is a developing consensus about the evolution of cooperation among kin, which incorporates both constraints to breeding and the benefits of philopatry (Koenig et al. 1992, Emlen 1994), explanations for cooperation among unrelated birds are less developed and a number of disparate factors have been invoked. Theory for the evolution of cooperation among close relatives usually revolves around the concept of kin selection (Brown 1987), which cannot play a role in cooperative systems comprising nonrelatives. When nonrelatives are helping without mating, neither current direct nor indirect components of fitness occur. Explanations for cooperative breeding in these species is more likely to rely on classical direct selection rather than kin selection, with the selective advantage of cooperation deriving from enhanced lifetime productivity rather than from any one breeding occasion.

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