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**COOPERATIVE BREEDING IN THE SKUAS
OF THE CHATHAM ISLANDS**

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A thesis submitted in partial fulfilment of the requirements

for the degree of

Doctor of Philosophy in Zoology

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"At length I was no longer able to resist the conclusion that the married 'pair' consisted not of two hens and a cock, but of two cocks and a hen..... So rigid, however, is the human mind in regard to questions of sex that for long Byron's sneer was of frequent occurrence. I confess that at first I spent time in attempting to discover which was the wise Catullus and which his friend Hortensius. That I was never able to decide. It was, indeed, a decision impossible to determine, impossible for long to contemplate in regard to a union so evidently proper according to Sea Hawk habit and custom..... Exclusive possession of the female as mistress, companion, or nurse is the ideal of man. It is not the ideal of the Sea Hawk."

H. Guthrie-Smith. Bird Life on Island and Shore. 1925

"Still further to the south, on Solomon and Big South Cape Islands, Skuas breed in great numbers, and there about half of the nests have three birds in attendance."

E. Stead. The Life Histories of New Zealand Birds. 1932

"The phenomenon of three adult Skuas at a nest, each one apparently equally devoted to the chicks, has usually caused sceptical comment whenever I have mentioned the fact in Northern Hemisphere circles. Among New Zealand observers, however, this fact has been common knowledge for at least the last 40 years."

L.E. Richdale, Transactions of the Zoological Society of London 27: 11. 1965

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John Croxall, at the British Antarctic Survey, responded to my unilateral declaration of interest in skuas when I was in the Antarctic in 1980. By telex then, in person back in Cambridge from 1983, and subsequently, he has continued to encourage and kindly find time to comment upon manuscripts and ideas. I am most grateful.

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group was but a name on a map to me, and has continued as the ultimate source of hard-to-find documents on the sub-Antarctic islands. Where else could one ask a friend to check some details of an early 19th Century sealing expedition to the group, and receive a photocopy of the ship's manuscript log through the mail a week later! Thank you Bob Headland. In Auckland, I thank Flavia Clifford-White and the staff of the Biological Sciences Library at the University for help with their own collection and the inter-library loans system. The Library at the Auckland Institute and Museum was especially useful for its comprehensive collection of early New Zealand ornithological literature and its excellent (and apparently little known) collection of current European ornithological and behavioural journals. I thank the staff for their always friendly assistance, and for access to the second collection in their charge, the Ornithological Society of New Zealand Library. I also acknowledge the access to collections at the University of Canterbury Library.

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ABSTRACT

Hemmings, A.D., 1995. Cooperative Breeding in the Skuas of the Chatham Islands. PhD Thesis, University of Auckland, New Zealand.

Cooperative breeding, widely reported in birds, is found in <1 - 5% of territories in some populations of the Brown skua, Catharacta lonnbergi. In the New Zealand region, up to 30-50% of skua territories may be occupied by trios or larger groups. This study examines its occurrence at the Chatham Islands, east of New Zealand. Here 16% of territories are occupied by trios and 2% by groups. All members of skua trios and groups participate in sexual and other breeding activity, and the associations are thus communal. Sexual discrimination of breeding birds by morphometric measurements shows that all communal groups known since 1978-79 have been polyandrous. These groups are long-lived associations, some of which are known to have persisted for at least 14 years. Trios are as long-lived and stable as pairs, and birds on communal territories do not move from them even when an appropriate-sex space becomes available on an adjacent pair territory. The members of trios are not close kin. All members of communal associations participate in territorial defence and chick rearing. In trios, the males appear to be equals, although in any one year the actual paternity of offspring may reside with only one of them. Overall reproductive success for Chatham Island skuas is high, for both pairs and communal groups, compared with other populations. However, communal trios and groups have lower reproductive success than pairs even over a 10 year period, particularly when considered on a per adult basis. Furthermore, no improvement in chick 'quality' is discernible. Unusually for skuas, the breeding population at the Chatham Islands is non-migratory. Skuas are present on their breeding territories during the winter, and exhibit characteristic territorial and agonistic behaviours, albeit at lower intensity than during the breeding season. It is

suggested that communal breeding in this skua population is not adaptive per se, but a secondary consequence of year-round residence. This is a departure from the conventional resolution of communal breeding. Residence is facilitated by benign climatic conditions and year-round prey availability. When territory space becomes available outside the breeding season, in a small number of cases more than a pair of skuas are able to establish themselves. Thereafter, trios and larger groups persist and behave in the same manner as pairs. The flux between trios and pairs when birds are lost is determined, in part, by the sex of that bird. Thus a trio which loses its one female will 'acquire' a replacement female and persist as a trio, whereas a trio which loses one of its two males will thereafter continue as a pair.

Keywords: Cooperative breeding, communal breeding, polyandry, Stercorariidae, skuas, skua trios, skua behaviour, skua breeding, Chatham Islands

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NOTE ON THE FORMAT OF THE THESIS

This thesis has been written as a series of interlinking papers, following a style widely used in zoological theses at the University of Auckland since that of I.G. Jamieson in 1986*. A number of the Chapters presented here have already been published in international journals, and others have recently been submitted. The journal locations for Chapters are indicated on each title page. Citations in the text are to the appropriate published or submitted paper, rather than to a Chapter number. All of the Chapters, and the corresponding papers, are the sole authorship of the candidate.

The strengths of this approach are, one hopes, that the specific areas of enquiry within each Chapter are subjected to wider peer review, must be presented as intelligible pieces of work in their own right, and that research findings and conclusions are more effectively placed in the public and professional domain. In addition, in my own experience, it is easier to use a work which is organised into self-contained sections, than a single unleavened tome. The 'drawback', as Jamieson pointed out, is that this style inevitably results in some repetition. Certain themes are repeated in introductory sections, as are some conclusions which are developed over several Chapters. Naturally there is also repetition of methodological information, references and acknowledgements. I trust that these minor disadvantages are outweighed by the advantages of this style of presentation.

* Jamieson, I.G. An Epigenetic study of the Social Behaviour of the Communally Breeding Pukeko (*Porphyrio p. melanotus*). PhD Thesis, 1986.