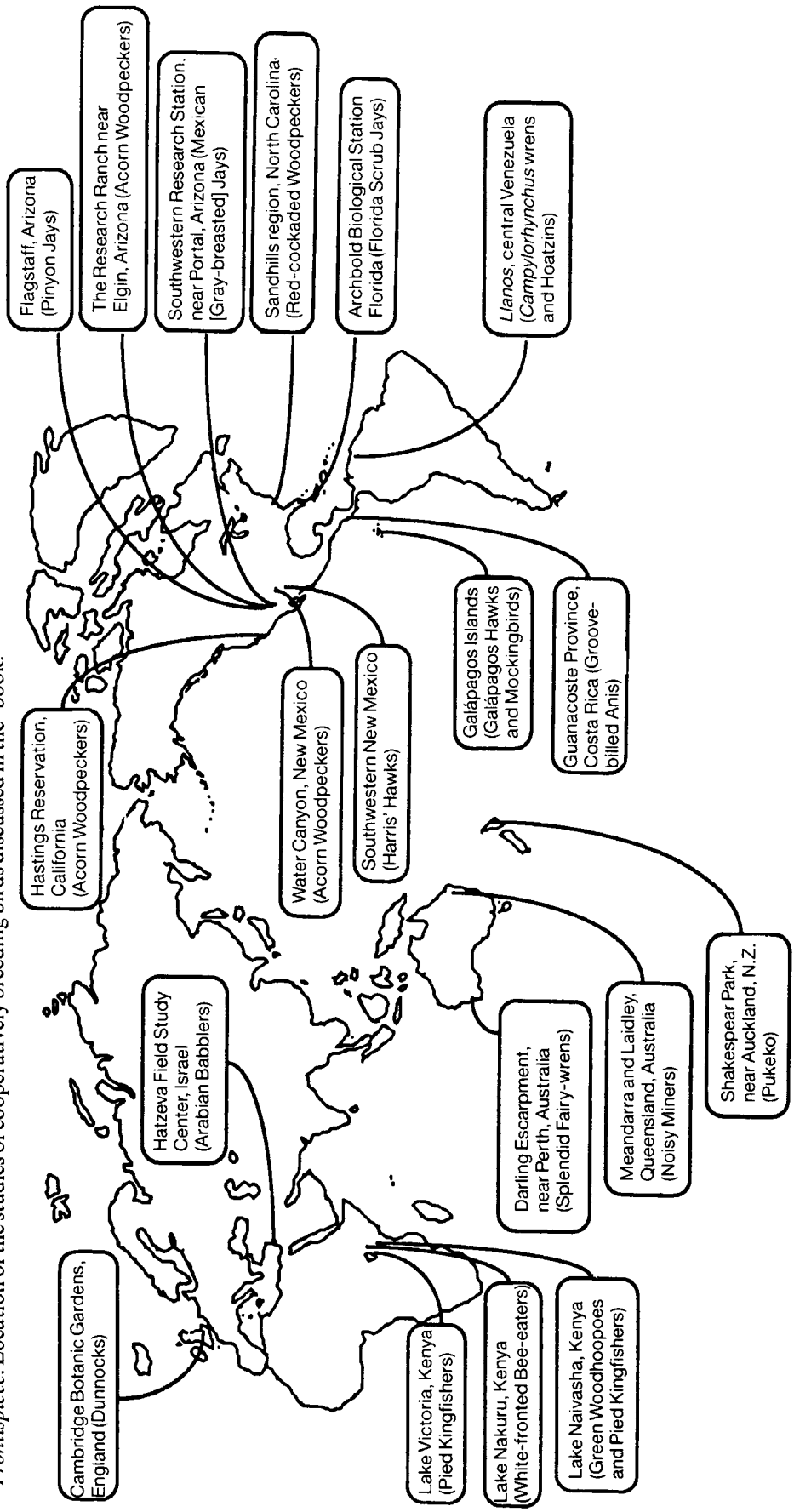
COOPERATIVE BREEDING IN BIRDS:

long-term studies of ecology and behavior



Frontispiece. Location of the studies of cooperatively breeding birds discussed in the book.

COOPERATIVE BREEDING IN BIRDS:

long-term studies of ecology and behavior

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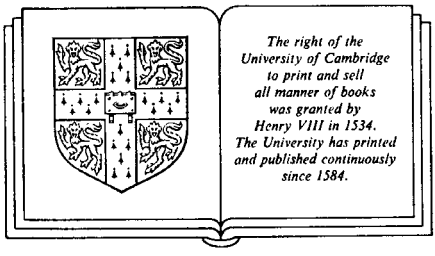

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INTRODUCTION

P. B. STACEY AND W. D. KOENIG

Cooperative breeding is a reproductive system in which one or more members of a social group provide care to young that are not their own offspring. The aid-givers may be non-breeding adults, in which case they are usually called 'helpers' or 'auxiliaries', or they may be co-breeders, and share reproduction with other group members of the same sex. Although the care given usually includes providing food, it may involve other parental-type behaviors as well, including territorial defense, nest or den construction, incubation and defense against predators.

Cooperative breeding is relatively rare: it is currently known to occur in about 220 of the roughly 9000 species of birds, and a smaller number of mammals and fish (for recent compilations, see Emlen 1984; Brown 1987). However, several theories of cooperative breeding suggest it should occur most frequently in tropical and warm temperate habitats, rather than in cold temperate or highly seasonal areas (see e.g. Fry 1972; Brown 1974; Stacey and Ligon 1987), and the reproductive biology of most species in these regions is presently unknown. In some habitats, such as the savannahs and woodlands of Australia, cooperative breeding is very common among some groups such as ground-foraging insectivorous birds (Ford *et al.* 1988). It also appears frequently in certain taxonomic groups, such as the New World jays (family Corvidae: Hardy 1961, Hardy *et al.* 1981), the Old World babblers (family Timaliidae: Gaston 1978), mongooses (subfamily Herpestinae: Rood 1984), and some primates such as tamarins and marmosets (family Callitrichidae: Terborgh and Goldizen 1985; Sussman and Garber 1987).

Although the existence of helpers at the nest has been known for many years (Skutch 1935), cooperative breeding has been studied in detail only over the last two decades. There were a few good early studies of

cooperatively breeding birds, particularly those of Davis (1942), Robinson (1956), Selander (1964) and Rowley (1965). However, a major difficulty was the absence until 1964 of an adequate theoretical framework within which the evolution of the apparently altruistic behavior of helpers could be understood. For example, one of the most widely mentioned early examples of alloparental care involved a photograph of a Northern Cardinal (*Cardinalis cardinalis*) feeding goldfish in a small pond (see e.g. Welty 1975). It was difficult to see how such behavior could be adaptive. The most reasonable explanation was simply that the cardinal had recently lost its own nest, and because such a bird would be highly motivated to feed young, it had simply been responding to the most available stimulus (as often occurs in domestic sheep and cattle). Although there were other examples of helping that did involve members of the same species, the origin and relationships of the animals to each other were usually unknown. It seemed plausible that many of these cases also involved 'mistakes', and the phenomenon of helping was generally relegated to the back shelf of biological curiosities.

Cooperative breeding reappeared briefly in 1962 when it was discussed by Wynne-Edwards in *Animal Dispersion in Relation to Social Behaviour* (1962), as a possible example of a self-limiting reproductive behavior. He hypothesized that for the Acorn Woodpecker (*Melanerpes formicivorus*: see Chapter 14), group storage of acorns and other food constituted an 'epideictic' display, which allowed the local population of woodpeckers to measure the amount of available resources, and, if they were too low, would lead some individuals (the helpers) or entire groups to forgo breeding for that season. Since such behavior seemed to require a form of group selection for its evolution, and the mechanisms by which group selection could occur in natural populations were not well understood, cooperative breeding again disappeared from the spotlight.

It was not until Hamilton (1964) and Maynard Smith (1964) developed the theory now referred to as kin selection that there was a firm basis upon which the empirical study of cooperative breeding could begin. These authors argued that the fitness of each individual is determined by the total number of genes present in following generations that are identical by descent with its own. Copies of genes could arise either directly through the production of the individual's offspring (the usual or 'direct' component of inclusive fitness: Brown and Brown 1981) or indirectly, through the reproduction of the individual's relatives (the 'indirect' component). Kin selection was applied initially to the evolution of the sterile, or non-reproductive, worker castes in social insects, and helping at the nest among

vertebrates was not mentioned in either initial article. However, it soon became apparent that helpers in birds and mammals might constitute an analog of worker castes in insects. In both cases, certain individuals appeared to act altruistically: they appeared to sacrifice their own individual reproduction to help to care for the offspring of others.

By the mid 1970s, a number of studies had been started on cooperative breeding, most dealing with birds. Although relatively rare, this breeding system presented excellent opportunities to test various hypotheses about the evolution of cooperation and competition in social behavior. It has been of wide interest therefore to both the specialist and to the general public. Several fundamental questions had to be addressed for each species. First, what was the origin of the 'extra' group members? Individual marking, usually by color banding, quickly showed that in most species (but not all) helpers are usually the previous offspring of the breeding pair that had remained in their natal group or territory. Once this had been demonstrated, the problem then became: why, on reaching physiological maturity, would the young fail to disperse and breed on their own, as they do in most other species? Are there specific ecological conditions that would lead to juvenile philopatry in some species but not in others? This failure to disperse was particularly puzzling, since by remaining at home, most helpers are not able to breed. (It had originally been suggested that helpers are physiologically immature and not capable of individual reproduction, but this has been shown to be incorrect for almost all species studied.)

The second key question is closely related to the first: given that a helper does stay at home, why would it provide care to young that are not its own offspring? For those cooperative breeders that nest in colonies rather than in group territories, such as the White-fronted Bee-eater (Chapter 16) and the Pied Kingfisher (Chapter 17), the analogous question is: why would the helper associate itself with another breeding pair within the colony, and help to raise that pair's offspring? To the extent that finding and bringing food to the young (or other forms of alloparental care) require both time and energy, these behaviors may be costly to the fitness of the helper. Is there a compensating benefit that is derived from helping and that might outweigh the apparent costs of not dispersing and attempting to breed individually? Is helping really altruistic, or is it simply an extraordinary (albeit obscure) type of selfish behavior?

It is now clear that answering these questions requires a combination of long-term observations of individual behavior and population level analyses of demography and genetic structure based either on a cross-sectional

sample of many different groups observed over a short period of time, or, as more recently, on the histories of individual animals that are followed throughout their lifetimes. In addition, because this type of reproductive system has repercussions on almost all aspects of a species' biology, from physiology to social behavior and foraging ecology, studies of cooperative breeders have produced some of the most detailed portraits of free-ranging animal populations now available.

Although considerable progress has been made in our understanding of cooperative breeding, the chapters of this volume illustrate clearly that considerable controversy continues to exist, even for the basic questions posed above. There have been several general reviews of cooperative breeding (e.g. Brown 1978, 1987; Emlen and Vehrencamp 1983), as well as numerous theoretical papers on individual topics (e.g. Brown 1974; Gaston 1978; Woolfenden and Fitzpatrick 1978; Vehrencamp 1979; Koenig and Pitelka 1981; Emlen 1982*a*, *b*; Stacey 1982; Ligon 1983; Wiley and Rabenold 1984; Jamieson and Craig 1987; Stacey and Ligon 1987; Mumme *et al.* 1988; S. Zack, 1989, unpublished results). The primary literature for most species, however, is highly fragmented. Many studies have now lasted for 10, 15, or more years, and include several generations of helpers and breeders. Sufficient information is now available from many studies to begin testing the hypotheses and models of cooperative breeding using empirical data rather than simply relying on logical argument and selected examples. As editors, we felt that this was an opportune time for a volume in which researchers could summarize the central results of their studies in a single location.

Another important development is that a sufficient number of long-term studies on different species now exist to make it possible to undertake a search for common themes and patterns. To facilitate this process, we provided each contributor to the volume with a list of suggested topics to be included in their chapters whenever possible. The topics ranged from such basic ecological factors as the species' habitat requirements and foraging behavior, through patterns of social interaction and the group mating system, to various population-level parameters such as dispersal, reproductive success and survival. We also asked the authors to present specific and quantitative data whenever possible, and to provide several figures or tables that we believed would be most useful for interspecific comparisons. These included information on the distribution of group sizes throughout the study, the relationship between group size and reproductive success, and the stability of population numbers over all years of the study.

Not surprisingly, each study has focused on different aspects of cooperative breeding, and each has lasted for a different length of time. None of the chapters includes all of the suggested topics. However, most authors were themselves extremely cooperative, and provided extensive new analyses and unpublished data in their chapters.

We also suggested that each chapter should include a section in which the authors discussed what they believed to be the critical unanswered questions for their species and for the field of cooperative breeding as a whole. It is our goal that not only will this volume be a compendium of information about specific studies but that it will also serve as a source of new ideas and direction for students interested in research on cooperative breeding. The health of this field is indicated by the wealth of ideas and diversity of opinions found in these concluding sections.

There have been a large number of high-quality studies of cooperative breeding, and one of the most difficult problems we faced as editors was to decide which studies to include. It simply was not possible for the volume to contain all of them and still be of reasonable length. There are excellent studies of cooperative breeding in vertebrates other than birds, including a cichlid fish (Taborsky 1984), many mammalian carnivores (for reviews, see MacDonald 1983; Emlen 1984; Bekoff and Daniels 1984), and at least one rodent, the naked mole-rat, *Heterocephalus glaber* (Jarvis 1981). An intriguing possibility is that the social organization of many primates can be viewed as cooperative breeding (see e.g. Terborgh and Goldizen 1985; Sussman and Garber 1987). Finally, the behavior of many invertebrates, such as social spiders, might also fit the definition of cooperative breeding given above, although they also have not been considered as such traditionally.

Given the potential range of studies that could be included, we felt it necessary to limit the focus of the volume to a single group, birds. Birds have several advantages for testing hypotheses about cooperative breeding. Most species either nest in colonies or have small territories, and it is not uncommon to be able to obtain accurate data on 20 to 30 groups each year. This allows the researcher to examine the range of different social contexts that normally exists within any population, as well as to consider both the mean and variance of each demographic parameter. Birds are easily and permanently marked through banding, which makes it possible to follow individuals throughout their lives, even if they disperse from their natal groups or territories. Finally, most cooperatively breeding birds have relatively short generation times, and one or more complete generations can be included in a single 10 or 15 year study.

Because demography plays a central role in all current theories of cooperative breeding, we decided to emphasize long-term studies whenever possible, since these would be most likely to include the widest range of information about the biology of the species and would provide the most quantitative data for interspecific comparisons. This meant that we were unable to include many excellent studies, which, although of relatively short duration, have none the less made very important contributions to the field. The reader is referred to the text by Skutch (1987) and Table 2.2 of Brown (1987) for references to many of these studies.

Our second goal was to illustrate the great diversity that exists among cooperatively breeding birds. Although all species have individuals that act as helpers at the nest, it has become clear that cooperative breeding can and is expressed in an extraordinary number of different contexts. The classical picture of a single territorial pair with a small number of non-breeding helpers that are previous offspring is only the simplest. It is represented here by chapters on the Splendid Fairy-wren (Rowley and Russell), the Green Woodhoopoe (Ligon and Ligon), the Red-cockaded Woodpecker (Walters), the Arabian Babbler (Zahavi), the Hoatzin (Strahl and Schmitz), and *Campylorhynchus* wrens (Rabenold). We then include a series of chapters on New World jays, illustrating how variable cooperative breeding can be, even within the same taxonomic group. A very primitive form is represented by the Pinyon Jay (Marzluff and Balda). This species lives in large flocks and nests in loose colonies. Helping is restricted almost exclusively to yearling males, and then only in certain lineages (the most productive). The Florida Scrub Jay (Woolfenden and Fitzpatrick) is highly territorial and has single breeding pairs that may be assisted by one or a few helpers. Only males help after their first year, after which all females disperse. In the Gray-breasted or Mexican Jay (Brown and Brown) several pairs join together to defend a common territory. Each pair nests separately, and at least some helpers are believed to move between different nests. A similar system of plural nesting, but with occasional instances of two females laying eggs in the same nest, is also found in the Galápagos Mockingbirds (Curry and Grant). Joint breeding is also found in the Groove-billed Ani (Koford *et al.*), but here the females always lay their eggs together in the same nest. Since each bird feeds all of the young in the nest, one individual will be both a breeder and a helper for another's offspring at the same time. These groups also may contain unpaired birds, who act as 'typical' helpers.

Superimposed upon this diversity of spatial systems is a wide range of mating systems that can exist within the social unit. In most of the species

described above, breeding is restricted to one or more monogamous pairs. Many other patterns are possible. In the Galápagos Hawk (Faaborg), for example, groups consist of one female and several unrelated males, each of whom may mate with the female and presumably share parentage of the young. Offspring are not recruited into the group, but become non-breeding floaters until a new group forms. Another raptor, the Harris' Hawk (Bednarz), also occurs in multi-male groups, and was originally believed to be polyandrous as well. However, Bednarz's recent evidence indicates that the extra males are usually non-breeding yearlings that help primarily through cooperative hunting rather than actually feeding the young. In the Pukeko of New Zealand (Craig and Jamieson) and Acorn Woodpecker (Koenig and Stacey), not only can several males mate with one female, but several females may lay eggs in the same nest. Groups also usually include one or more non-breeding helpers as well. This combination of within-group polyandry and polygyny (or polygynandry) can produce extremely mixed parentage of the young in these species, and makes determination of individual reproductive success difficult. Perhaps the extreme example of variable mating systems is the Dunnock (Davies). These small birds exhibit an incredible combination of both spatial and reproductive patterns in the same population, including monogamy, polyandry, polygyny and polygynandry. Each spring new units may form, often in a combination different from that of the previous year. The ecological reasons behind this extraordinary pattern are just beginning to be unraveled.

Most of these species live and breed within all-purpose territories. Another group of cooperative breeders are colonial nesters. These include the White-fronted Bee-eater (Emlen), where individuals may also hold feeding territories away from the nesting colony, and the Pied Kingfisher (Reyer), where they do not. Helpers in these species join already established pairs at the colony, and they may play an important role in bringing food to the nest. An intriguing and somewhat intermediate form between the colonial and territorial species, and certainly the most complex system of cooperative breeding studied to date, is the Noisy Miner of Australia (Dow and Whitmore). Here, large numbers of birds occupy a common 'territory' that is defended from all other birds, including other species. Each colony is further divided into coteries, and within each coterie, females nest individually. A female can be helped by many different males, and each male may help a number of different females. (Pinyon Jay flocks, mentioned above, may represent a primitive form of this type of organization.) Although the colonial species are ecologically very different from territorial

ones, many of the same questions can be asked about the adaptive nature of cooperative breeding.

As this volume illustrates, the study of cooperative breeding is a dynamic and active field. All the puzzles posed by this type of breeding system are far from being solved. A central challenge is to understand the diversity of patterns described herein. Cooperative breeding has arisen independently in many different taxonomic lines and it can occur in a wide variety of habitats. Is there a single model that can explain the origin of this system, or is its occurrence in each species a unique event? New theories have recently been proposed, to explain both the ecological basis of philopatry among young birds and the selective nature (or lack thereof) of helping behavior itself. Our goal in this book is to present an overview of what is currently known about a diverse group of cooperatively breeding birds. We hope this will facilitate the search for common patterns among the species, and provide directions for new research in the field.

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