Introduction

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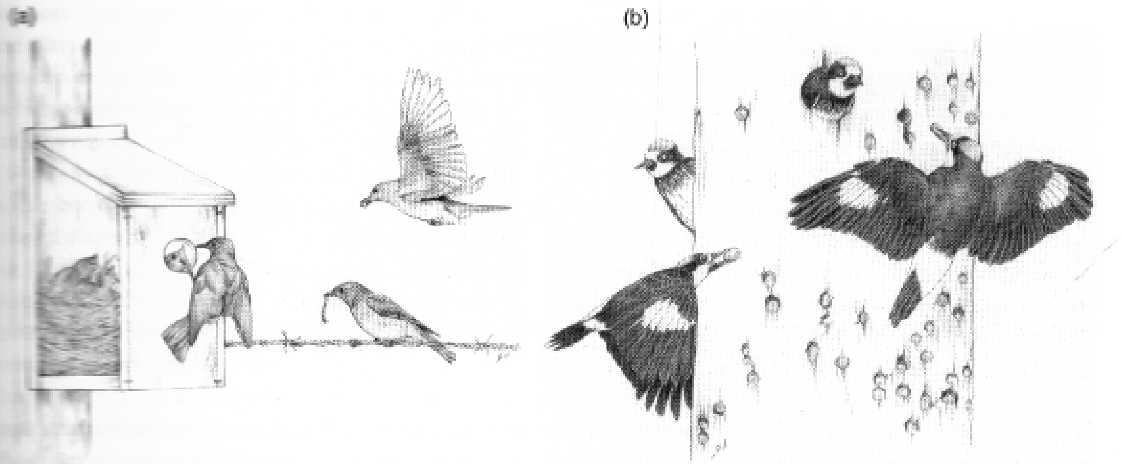

Cooperative breeding was described by naturalists as early as the nineteenth century (Boland and Cockburn 2002) and refers to breeding associations with three or more individuals collectively raising young in a single brood or litter. Breeding in groups was little more than a biological curiosity, however, until nearly 30 years after Skutch (1935) first introduced "helpers at the nest" to refer to individuals that forgo breeding to help raise young that are not their own. In the 1960s, evolutionary studies of animal social behavior were quickly transformed by the realization that selection acts mainly on individuals and only rarely on groups (Williams 1966). This insight spawned the field of behavioral ecology, and, in particular, kin selection and inclusive fitness theory (Hamilton 1963, 1964), which provided a firm theoretical basis for understanding the paradox of helping and other forms of cooperative breeding that appeared to involve a sacrifice in personal reproduction. This book provides examples of studies that test specific predictions based on individual selection and inclusive fitness theory, using a combination of experimental and observational studies designed to measure the socioecological drivers and fitness consequences of giving up at least a share of personal reproduction to help others breed.

Relatively quickly after Hamilton's seminal papers, cooperative breeders became subjects of several

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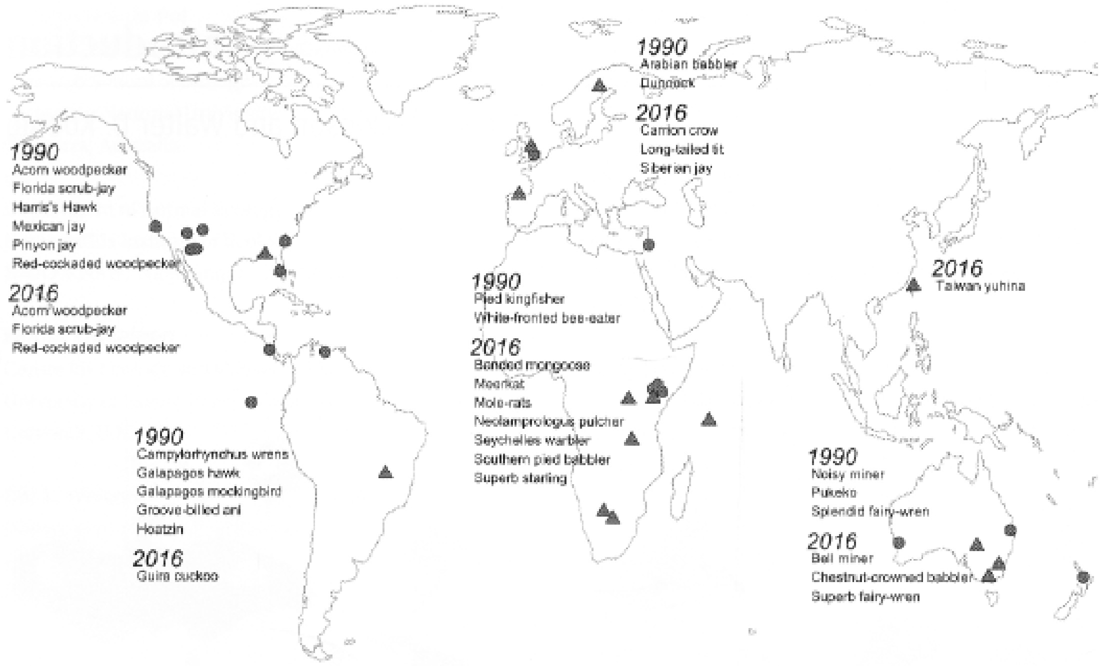

Figure I.1. The geographic distribution of studies represented in Stacey and Koenig (1990; circles) and this book (2016; triangles).

long-term studies, many of which were summarized species by species in Stacey and Koenig (1990) and topic by topic in Koenig and Dickinson (2004). This latter volume reviewed theory and evidence by summarizing the literature across a range of relevant topics. The book we introduce here returns to the earlier model, examining advances based on population studies of vertebrate species across the globe (Figure I.1) with the goal of exploring the ways in which new theory and empirical evidence have altered our perspective on cooperation over the last 25 years. We believe that new insights usually come from exploring the diversity and complexity of animal societies within the context of theory; our hope is that having summaries of these studies all in one place will generate new thinking, while helping to foster generalities and illuminate holes in current thinking.

The chapters in this book include contributions from both new and more senior researchers; three chapters are updates of studies summarized earlier in Stacey and Koenig (1990), demonstrating the added value that comes with increased longevity of studies in this field. The remaining studies highlight the many advances that have been made with the addition of new, and often exceptional, study systems and experimental approaches.

Results from such studies indicate that what we know today about cooperative breeding may not be representative of the different kinds of systems that are out there, making it difficult to draw general conclusions. Within the complexity that has been uncovered, however, are both consistent patterns and new gems of ideas that help push the field forward. It is only in bringing together and synthesizing the evidence that already exists that a story begins to emerge for each species, allowing us to get a sense of what matters in a system, what the important design features are, and how natural selection has shaped them variously among species. We have particularly enjoyed seeing the insights that emerge when researchers have the opportunity to tell the whole story in one place, rather than piecemeal in technical publications.

What has happened since the last collection of long-term studies was published in 1990? While reproductive skew theory had already been around for a while (Vehrencamp 1983), it really took hold, generating an array of models and ideas that improved understanding of the extent of reproductive sharing in animal societies and the complexities surrounding measuring and modeling reproductive division of labor (Magrath et al. 2004). Although the original insights provided by reproductive skew theory have proven problematic for most cooperatively breeding vertebrates (Haydock and Koenig 2002; Magrath et al. 2004), the interplay between empirical studies and theory continues to produce new generalizations and understanding of how and why reproductive sharing varies across taxa.

Study systems chosen as exceptions appear early in the book, beginning with a species that exhibits delayed dispersal in the absence of cooperative breeding (Chapter 1), as well as two cases of cooperative breeders that have fluid systems of helping that become possible when localized dispersal of offspring leads to breeding in kin neighborhoods (Chapters 2 and 3). Chapters 2 through 13 focus on cooperatively breeding birds in which relatedness and kin selection are generally critical to the evolution of cooperative behaviors, although beyond that they encompass a wide range of social organizations ranging from socially and genetically monogamous pairs with helpers (Chapters 4, 5, and 7) to species with helpers in which extra-pair matings are common (Chapters 2, 8, and 12), species organized into complex and in some cases multileveled groups (Chapters 9, 10, and 11), and cooperatively polygamous groups with helpers (Chapters 6, 12, and 13). In addition to these are chapters covering species of vertebrates in which individuals cooperating with one another are apparently *not* related, with the idea that these can provide strong, complementary tests of alternative hypotheses for the evolution of cooperation (Chapters 14 and 15).

Great strides have been made in understanding cooperation in non-avian vertebrates, including fishes (Chapter 16) and mammals (Chapters 17, 18, and 19), with several of these studies combining field research with field and laboratory experiments to test important hypotheses concerning the evolution of helping behavior that are difficult to address in the field alone. In bringing these newer studies together with the three landmark, older studies, which were largely focused on such classic ecological constraints as habitat and cavities (Chapters 4, 5, and 13), it becomes possible to assess current understanding of cooperative breeding in vertebrates and to develop the broad perspective needed to foster new thinking. Significantly, the 19 studies summarized here include some of the most extensive and detailed population studies of wild living vertebrates ever undertaken.

Perhaps the most important technical advance since the 1990 volume is the widespread availability of molecular tools to assess parentage, especially the advent of hypervariable microsatellites, which allow study-wide parentage assignment. While Nick Davies' (1990) dunnock (*Prunella modularis*) chapter was the only study to integrate molecular parentage assignment in the previous book, molecular tools are commonly used today, allowing for assessment of such critical measures as relatedness, incest, inbreeding, reproductive skew, and, of course, inclusive fitness.

Since Hamilton (1963, 1964), the primary body of theory informing studies of social behavior has been inclusive fitness theory, which compares the direct fitness benefits of producing offspring with the indirect fitness benefits of helping relatives produce additional offspring over what they might otherwise produce, weighted by relatedness (Brown 1980). The minimal predictions of inclusive fitness theory are that helpers should prefer, or at least be more likely to aid, relatives over nonrelatives, that the inclusive fitness advantages of helping should be greater than what helpers (as individuals) might otherwise achieve (i.e., Hamilton's rule, which infers that helping must be better than actual outside options), and that if breeding is the better option, helpers should breed independently when they have the opportunity to do so.

The studies presented here provide a breadth of evidence supporting the importance of indirect fitness benefits, which often, but not always, act in concert with limitations on independent breeding to drive decisions to help or cobreed with relatives. In general, studies of cooperative breeders indicate that even when indirect fitness benefits are small, they can still be an important driver of helping behavior – because the outside options are even worse. Most of the chapters in this book present strong evidence for the importance of kinship and kin recognition in the behavioral choices that individuals make, especially choices of whether to help and whom to help (Chapters 2, 3, 7, and 11). Explicit tests of Hamilton's rule (Chapters 2 and 3) provide insights that further demonstrate the value of kin selection and inclusive fitness thinking. This large body of evidence supporting the importance of kin selection to helping stands in direct opposition to challenges based on modeling efforts and spotty interpretation of empirical evidence (Nowak et al. 2010).

Unsurprisingly, relatedness and indirect fitness benefits are much less prevalent among same-sex cobreeders in species that exhibit cooperative polygamy, over half of which are thought to involve cobreeding by nonrelatives (Riehl 2013). Such partnerships among nonrelatives are, of course, driven by direct fitness benefits, rather than indirect fitness benefits arising through collateral kinship (Hartley and Davies 1994). Here we feature two cooperative breeders, both joint-nesting, that exhibit cobreeding by nonkin (Chapters 14 and 15). Despite these examples, studies of species whose cooperative behavior is not based on kinship remain relatively rare, and even ruminating about why unrelated males might help raise offspring of nonkin is intriguing: reciprocity; potential to inherit a mate; experience; high costs of floating or maintaining a territory as an individual?

At a time when funding is challenging to obtain and granting agencies are shying away from the complexity of demographic studies in favor of the "ooh, shiny" payoffs that can arise from short-term, mechanistic questions (Zuk and Balenger 2014), we hope this book inspires renewed interest in long-term studies of social behavior for their value in addressing lifetime fitness consequences of behaviors, their corrective potential (most authors in this book would, we think, agree that their ideas and evidence have changed significantly since they first began their study), their importance to conservation (Chapters 4, 5, and 12), and their capacity to uncover the complexities underlying the evolution of social behavior. Ideally, long-term studies of social behavior knit together multiple approaches by integrating ecology, life-history theory, behavioral genetics, physiology, and behavior, while forging new connections by measuring the traits, trajectories, and demography of individual agents. Such efforts provide important fodder for new theory and ideas.

Most importantly, in an age when there is a large focus on analyzing existing data, we believe this book illustrates the vital interplay between natural history observations and the development of new ideas, which when situated within a rich domain of accumulated knowledge can be tested rigorously and in ways that advance our understanding of the evolution of social complexity. All of the authors in this book are dedicated naturalists whose propensity to take on the unforgiving commitment of embarking on the long-term study of marked populations of animals is integral to the insights they have had and the discoveries they continue to make.

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