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Edited by Reinmar Hager and Clara B. Jones

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Reproductive Skew in Vertebrates

Reproductive skew is the study of how reproduction is partitioned in animal societies. In many social animals reproduction is shared unequally, leading to a reproductive skew among group members. Skew theory investigates the genetic and ecological factors causal to the partitioning of reproduction in animal groups and may yield fundamental insights into the evolution of animal sociality. This book brings together new theory and empirical work, mostly in vertebrates, to test assumptions and predictions of skew models. It also gives an updated critical review of skew theory. The team of leading contributors cover a wide range of species, from insects to humans, and discuss both ultimate (evolutionary) and proximate (immediate) factors influencing reproductive skew. Academic researchers and graduate students alike with an interest in evolution and sociality will find this material stimulating and exciting.

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Reproductive
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*Proximate and
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Foreword

A brief history of skew theory

New ideas in science don't spring out of nowhere; they combine and build from earlier ones. The concept of reproductive skew is no different, and it is nice to have this opportunity to look back, over 30 years ago now, and identify the various sources and give credit where it's due. The story begins in 1974 at the 16th International Ornithological Congress in Canberra, Australia. During that long flight to Australia from Johannesburg, South Africa, the pilot came on the loudspeaker and announced that the United States President Richard Nixon had just resigned in disgrace over the Watergate scandal. Having been in the field in Africa all summer, this was a shocking return to civilization. Ian Rowley had convened the first symposium on cooperative breeding in birds, with himself, Lew Grimes, Glen Woolfenden, and Amotz Zahavi presenting surveys of the cooperatively breeding species in their respective continents (Australia, Africa, the Americas, and Europe) (Grimes 1976, Rowley 1976, Woolfenden 1976, Zahavi 1976). All four speakers noted that the helper-at-the-nest form of cooperative breeding, where offspring remain on the parental territory, delay breeding, and assist with the care of subsequent broods of their parents, was by far the most common one. Cooperative breeding was associated with a variety of habitats and climates, but most were characterized by sedentary residence on territories or fixed home ranges. Habitat saturation was identified by Woolfenden and Zahavi as the primary force favoring prolonged retention of offspring on the parental territory.

During the contributed talk sessions, two of us, John Craig and I, spoke about our work on two species that differed significantly from the usual pattern in having multiple males and females breeding in a communal nest: groove-billed anis and pukeko. A lively workshop discussion followed, in which we argued about whether kin altruism or individually selected selfish

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behavior was the more important driving force for the evolution of cooperation. I tried to focus the discussion on the question of what might be driving the two different forms of cooperative breeding, the helper system versus the communal system, and suggested that lack of reproduction by helpers was the more pressing question to answer. Woolfenden glared at me and said no, the burden was on me, Craig, and others to explain when communal nesting would be favored, since helping was the norm and communal nesting the rarer form. The gauntlet had been thrown down, and I left the meeting determined to answer this question.

In 1976, with my thesis finished and my first academic job beginning, a second motivator arose: teaching a new course (jointly with spouse Jack Bradbury). E. O. Wilson’s *Sociobiology* (Wilson 1975) had just appeared, and became the textbook for our course of the same name. Wilson’s review of the two alternative routes to sociality, the familial and the communal routes, was inspiring, and it quickly became clear that many animal groups, including social insects, spiders, birds, and mammalian carnivores, all showed these two forms of cooperative breeding (Eisenberg 1966, Wilson 1971, Lin & Michener 1972, Brown 1974). I felt compelled to come up with an explanation for the students. Hamilton’s rule (Hamilton 1964) could explain the altruism of helpers towards close kin, but it couldn’t explain the aggregation and mutual cooperation of unrelated individuals in a communal system. Richard Alexander’s insightful review of animal social behavior (Alexander 1974) held the next major key: he clearly articulated that an individual’s gain from remaining in a social group had to be compared to the alternatives of living alone or taking the risk of finding and joining another group. He also noted that different competitive dynamics were likely to occur in different types of groups, i.e. family groups versus groups of unrelated individuals. Finally, he asserted that group-living animals invariably form dominance hierarchies in which dominants often gain at the expense of subordinates, and coined the phrase “parental manipulation of progeny” to describe selection on parents to reduce the reproduction of certain offspring in order to increase their inclusive fitness via other offspring.

A new perspective started to emerge: a focus on the power of the dominant and its greater ability to shape group composition and bias reproductive shares to its advantage. But the leverage of the dominant had limits if subordinates could opt to leave. Under conditions of habitat saturation, offspring would have poor outside options and therefore would be forced to remain with their parents, where they could be prevented from breeding by parental domination but able to increase their inclusive fitness by helping. By contrast, in unsaturated conditions groups would only form if there were some

It took a few more years to completely vet the mathematics of the model and explore the parameter space with different values of relatedness, group benefits, and ecological constraints. I appreciate the feedback from my mathematically competent colleagues at UC San Diego, Mike Gilpin, Ted Case, and Kurt Fristrup. I was pleased when John Maynard Smith took an interest in the model during our 1980 sabbatical leave in Sussex, UK; he not only incorporated it as an example of a two-stage game into the game theory book he was writing (Maynard Smith 1982), but he “did the sums” in a slightly different way by assuming that in larger groups subordinates made individual decisions about whether to stay or leave. To explain the occurrence of equitably breeding groups of relatives within the model’s framework, some factor that prevented enforcement by dominants such as constraints on control, reproductive inefficiency caused by within-group conflict, or coalitions of subordinates had to be invoked. If these factors were widespread, such that observed skew was often less than the maximum predicted by the model, I surmised that the original model would not be very useful. Occurrence of skews greater than predicted by the model would certainly falsify it. In the final revision of the 1983 paper (Vehrencamp 1983), a reviewer and editor were critical of the use of the word “skew” as a verb and insisted I use the term “bias.” Once the paper was published, I figured the idea would have to cook. Since it seemed very difficult to conduct experimental tests and manipulations on birds, and the molecular means for determining paternity and maternity were not fully developed, I switched to research on animal communication.

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Kern Reeve, along with colleagues Francis Ratnieks and Laurent Keller, gave the theoretical model a shot in the arm in the early 1990s by simplifying the math, limiting group size to two, greatly clarifying the specific predictions and tests of the model, and extending the model to make predictions about when groups should be stable versus unstable (Reeve 1991, Reeve & Ratnieks 1993, Keller & Reeve 1994). In addition, they added the possibility that the degree of skew might be limited by subordinate fighting for complete control of the group's resources, derived skew in parent-offspring associations, and generalized the skew model to N-person groups with diminishing group benefits as group size increases (Reeve & Keller 1995, 1997, Reeve & Emlen 2000). With their background in social insects, they shifted the terminology and mechanisms of group formation to a perspective different from my vertebrate approach. Whereas I conceived of groups of potential breeders initially forming for reasons of birth location or ecological conditions, followed by the emergence of a dominance hierarchy and the subsequent suppression of reproduction by subordinates just short of the point where they should leave, Reeve envisioned a dominant overwintering queen returning first to the birth nest site and then enticing later arrivals to join in a group. Words like "incentive," "payment," "concession," "negotiation," and "social contract" were incorporated to describe the processes of group formation and reproductive partitioning. Many lab groups were engaged in empirical testing of the model's predictions. To my surprise, the reproductive biasing models suddenly became "skew theory."

A symposium devoted to skew theory was held in Sheffield in 1997 to bring together vertebrate and invertebrate perspectives. Along with the notoriety and testing came a wave of skepticism articulated by Tim Clutton-Brock, who expected dominants to have perfect control and both dominants and subordinates to have perfect knowledge of reproductive shares and the availability of outside options (Clutton-Brock 1998). Beginning in 1998, an explosion of new skew models by Reeve, Michael Cant, Rufus Johnstone, Hanna Kokko, and others appeared (Cant 1998, Reeve *et al.* 1998, Cant & Johnstone 1999, Johnstone & Cant 1999, Johnstone *et al.* 1999, Kokko and Johnstone 1999, Crespi & Ragsdale 2000, Reeve 2000, Cant & Field 2001, Kokko *et al.* 2001, to mention only a few). In response to the criticism, these models variously modified the assumptions and mechanisms of dominant control, incorporated additional fitness components such as the potential for subordinates to inherit the dominant position, and considered the costs of enforcing skew and producing more young. A major alternative model was also developed, the tug-of-war model (Reeve *et al.* 1998), which assumed that

reproductive shares were the outcome of a costly conflict between two individuals of different competitive abilities. Ecological constraints do not influence reproductive partitioning in this model, but both participants reduce their combative effort when more closely related so skew tends to be unaffected or even lower than when they are less closely related. Renewed efforts to test the alternative predictions of the tug-of-war and optimal skew models sometimes found better support for the tug-of-war predictions.

A new synthetic model by Reeve and Shen (2006) that combines the tug-of-war process within the constraints of options outside the group, called the bordered tug-of-war model, holds great promise as a single flexible model. This model assumes that dominant and subordinate continually adjust their payments and selfish tug-of-war efforts in response to each other (K. Reeve, personal communication). In a real way, it better incorporates the biasing mechanisms and constraints that I envisioned 30 years ago. By varying parameters that set whether one, both, or no parties concede some direct fitness to the partner to keep her/him from leaving, one can cover the whole range of traditional concessions, bordered tug-of-war, and pure tug-of-war models. Each of these three processes appears to operate under different conditions of ecological constraint, benefit to grouping, and relatedness.

The current state of skew theory is well represented in the chapters of this book. Chapters by Taborsky on cooperatively breeding fish and by Kutsumake and Nunn on primates highlight the extreme range of ease and difficulty, respectively, of manipulating and measuring the key skew-determining parameters. It is heartening to read in the review of avian cooperative breeders by Koenig *et al.* that a meta-analysis largely supports the predictions of the traditional optimal skew model for birds. Chapters by Abbott *et al.*, Faulkes and Bennett, and Young argue that in mammals, despite the high cost of offspring production, dominant females can attain a high skew through hormonal suppression and infanticide, for example. Jones, on the other hand, argues that high variability and unpredictability of ecological conditions limits the ability of dominants to control subordinates in socially flexible mammals. A useful review of reproductive skew studies in primitively eusocial wasps by Field and Cant points out that skew is often greater than predicted by the concessions model. They discuss whether this outcome is a clear falsification of the model, or whether either ecological constraints or inheritance of the dominant position has not been properly measured and considered. Hager also reports that future reproductive potential may be driving the observation of high reproductive skew in male langurs. Holekamp and Engh demonstrate the impact of the control one sex may have over skew in the opposite sex, a problem that continually arises in cases of vertebrate cooperative breeders containing

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multiple members of both sexes. Cant and Johnstone explore a model similar to the bordered tug-of-war, but where mutual adjustments between dominant and subordinate are not allowed.

Despite the skepticism and sometimes-heated disagreements (for example, see Magrath and Heinsohn 2000, Nonacs 2006, Nonacs 2007, and chapters by Hodge and Crespi), the collective body of theoretical and empirical work on reproductive skew has been and continues to be an engaging and fruitful field of study with broad ramification to many aspects of social behavior in animals and humans.

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References

Alexander, R.D. (1974). The evolution of social behavior. *Annual Review of Ecology and Systematics*, **5**, 325–384.

Brown, J.L. (1974). Alternative routes to sociality in jays. *American Zoologist*, **14**, 63–80.

Cant, M.A. (1998). A model for the evolution of reproductive skew without reproductive suppression. *Animal Behaviour*, **55**, 163–169.

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Cant, M.A. & Johnstone, R.A. (1999). Costly young and reproductive skew in animal societies. *Behavioral Ecology*, **10**, 178–184.

Clutton-Brock, T.H. (1998). Reproductive skew, concessions and limited control. *Trends in Ecology & Evolution*, **13**, 288–292.

Crespi, B.J. & Ragsdale, J.E. (2000). A skew model for the evolution of sociality via manipulation: why it is better to be feared than loved. *Proceedings of the Royal Society of London B*, **267**, 821–828.

Eisenberg, J.F. (1966). The social organization of mammals. *Handbuch der Zoologie*, **10**, 1–92.

Emlen, S.T. (1982). The evolution of helping. I. An ecological constraints model. *American Naturalist*, **119**, 29–39.

Grimes, L.G. (1976). Cooperative breeding in African birds. *Proceedings of the International Ornithological Congress*, **16**, 666–673.

Hamilton, W.D. (1964). The genetical evolution of social behavior, I & II. *Journal of Theoretical Biology*, **7**, 1–52.

Johnstone, R.A. & Cant, M.A. (1999). Reproductive skew and the threat of eviction: a new perspective. *Proceedings of the Royal Society of London B*, **266**, 275–279.

Johnstone, R.A., Woodroffe, R., Cant, M.A., & Wright, J. (1999). Reproductive skew in multimember groups. *American Naturalist*, **153**, 315–331.

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- Kokko, H. & Johnstone, R. A. (1999). Social queuing in animal societies: a dynamic model of reproductive skew. *Proceedings of the Royal Society of London B*, **266**, 571–578.
- Kokko, H., Johnstone, R. A., & Clutton-Brock, T. H. (2001). The evolution of cooperative breeding through group augmentation. *Proceedings of the Royal Society of London B*, **268**, 187–196.
- Lin, M. & Michener, C. (1972). Evolution of sociality in insects. *Quarterly Review of Biology*, **47**, 131–159.
- Magrath, R. D. & Heinsohn, R. G. (2000). Reproductive skew in birds: models, problems and prospects. *Journal of Avian Biology*, **31**, 247–258.
- Maynard, Smith J. (1982). *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.
- Nonacs, P. (2006). The rise and fall of transactional skew theory in the model genus *Polistes*. *Annales Zoologici Fennici*, **43**, 443–455.
- Nonacs, P. (2007). Tug-of-war has no borders: it is the missing model in reproductive skew theory. *Evolution*, **61**, 1244–1250.
- Reeve, H. K. (1991). The social biology of *Polistes*. In K. Ross & R. Matdiews, eds., *The Social Biology of Wasps*. Ithaca, NY: Cornell University Press, pp. 99–148.
- Reeve, H. K. (2000). A transactional theory of within-group conflict. *American Naturalist*, **155**, 365–382.
- Reeve, H. K. & Emlen, S. T. (2000). Reproductive skew and group size: an N-person staying incentive model. *Behavioral Ecology*, **11**, 640–647.
- Reeve, H. K. & Keller, L. (1995). Partitioning of reproduction in mother–daughter versus sibling associations: a test of optimal skew theory. *American Naturalist*, **145**, 119–132.
- Reeve, H. K. & Keller, L. (1997). Reproductive bribing and policing evolutionary mechanisms for the suppression of within-group selfishness. *American Naturalist*, **150**, S42–S58.
- Reeve, H. K. & Ranieks, F. L. W. (1993). Queen–queen conflict in polygynous societies: mutual tolerance and reproductive skew. In L. Keller, ed., *Queen Number and Sociality in Insects*. Oxford: Oxford University Press, pp. 45–85.
- Reeve, H. K. & Shen, S. F. (2006). A missing model in reproductive skew theory: the bordered tug-of-war. *Proceedings of the National Academy of Sciences of the USA*, **103**, 8430–8434.
- Reeve, H. K., Emlen, S. T., & Keller, L. (1998). Reproductive sharing in animal societies: reproductive incentives or incomplete control by dominant breeders? *Behavioral Ecology*, **9**, 267–278.
- Rowley, I. (1976). Cooperative breeding in Australian birds. *Proceedings of the International Ornithological Congress*, **16**, 657–666.
- Vehrencamp, S. L. (1980). To skew or not to skew? In R. Nöhring, ed., *Acta XVII Congressus Internationalis Ornithologici*. Vol. I. Berlin: Verlag der Deutschen Ornithologen-Gesellschaft. pp. 869–874.

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Wilson, E. O. (1971). *The Insect Societies*. Cambridge, MA: Belknap Press.

Wilson, E. O. (1975). *Sociobiology: the New Synthesis*. Cambridge, MA: Belknap Press.

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Zahavi, A. (1976). Cooperative breeding in Eurasian birds. *Proceedings of the International Ornithological Congress*, **16**, 685–694.

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Preface

We have collaborated on projects since 2001, and it became evident to us by 2004 that a book about reproductive skew incorporating theoretical, empirical, and review chapters might be timely. Because of our own research specializations, and because a large body of literature exists on skew in social insects, we generated a plan to prepare a volume on reproductive skew in vertebrates, approaching Cambridge University Press with a proposal. The present text represents our attempt to provide a “state of the art” overview of reproductive skew in vertebrate societies by some of the most active and highly regarded researchers in this field. It is our intention to highlight the most fundamental questions for students of reproductive skew, to assess the strengths and weaknesses of skew models, to critically evaluate skew in insect societies and skew in social vertebrates, and to identify important directions for future theoretical and empirical work.

In her foreword to our volume, Sandra Vehrencamp has provided a brief overview of the history, theory, and empirical highlights of models of reproductive skew. It is clear from her personalized account that advances in the study of reproductive skew (the within-sex partitioning of reproduction within social groups) were presaged by early work in behavioral ecology demonstrating a relationship between dispersion and quality of limiting resources, in particular, food and nesting sites, as well as variations in social behavior, social organization, and mating systems within and between populations. The relationship between these factors is analyzed in models of reproductive skew that attempt to explain the partitioning of reproduction among individuals of the same sex in animals and offer a theoretical framework for understanding the formation of social groups. In addition to the central role of kin selection, skew theory identifies other fundamental processes that are key to the evolution of complex sociality, such as suppression of reproduction or the control of group membership, and it may thus enable us to

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study one of the major transitions in evolution, from primarily solitary to social lifestyles, across a range of different taxa.

Our book provides the reader with theoretical, empirical, and review chapters on a variety of model vertebrate systems exemplifying high, intermediate, and low skew and the causes and consequences of biased reproduction within groups. Furthermore, since social insects have been the classic exemplars of high-skew societies, we include a chapter on these organisms and their similarities and differences to social vertebrates. We think that a particularly helpful feature of our text is its future value as a reference tool. A related utility is the book's presentation of many ideas for future research that have not been thoroughly investigated to date: for example, the evolution of low-skew societies and underlying mechanisms of suppression. An additional feature of *Reproductive Skew in Vertebrates: Proximate and Ultimate Causes* is its presentation of caveats about skew models for those who may be uncritically enthusiastic about these paradigms. The investigation of all aspects of reproductive skew is in its early stages, and we hope that our volume will help this field develop into a more mature, and critical, enterprise.

As editors, we would be remiss if we failed to acknowledge and to express gratitude to the many individuals who have facilitated the process of our book's actualization – from initial proposal to published text. We thank our initial contacts at Cambridge University Press whose interest in our ideas never faltered. Our editor at Cambridge, Martin Griffiths, has provided significant input, guidance, support and encouragement for our project. Without Martin's expert ability to diagnose and to resolve challenges, our book may not have gone to press. Subsequent to the decision by Cambridge University Press to invite our initial book proposal and to distribute it for review, we received helpful and constructive criticism and advice from several researchers investigating the topic of reproductive skew. These critiques influenced our final decisions regarding our volume's conceptual framework and organization, and also prompted us to include additional chapters on topics we had not previously considered. Indeed, the initial feedback we received from reviewers of our proposal was critical in stimulating our thinking about target questions and heightened our enthusiasm for our project, and we gratefully acknowledge the comments of these researchers.

Our most profound thanks are extended to our contributors, who have demonstrated professionalism, expertise, patience, and, most important, good humor at every stage of our project. Without the willingness of these individuals to engage in frequent communication about their submissions and to receive our suggestions with grace, even when they may have disagreed with them, our book would not have been realized. We hope that our contributors

will be pleased with the final text, as we are, and that they, their colleagues, and their students will value their contributions to *Reproductive Skew in Vertebrates: Proximate and Ultimate Causes* for many years to come. Among the contributors to our book that we wish to acknowledge by name are Sandra Vehrencamp and Bernard Crespi, who assumed responsibility for writing the foreword and the concluding chapter, respectively. These experts met unique challenges requiring the ability to summarize the field of reproductive skew, both retroactively and for the future. We hope that both of these contributions will help to place the book’s chapters in a broad context by linking each topic with past work, with the present state of the field, and with the literature on reproductive skew and related topics yet to be published. Finally, we wish to express personal thanks to those who have been particularly influential in our careers. Reinmar Hager is especially grateful to Rufus Johnstone, his thesis advisor at Cambridge University, for introducing him to skew theory, and to Yfke Hager, for help with editing. Clara B. Jones, likewise, thanks her dissertation advisor at Cornell University, William C. Dilger, for encouraging her interests in plants and animals and for facilitating her research interest in the evolution of social behavior. In the final analysis, it may be both necessary and sufficient to stress that we hope you find our volume a “good read” that will provide information, stimulate thinking, and generate original research, both theoretical and empirical, for its readers and their extended academic families. We look forward to these outputs as well as your measured feedback.