Book review

Birds of a feather flock together

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The Social Lives of Birds: Flocks, Communes, and Families
Joan E. Strassmann
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As dusk approaches, you might be lucky enough to watch a synchronized spectacle where millions of European starlings perform a collective aerial ballet as they settle down to their nighttime roost. These birds have taken this wondrous murmuration behavior with them as they have expanded their range globally. Birders are now drawn to renowned starling roost sites in the fall and early winter, when these shape-shifting clouds of birds are reliably witnessed. Starling murmurations are one of the true marvels of the avian world: an airborne manifestation of the sociality that brings birds together in groups of many kinds.

As I write this piece gazing outside the tent at my Kenyan field site, I can see four different species of starlings, each adorned with varying shades of iridescent blue-green plumage that shimmers in the early morning sunlight. Although each of these species occasionally forms small flocks and individuals often roost together at night, none perform an intricate bedtime dance routine like their European starling cousins. Yet each starling species here has its own manifestations of intricate social behavior. For example, all superb starlings — the species that I have studied for more than 25 years[1] — spend their lives in large, extended family groups that are among the most complex societies of any bird on Earth (Figure 1). Although their plumage is truly 'superb' and accordingly draws the eye, at just one site here you might also notice dozens of other birds engaging in a wide range of interactions. Most bird species are social at some point during their lives, and a large number form permanent groups or temporary associations, with the nuances of their social lives sometimes an obvious part of their biology. On the African savanna, much of that social variation is on full display. Green wood hoopoes wander noisily in family groups along wooded stream courses. When it rains and breeding begins, male widowbirds summersault themselves above the vegetation, displaying vigorously to inquisitive females. And dangling from the tips of acacia trees are the clustered nests of the colonial black-capped social weaver, which author Joan Strassmann terms 'supersocial groups' in her charming new book *The Social Lives of Birds*.

This book offers a grand tour of the full diversity of avian lifestyles. Strassmann, an expert on animal social evolution, has been an avid birder since childhood, though her own research has focused primarily on social behavior in wasps and slime molds, not birds. Perhaps this gives her an informed but unbiased lens to appreciate the complex and rich behavioral variation that we see across birds.

Much of what we know about avian social behavior comes from studies of individually marked birds that are followed over space and time for generations. These long-term field studies have dramatically shaped the field of behavioral ecology for at least the past six decades. In many ways, her book is as much about the principles of animal behavior and social evolution as it is about the rich lifestyles of birds. Strassmann organizes her text by devoting each chapter to a different form of avian sociality (noted here in *italics*), focusing on interesting bird biology and the stories of those that study it, rather than getting bogged down in the confusing terminology that scientists often like to use and argue about.

Many species of birds associate temporarily, ranging from the *flocks* they form to help escape predation, to the *mixed-species flocks* they form to find food, to the *roosts* they form to stay safe at night. In each of these initial chapters, we are presented with a compelling series of examples of how the forces that ecologists term 'bottom-up' (food availability) and 'top-down' factors (predation risk) jointly shape avian social behavior. In the simplest terms, groups tend to form when the benefits of associating outweigh the costs. For many individuals it is often safer to be in a group, where there are more eyes to spot predators and more neighbors to dilute the risk of

Figure 1. A supersocial bird.
Superb starlings form social groups with a mix of kin and non-kin that together cooperate to raise offspring in the unpredictable savanna environment of East Africa. (Photo: © D. Rubenstein.)

being eaten. Yet there are also costs to group-living: more competitors for food and other resources, the risk of disease or parasite transmission, and so on. In some species, temporary groups form — even among different species — precisely because flocking helps individuals find more food, despite the downsides of competition with flockmates. Using mixed-species flocks, which are common at backyard bird feeders around the world, Strassmann introduces us to the varied roles that individual species take on in these aggregations and how flocks with entirely different membership from different continents often host species with notably similar roles, such as the sentinel species that keep watch and alarm call when they spot an approaching predator.

In these pages we are also often reminded of what Strassmann has learned from her friends and family, as well as from both her mentors and her mentees. Taking a central role is her undergraduate mentor at the University of Michigan, Richard Alexander, who shaped much of Strassmann's own view on social behavior, as he influentially did for a great number of today's behavioral biologists. In Alexander's classic paper 'The evolution of social behavior'[2], he noted that there are no automatic benefits to group-living, only automatic costs. These costs are explored in more detail in *colonies*, where cliff swallows are a compelling protagonist. Via a long-term study in Nebraska, USA that has spanned nearly half a century, we learn about the swallow bug ectoparasites transmitted among densely packed swallow nests and about how the birds have evolved greater parasite resistance over just the last few decades. Yet there are also benefits to living in colonies, and in *seabird colonies* Strassmann explores species that forage in the ocean — often for months or years at a time — but that must return to land to breed. Nearly 98% of seabirds nest in colonies, often for the same reasons that terrestrial species do, such as information transmission about food, avoiding predators to safely rear young, and even finding mates.

Forming groups to find mates is the basis for *leks*, our first foray into the topic of sexual selection. Males of most lekking species like to put on a show. They congregate at arenas frequented by females to dance, drum, or strut their way to (reproductive) success. Males in lekking species compete intensely for mates, and in most species reproduction is monopolized by one or only a few individual males on a lek. This intense male–male competition leads to strong selection on the ornamental traits that females find most attractive, as well as on behavioral strategies that maximize a male's chance of obtaining a mate. Here we are introduced to ruffs, a shorebird that is among my own favorite exemplars of bizarre forms of avian sociality. Males of this species have evolved three fundamentally alternative mating types that differ in color, size, and behavior. These differences are collectively controlled by chromosomal rearrangements that link the underlying genes together into complexes called supergenes. Once thought rare in birds, these 'chromosomal inversions' are turning out to be quite common in many avian genomes[3], and supergenes likely underlie many other behaviors in birds.

Unlike lekking species in which only females care for young, in the majority of birds both sexes provide parental care. In *mate choice and parental care*, we learn how social monogamy (one male pairing with one female) is the norm, yet genetic monogamy (one male mating with one female) is much less common. Meanwhile, most bird species commonly exhibit some degree of extra-pair paternity in their nests, where multiple males fathering chicks with the same female is more the rule than the exception. Females also occasionally lay their eggs into the nests of other females, a behavior that has been taken to the extreme in obligate brood parasites such as cowbirds and some cuckoos that must lay their eggs in the nests of other species. Although biparental care is widespread in birds, we also learn about cases of male-only care, which may be the ancestral form of avian parental care, having first evolved in dinosaurs.

As we shift focus from avian mating systems to social systems, Strassmann introduces us to the full range of more permanent associations that birds can form. In *families with helpers*, we learn about species in which more than two individuals are needed to care for young. These cooperative breeders tend to occur in unpredictable environments where food is limited and availability fluctuates from year to year. Central to these later chapters is the concept of kin selection, where some individuals — helpers — gain fitness not by breeding on their own but rather by helping to raise the offspring of their relatives, with whom they share genes. We move from small family units of related individuals to groups of largely unrelated individuals in *communal nesters*. Here the indirect fitness benefits of helping relatives are less likely to be important and, as one would predict from kin selection, reproduction is shared more equitably among the non-kin group members, and non-breeding helpers are rare. Although communal breeders cooperate to defend the nest and care for young, there is also a great deal of conflict within the group over egg laying. Dominant females often destroy the eggs of subordinate females in an attempt to monopolize more of the reproduction. Finally, in *supersocial groups*, we learn about some of the most socially complex bird species. Much like the superb starling that I study in Kenya, these species often form groups that contain a mix of relatives and non-relatives. Some species breed separately on a group-defended territory, some breed in a colony, and still others breed jointly in a shared nest. Reproduction is less equitable than in communal breeders but more equitable than in family-living species. These supersocial species tend to live in the most variable and unpredictable environments, and having helpers is necessary for successful reproduction in these harsh conditions.

With personal anecdotes, captivating stories, and rich details, *The Social Lives of Birds* offers a balanced and nuanced perspective on avian sociality that is equally appropriate for the casual reader, the interested student, and even a professional such as myself. As we learn throughout the book's pages, the field of vertebrate social evolution has a rich history, but it continues to advance, with studies

of birds often leading the way. New theory is moving us beyond an understanding of family group formation to the maintenance of more complex supersocial groups. As more social trait data and more powerful comparative methods become available, interspecies comparisons will continue to identify global patterns and generate new hypotheses. As additional chromosomal-level genome assemblies become available for birds, evidence for the role of supergenes in other behavioral differences will surely be found. And as environments continue to transform due to climate change, habitat loss, overfishing, and urbanization (all topics that Strassmann weaves into her narrative), birds will be affected in myriad ways. Behavior is often flexible and can change rapidly as environmental conditions shift. Some species may be able to buffer these shocks by living in cooperative groups, while others may be able to thrive in human-modified landscapes. Yet still other species — social and non-social ones alike — may not be able to cope with declines in food or habitat. Ultimately, we must hope that people continue to watch, appreciate, and conserve birds and their homes. After all, birding is a big business: in the US alone, amateur birders spend more than $100 billion a year on their passion. So, continue to feed backyard birds and add them to your life lists, but as you do so also watch them, observe their behavior, and enjoy their rich and fascinating social lifestyles.

DECLARATION OF INTERESTS

The author declares no competing interests.

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Q & A

Miltos Tsiantis

Miltos was born in the UK and studied biology in Athens, Greece before obtaining his DPhil from the University of Oxford. He conducted postdoctoral research at Oxford holding a number of research fellowships and spent some of that time on research visits to Berkeley. He then started his lab in Oxford, where he became Professor. Since 2013, he has been a Director at the Max Planck Institute for Plant Breeding Research in Cologne.

What turned you on to biology in the first place? I have always been interested in science. I was very inquisitive as a child and remember watching the Carl Sagan *Cosmos* series, which made me very interested in research. In my late teens I was also interested in history and political theory, but I think I decided that biology was more exciting from a hands-on perspective.

And what drew you to your specific field of research? As an undergraduate in Greece I learnt a lot about animal development, for example the genetics of animal body plans, and the role of homeobox genes and transcriptional control in development. I found this type of work very exciting. Initially, I wasn't interested in plants but eventually realised that a whole suite of questions in plant development were open and exciting. For example, as plants evolved multicellularity independently of animals, this raises the question of what are the mechanisms through which body plans are established and organogenesis occurs in this different context. I remember reading the papers on transposon tagging of floral homeotic genes by Enrico Coen and the maize *Knotted-1* homeobox gene by Sarah Hake and being inspired by these findings. That's probably when I decided to pursue a PhD in plant biology. I also remember the work of Mike Levine on transcriptional regulation in *Drosophila* development and Sean Carroll's and David Kingsley's work on animal diversity being very exciting.

If you had to choose a different field of biology, what would it be? Maybe developmental biology in animals since I love questions relating to pattern formation, cell fate decisions and the natural diversity in developmental processes. I find the limb bud a really fascinating system.

What's your favourite experiment? I think most experiments are exciting in their own way, particularly those that give you valuable insight no matter what the outcome is. One experiment from our group that I found very rewarding was transferring one transcription factor-encoding gene between species and observing that it is sufficient to make the leaf morphology of the recipient species become like that of the donor one. This was done by Daniela Vlad, a very talented postdoc in our group when we were in Oxford.

What are your favourite conferences? The FASEB conference in plant development is one of my favourites. It's an excellent opportunity to see so many developmental biologists at different stages of their careers presenting exciting work and to have a lot of animated discussions over a drink. Also, I was lucky enough to attend two Fondation Les Treilles meetings in a beautiful setting in France. A small number of scientists come together for about a week to give presentations, and there is ample time for informal discussions; it is a true science discussion paradise. In one of them, organised by Nicolas Gompel