The Secret Lives of Starlings

An unpredictable habitat sets the stage for cooperation and conflict in African starlings—and influences who cheats on whom.

BY DUSTIN R. RUBENSTEIN

With its glossy blue back and neck, jet black head, rusty underbelly, and characteristic white breast band, the superb starling (Lamprotornis superbus) is hard to miss. It lives in savannas in eastern Africa, where it is one of the most common birds.

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Superb starlings live in cooperative family groups of as many as thirty individuals; their social structure is one of the most complicated in the avian realm.

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When love is in the air, beautifully turned-out males trail their equally dazzling mates everywhere to ensure their fidelity. And still some of those females, albeit a minority, manage to elude their bodyguards and cheat on their partners. Some females do it for better genes, while others trade sex for extra food for their young. And when a female does cheat, it can be with a mysterious stranger—or with a close relative of her partner: his brother, cousin, or even nephew! What sounds like a sordid soap opera is conventional life for a group of African birds. Their social structure just happens to be one of the most complex in the avian world.

The superb starling (*Lamprotornis superbus*), which dwells in eastern Africa from Sudan to Tanzania, is one of 110 or so species of starlings, forty-five of which are found only in Africa. The superb starlings live in large communal groups and cooperate with one another to raise offspring, but not without some conflict, competition, and varying amounts of cheating, from rare to rampant. Their groups consist of breeding pairs as well as helpers that don't breed themselves, but aid multiple nests simultaneously. Although males do most of this helping, both sexes help.

Nearly 40 percent of African starling species are so-called "cooperative breeders," meaning that additional individuals help raise one breeding pair's young, but superb starlings are "plural cooperative breeders," with several breeding pairs sharing a large pool of helpers. Their family groups, which include parents, stepparents, siblings, aunts, uncles, nieces, and nephews, can swell to upwards of thirty individuals, more than almost any other group-living avian species. Within those groups, up to six breeding pairs build individual nests inside thorn-encased acacia trees, on a large territory that the whole group then defends year-round. The males of the group are often related, because, as with most family-living birds, female superb starlings are more apt to disperse from the group than are males, creating a patrilineal society.

Within that complex web of cooperative familial relationships, mating conflict lurks. While superb starlings form mating pairs for as long as five years and are often strictly monogamous, promiscuity rates can be as high as 32 percent in some family groups. What drives some to cheat and others to stay faithful? And what environmental factors incline particular individuals to breed themselves or to help raise others' offspring? The answers are only just emerging—and they shed new light on the evolution of mating and social behavior.

Evolutionary biologists have long recognized that nurturing close relatives has enough of a genetic payoff to explain why some individuals forgo or delay reproduction and instead remain in their group as helpers. Beginning with studies of ants and other social insects, the importance of kin in the evolution of cooperation was recognized by William D. Hamilton in the 1960s [*for more about Hamilton, see "Life Zone" on page 16*]. The insight was soon extended to cooperatively breeding birds and mammals. Simply put, cooperating with kin and living with family is behavior that can pass the acid test of natural selection, since it perpetuates one's own genes.

By the 1980s, as studies of family living in birds began to accumulate, it also became clear to Cornell University behavioral ecologist Stephen T. Emlen and others that environmental factors might influence the decision to be a breeder or a helper. A shortage of suitable nesting sites might, for instance, constrain birds from leaving their natal territory in search of opportunities to breed, and might thus favor taking on the role of helper. Today, we recognize that both ecological constraints and kin relationships likely figure into cooperative-breeding decisions. Individuals must balance the costs and benefits of trying to disperse from their natal territory to breed independently against those of staying home to help raise relatives, a calculation that will vary depending on the availability of food, turf, mates, and more.

Ever since the naturalist Alexander F. Skutch made the first observations of cooperative-breeding behavior

Elephants head to a watering hole on the Serengeti Plain. Along with lions, hyenas, and wild dogs, elephants are among the well-known savanna mammals that raise their young cooperatively. Superb starlings also rely on cooperative breeding to successfully raise young during the harsh times when the rains are meager or late.

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in birds, nearly seventy-five years ago in the forests of Costa Rica, scientists have wondered why some species cooperate and others do not, particularly when cooperative and noncooperative species are closely related. It has long been suspected that some trait shared among cooperatively breeding species explains why they live in family groups, but the evidence for any one trait is weak at best. Take life span, for instance: cooperative breeders tend to be long-lived—but there are also plenty of long-lived species that do not cooperate.

If no single intrinsic trait promotes cooperation, perhaps some extrinsic one related to the environment plays a role? African starlings offer an excellent opportunity to examine that question, because their many species not only exhibit a range of family lifestyles, but also live in a variety of habitats. Africa is an ecologically diverse continent with harsh and forbidding deserts, lush rain forests, and wildlife-rich savannas. It is no less common to see a starling darting through a forest canopy than it is to see one riding atop a Cape buffalo in a savanna [*see photograph on page 33*]. However, the cooperative species live only in savannas, whereas the noncooperative species live primarily in forests.

A similar observation has been made in Australia, where an unusually high 13 percent or more of bird species are cooperative breeders: the cooperative species tend to reside in savanna–woodlands habitat. If savannas on two of the more arid continents in the world harbor so many cooperative species, what is it about these semiarid habitats that promotes family living? The answer hinges on how semiarid savannas differ from other ecosystems.

"African savanna" may conjure up images of the Serengeti and its open plains, covered with herds of migrating wildebeests and zebras, stalked by ferocious predators such as lions, hyenas, and cheetahs. Most African savannas, however, are actually savanna–woodlands, characterized by a mixture of trees and grass. Large animals are common, but the mosaic of trees and grass also supports an abundance of smaller animals, including numerous species of birds. Rain—the lifeblood for all savanna plants and animals—is seasonal, and for many months each year the savanna is dry and barren. That seasonality in rainfall explains the great wildebeest migrations, but it cannot explain why cooperative breeders are common in savannas. After all, seasonality is also characteristic of temperate and tropical forests, and even of arctic tundras.

But there is a crucial difference in savannas: the *unpredictability* of rainfall. Although there are pronounced annual dry and wet seasons, the start and duration of the rains vary from year to year, making these semiarid ecosystems some of the most environmentally unpredictable places on Earth. The absence, or even delay, of the annual rains can mean the difference between success and failure for most savanna inhabitants, including starlings.

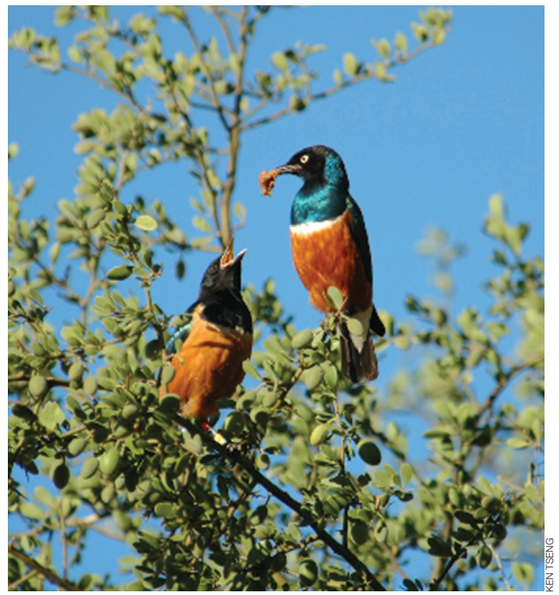
Cornell ornithologist Irby J. Lovette and I have constructed an evolutionary tree based on the DNA of all forty-five species of African starlings—primarily collected during trips we took across the savannas, forests, and deserts of Kenya. Using this tree, we have shown that the cooperative breeders are indeed found in the more seasonally unpredictable parts of Africa. When the rains fail to come or when they are scant, it may be impossible for many of the noncooperatively breeding starlings to successfully raise their young. But for the cooperative species, with helpers to share the burden of feeding their offspring, life is easier during the bad times. In fact, superb starling pairs with more helpers successfully raise more young. It is thus no coincidence that cooperative breeding is common in numerous other groups of birds that live in savannas, as well as in a variety of well-known savanna-dwelling mammals such as lions, hyenas, wild dogs, and elephants, and perhaps even early human ancestors [*see "Meet the Alloparents," April 2009*].

Cooperation in superb starlings may offer security in the face of unpredictable conditions, but conflict naturally arises, too. For one thing, same-sex individuals commonly fight over breeding opportunities. On average, only about four pairs per group breed, even though plenty of other birds are capable of reproducing. Since neither the availability of nest sites nor that of breeding partners seems to be a limiting factor, why do only a subset of the capable breeders in each group breed? Reproductive decisions seem to be related to rank: the more dominant individuals tend to breed, whereas the more subordinate individuals tend to help. However, it is not yet clear how dominance or social rank is determined in superb starlings.

Perhaps not surprisingly, reproductive conflict is influenced in part by the environment. Most fighting occurs during the dry season that comes immediately before the breeding period. That three-month period is when reproductive roles are determined, and it also happens to be the most unpredictable period in an already unpredictable environment, with the greatest variation in rainfall.

In drier years, the number of aggressive interactions between dominant and subordinate birds is higher. Those conditions are associated with higher levels of stress hormones in subordinates, more of which then adopt helping roles. Additionally, helpers do a greater proportion of the nestling feeding in drier years than they do in wetter ones. In contrast, during wetter years, conflict decreases; stress hormone levels in subordinates match those of dominant birds; and younger, inexperienced birds attempt to breed for the first time. Although stress hormones are not likely to determine breeding roles in this species directly, they are indicative of the level of social stress with which an individual must cope. Subordinate individuals must be adaptable in their reproductive strategies, gauging the conditions in a given year.

Attaining breeding status does not always mean that life is better, especially for male superb starlings. Preventing one's mate from straying and copulating with another individual is nearly as important as finding a mate in the first place. After all, failure to father the offspring of your mate would not only mean a wasted breeding attempt, but would also entail the costs of raising someone else's young. For decades ornithologists have known that 90 percent of bird species are socially monogamous, forming pair bonds to raise young. Now we also know that nearly 90 percent of bird species are promiscuous on the



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Superb starlings form monogamous pairs for up to five years, but some females are promiscuous. Securing a male helper to bring food to the nest is one reason for the cheating.

side. Indeed, molecular studies (bird paternity tests) have confirmed that the outwardly devoted, altruistic appearance of superb starlings is deceptive.

So which males do females choose to cheat with? Like everything else in the secret lives of starlings, the answer is not simple. Two distinct mating strategies are pursued by promiscuous females: half copulate with males from inside the group, and the other half with males from outside the group. A given female's choice of cheating partner depends upon her needs. Promiscuous females that choose mates from inside the group tend to have few surviving offspring from previous years, and thus few potential helpers. Those females target subordinate, nonbreeding males from inside the group that can, and eventually do, help at their nests. In other words, females without potential helpers are trading sex for child care to improve the odds of successfully raising offspring. On the other hand, promiscuous females that consort with males from outside the group gain some genetic diversity for their young. In comparison with females that do not cheat, they are more genetically similar to their mates, possibly as a result of inbreeding. Males from neighboring groups enable such females to provide any resultant offspring with a measure of genetic variation that the original mate lacks.

Given the two types of potential reproductive benefits of cheating in superb starlings—help feeding offspring and an increase in offspring's genetic diversity—one would think cheating would be the norm, as it is in many other cooperative breeders. But promiscuous matings are actually fairly rare in superb starlings, accounting for, on average, only 14 percent of offspring produced. A closer examination of the mating system reveals that promiscuous matings are extremely rare in some groups, but relatively common in others: promiscuity rates range from 4 percent to 32 percent among family groups.

Promiscuity rates do not vary from year to year, and are not related to variation in rainfall. Nor does rank or social structure seem to influence the patterns. Instead, promiscuity relates most closely to territory quality, which remains stable across years. Females living on high-quality territories, with plenty of food, are less promiscuous than those living on low-quality territories with little food. As New Yorkers might especially appreciate, it all comes down to real estate.

The highest-quality superb starling territories encompass large open grassy areas, or glades, where insects are readily available during the rainy season, and to a lesser extent during the dry season. Superb starlings are omnivorous throughout the year, but they need to feed their nestlings insects—primarily grasshoppers—during the breeding season. Securing that high-quality real estate seems to be the birds' prime reproductive strategy. Yet such glades are rare, and unevenly distributed across the landscape. The best real estate comes from abandoned livestock corrals, called *bomas* in East Africa, where an accumulation of dung and urine has enriched the soil—an effect that lasts at least forty to fifty years, and possibly as long as a hundred years or more.

Those nutrient-rich hot spots support large numbers of insects and attract a diversity of wildlife, ranging from large herds of antelopes to small creatures such as bat-eared foxes

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Superb starlings vigorously compete for food with other species, such as these gray-headed sparrows in Kenya's Samburu National Park. Despite living in cooperative groups, starlings can also experience intense conflict with each other: dominant and subordinate individuals tend to fight over breeding opportunities during especially dry seasons, when food is scarce.

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*A greater blue-eared glossy starling (*Lamprotornis chalybaeus*) rides atop a Cape buffalo in Kenya's Lake Nakuru National Park.*

[*see "The Natural Moment," page 2*]. Superb starlings build their nests around the edges of glades and forage throughout the year in those food-rich patches. The abundance of insects is essential to producing offspring during the breeding period, and groups with more, or larger, abandoned boma sites on their territories have greater access to food throughout the year. It is not yet clear how or why those nutrient-rich patches affect promiscuity patterns, but clearly they are important to starlings. Thus, resource availability as it varies unpredictably in *time*—rainfall patterns from year to year—has a greater influence on the social system of superb starlings, in terms of cooperation and reproductive conflict over breeding roles, whereas resource availability as it varies in *space*—insect location and abundance—has a greater influence on the birds' mating system, with respect to mating conflict and patterns of promiscuity.

Rainstorms on the African savanna are life-giving and life-changing events. Within only a day or two of the first storms of the season, life bursts forth from the dry, barren land as green grass sprouts from soil, bringing with it a flush of new insects. A few minutes after a particularly intense storm, millions of winged termites erupt from the ground, causing a feeding frenzy among the birds. As we've seen, starlings are adapted to the unpredictable nature of these rainstorms and to the savanna environment in general.

But humans are modifying these semiarid environments. Whereas traditional livestock practices have had generally positive effects on superb starlings by creating nutrient-rich glades, not all human-directed changes in land use are beneficial. In the coming months, I will begin to explore how overgrazing by cattle, goats, and sheep influences starling social behavior. Numerous studies have shown that overgrazing in Africa can lead to declines in bird and mammal populations, as well as to land degradation. My research suggests that such degradation could also have more subtle consequences for avian reproductive behavior.

In addition, as the Earth continues to warm at alarming rates, unpredictable and extreme weather events such as droughts, floods, and tornadoes are becoming increasingly common everywhere. In sub-Saharan Africa in particular, droughts are becoming more intense and more frequent. At my study site at the Mpala Research Centre in central Kenya, superb starlings have largely failed to breed during the past two years during the primary rainy season, which barely materialized. I will now begin to examine the reproductive physiology and social behavior of superb starlings living in different Kenyan habitats to see how they and other bird species might respond to global warming and its associated increase in environmental unpredictability. The secret and complicated lives of starlings still have a lot to teach us about adapting to uncertainty. Although research about them will not reduce the volatility in New York real estate prices, it may help predict the future biotic consequences of climate change and habitat degradation.

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