11

Superb starlings: cooperation and conflict in an unpredictable environment

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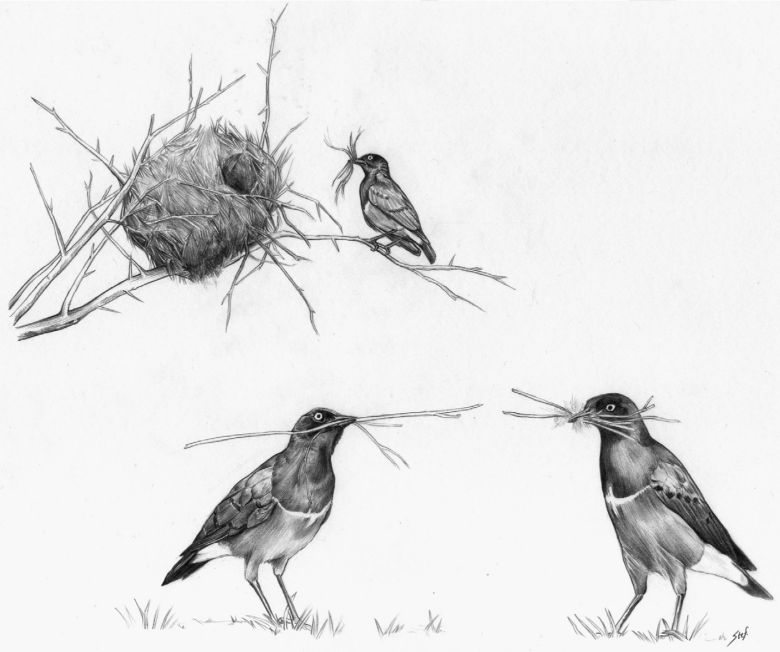

Introduction

The starlings are an Old World family of birds concentrated in the Indo-Malayan and Afrotropical regions (Feare and Craig 1999; Lovette and Rubenstein 2007). Because the European starling (*Sturnus vulgaris*) and common myna (*Acridotheres tristis*) – both of which originated in Eurasia (Lovette et al. 2008) – are among the world's most invasive avian species, starlings are now present on all continents except South America and Antarctica (Feare and Craig 1999).

The African clade of starlings, comprising approximately 45 species, is one of the most socially diverse groups of birds in the world, with nearly 40% of the

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species exhibiting cooperative breeding behavior (Rubenstein and Lovette 2007). Cooperatively breeding starling societies range from simple to complex. Singular breeding species live in simple societies with a single breeding pair and one or a few offspring that delay dispersal and help on the natal territory. In contrast, plural breeding species live in complex societies with multiple breeding pairs and helpers of both sexes (some related to the breeding pair and some not) that can provision multiple nests simultaneously.

In East Africa, the superb starling *(Lamprotornis superbus*) is one of the savanna's most easily recognizable species. It is one of approximately 22 species in the genus *Lamprotornis*, best known for its iridescent blue-green plumage (Lovette and Rubenstein 2007; Maia et al. 2013). Most *Lamprotornis* starlings are gregarious, with many living in cooperatively breeding groups (Feare and Craig 1999). Superb starlings live in large, boisterous kin-based social groups and have one of the most complicated social systems of any bird, making them a particularly good model system for the study of cooperation and conflict.

Study area

Since 2001, I have studied a population of superb starlings in central Kenya at the Mpala Research Centre, Laikipia (0°17' N, 37°52' E), between 1,740 and 1,800 m in elevation. This private property, over 200 km^2 in size, consists of savanna-bushland habitat, a matrix of trees, grass, and bare earth. Mpala lies in the middle of the Laikipia District, a plateau that stretches from the slopes of the Aberdare Mountains and Mt. Kenya in the south and east, to the edge of the Great Rift Valley in the west, to the drier low elevation regions in the north. Annual rainfall at Mpala ranges from nearly 600 mm in the south to less than 350 mm in the north. The study area, consisting of nine marked social groups, is approximately 15 km^2 in the southern portion of the property where rainfall is highest. Seven social groups have been continuously monitored since April 2001, and two additional groups were added to the study population in January 2002.

Rainfall in this region of central Kenya is highly variable in both time and space (Rubenstein 2011). From 1999 through 2013, the mean (± standard deviation [S.D.]) amount of annual rainfall at Mpala was 576 ± 184 mm (range = 280 mm in 2000 to 960 mm in 2011) (Figure 11.1a), with most rain falling during the short (October–November; mean = 138 ± 70 mm) and long (March–May; mean = 238 ± 99 mm) rainy seasons (Figure 11.1b). The most variable period of rainfall is the three-month dry season (the pre-breeding period; mean = 59 ± 57 mm, range = 10 mm in 1999 to 215 mm in 2010) between the two rainy seasons (Rubenstein 2011) (Figures 11.1c and 11.1d). Although I have not quantified spatial variation in rainfall within the study area, three of the marked groups occur in a slightly drier region than the other six groups. Thus, territories vary substantially in the amount and timing of annual rainfall, which affects the start and duration of the breeding seasons, and in some years whether groups breed at all during the short rains.

The high variation in rainfall within and across years strongly influences superb starling territory quality through its effects on grass cover, which in turn is highly correlated with insect biomass in this ecosystem (Rubenstein 2007d). Grass cover varies both spatially and temporally, but high quality territories are consistently better relative to low quality territories (Rubenstein 2011). Grass cover is not only influenced by rainfall, but also by topography and soil type, being generally greatest on the tops of ridges and lowest in the valleys where moisture accumulates and bushes and trees predominate.

At Mpala, there are two primary soil types – red sandy loams (Ferric and Chromic Luvisols containing roughly 50% clay and 24% sand; Young et al. 1998) and black cotton soils (Pellic Vertisols containing 15% clay and 74% sand; Augustine 2003). These two soil types support different communities of trees, grasses, and animals (Augustine et al. 2011). Superb starlings are found commonly on both types of soil, and some of the territories with the lowest grass cover occur in the transition zone between the two soil types. Five of the marked social groups in the study population occur on red soils and four on the transition between red and black cotton soils. I have not studied any groups occurring on pure black cotton soils, largely because roads in the black cotton ecosystem become impassable to vehicles during the rainy season when birds are breeding.

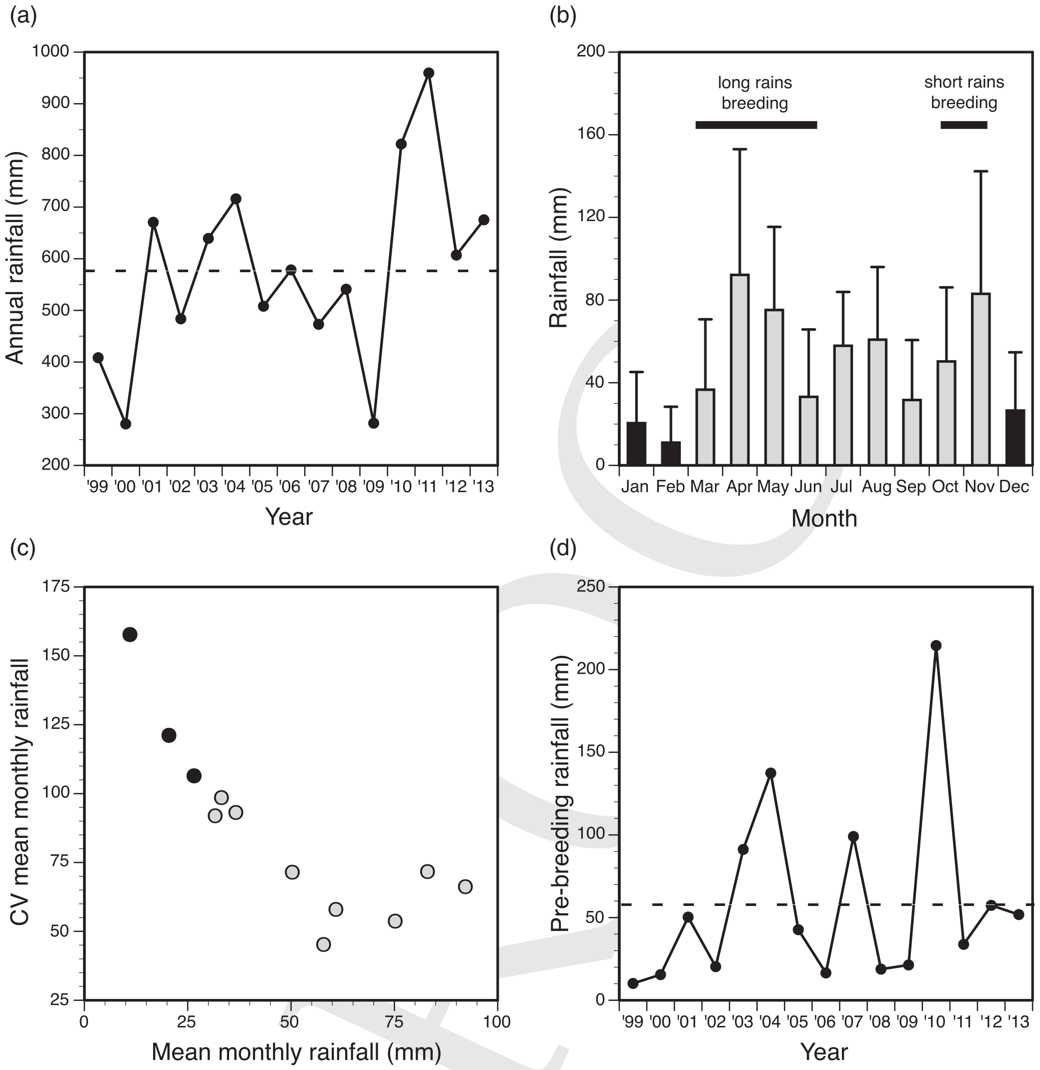

Figure 11.1. Rainfall patterns at the Mpala Research Centre, Kenya from 1998 to 2013. (a) Total annual rainfall from 1999 through 2013. The dashed line indicates the mean annual rainfall during this period (576 mm). (b) Mean (± S.D.) monthly rainfall from June 1998 through December 2013. Black bars indicate the pre-breeding period from December to February. The typical long and short rains breeding seasons are indicated above the bars. (c) Mean monthly rainfall is negatively related to the coefficient of variation (CV) in mean monthly rainfall, indicating that drier months are more variable than wetter months. The three most variable months occur during the pre-breeding period, and are indicated by black circles. (d) Pre-breeding rainfall from 1999 through 2013. The dashed line indicates the mean pre-breeding rainfall during this period (59 mm).

Life history and demography

Distribution and geographical ecology

Superb starlings live primarily in savanna-woodland habitat throughout much of East Africa, but can be found occasionally in arid regions, cultivated areas in wetter regions, and even in towns and suburban gardens. They are omnivorous, feeding on everything from termites, grasshoppers, Lepidoptera larvae, and ants, to berries, small fruits, and seeds (Feare and Craig 1999), and occasionally on mammal carcasses. During the breeding season nestlings are fed insects, primarily caterpillars and grasshoppers. Food resources are apparently not defensible during any season, and individuals do not appear capable of monopolizing food to the exclusion of other group members. Superb starlings are long-lived; in captivity they can live for more than 15 years, and in our study population, some individuals have lived for at least 14 years.

Superb starlings have large territories, often 50 ha or more in size. The landscape at Mpala is saturated with territories and social groups often border multiple other groups. Groups are territorial year-round, but birds spend extensive amounts of time each day off their territories, particularly during the nonbreeding season. When not on their territories, they are usually going to water or searching for food. In the nonbreeding season, groups will often mingle peacefully at the borders of territories to feed on the berries of dry season fruiting trees, and form mixed species flocks with other starling species such as the greater blue-eared glossy starling (*Lamprotornis chalybaeus*) and the Hildebrandt's starling (*L. hildebrandti*). Birds defend their territories in the breeding season, chasing away birds from other groups, particularly individuals that approach nests.

Territories are distributed heterogeneously in bushland habitat with a mix of grassy open areas that birds use for foraging and trees that they use for nesting. At Mpala, superb starling territories invariably encompass at least one grassy glade, a remnant of abandoned pastoralist livestock corals, called bomas, which were used for the overnight containment of livestock (Young et al. 1995). Because large quantities of livestock dung are concentrated in these small areas, both the soil and the vegetation inside glades are nutrient-rich, with insect abundance more than twice that in neighboring bushland sites (Huntzinger 2005). These nutrient-rich hotspots generate a positive feedback loop by attracting ungulate herbivores that continue to urinate and defecate in the glades, thus concentrating nutrients further and enhancing the abundance of insects and wildlife alike (Augustine 2003; Rubenstein 2007d). Nutrient-rich bomas persist as grassland glades on the landscape for decades, thus representing stable high quality areas in an otherwise depauperate landscape. Thus, these hotspots represent predictable patches of resources in otherwise climatically unpredictable environment that allow superb starling social groups to persist as dynasties for generations.

Group and demographic structure

Superb starlings are plural cooperative breeders that live in large territorial groups of up to 40 or more individuals with multiple breeding pairs per group. Mean (± S.D.) group size is 25.8 ± 5.9 (Table 11.1), with 4.3 ± 2.4 breeders per group during the long rains and 2.6 ± 1.7 breeders per group during the short rains. The remaining nonbreeding birds are a mix of helpers that provision nestlings and nonbreeder/nonhelpers that neither provision offspring nor breed, but can play an important role in defending nests from predators (Rubenstein 2007b). This category includes birds that would likely have provisioned at a nest had it not been depredated in the egg stage. However, some nonbreeder/nonhelpers do not contribute to breeding in any capacity, even through nest guarding.

The sex ratio of superb starling groups is roughly equal (Table 11.1). Importantly, both sexes of superb starlings help at the nest, although males provision more and make up a higher proportion of the helping individuals than females (Rubenstein 2006). In general, males are the primary philopatric sex and females the primary dispersing sex; from 2002 to 2005, 8 of 11 (73%) birds that immigrated from one marked social group to another were female (Fisher exact test; $P < 0.01$), and

Table 11.1. Patterns of genetic relatedness and demographic structure from nine superb starling social groups monitored from 2002 to 2012

Trait	Mean ± S.D.	Max	Min
Genetic relatedness (*r*)			
Male	0.12 ± 0.05	0.15	0.02
Female	0.07 ± 0.05	0.21	–0.04
Combined sexes	0.08 ± 0.04	0.14	0.01
Demographic structure			
Number of males	12.8 ± 3.0	19.8	7.8
Number of females	13.3 ± 3.2	23.7	7.8
Group size (males and females)	25.8 ± 5.9	43.6	15.6

Pairwise relatedness values were calculated using Kingroup v2 (Konovalov et al. 2004).

61 of 76 (80%) individuals that immigrated into the study population were females ($P < 0.001$). Dispersal records from the population are limited, but banded birds have been observed in new groups nearly 20 km from where they were born. The majority of dispersal and immigration into new groups occurs during the pre-breeding dry season, although some immigration takes place at other times of the year as well. Females delay dispersal and remain in their natal groups for an average of 2.0 years before they disperse, and 17 of 65 (26%) females remained for ≥ 3 years before dispersing (Rubenstein 2006).

Although some females never disperse from their natal groups, there have only been three apparent cases of a female breeding in the group in which she was born. However, all of these breeding attempts were depredated before parentage could be confirmed with microsatellite markers, so there is no genetic evidence of a female breeding in her natal group. In contrast, male breeders appear to be a mix of natal and immigrant individuals. Determining which birds were actually born into the group is difficult because birds are long-lived and many were alive when the project began in 2001. In any case, 43 of the 112 (39%) males that bred for the first time at least two years after the project began were confirmed to have been born in the group in which they bred. Although this number is almost certainly an underestimate, it suggests that as many as half of the breeding males in groups may be immigrants.

Breeding biology and life history

Although superb starlings have been observed nesting in every month of the year at Mpala, the primary breeding season occurs during the long rains from March to June with a secondary breeding season during the short rains in October to November. The mean (± S.D.) number of nest attempts per group was 5.1 ± 2.8 during the long rains breeding season and 3.4 ± 2.4 during the short rains breeding season. In contrast, the sympatric greater blue-eared glossy starling (a noncooperative breeder) and the Hildebrandt's starling (a facultative cooperative breeder) only breed during the long rains, except during El Niño years, when the rains are particularly prolonged. During these El Niño years, the short and long breeding seasons of the superb starling can blend into one extended breeding season because of high rainfall during the pre-breeding period.

Superb starlings build nests of woven grass in trees, often near the center of the group territory and around the central grassland glade. Breeding pairs always build nests in different trees, which can be both close together or far apart. Although the breeding pair does most of the nest building, helpers occasionally contribute. Nests consist of a closed dome structure, typically with a short tunnel entrance. Pairs will reuse nests in successive breeding seasons, although most get destroyed by weather or other animals within two years. Birds have also been reported to use the abandoned nests of other birds, including those of swallows, swifts, and a variety of species of weavers (Fry et al. 2000; Rubenstein 2006).

Across most of their range, superb starlings nest in thorn trees, primarily in the genus *Acacia* at heights ranging from < 1 m to > 9 m above the ground (mean = 2.8 m). There appears to be no effect of nest height or tree species on the probability of being depredated (Rubenstein 2006). The most abundant tree species in the black cotton soil and transition zone is the whistling thorn acacia (*Acacia drepanolobium*), which is protected from megaherbivores (primarily elephants) by one of four species of symbiotic ant (Goheen and Palmer 2010). Preliminary data suggest that superb starlings may preferentially place their nests in trees defended by the most aggressive ant species, presumably because the ants help protect the nest from predators.

Nest failure is extremely high. From 2001 to 2013, I monitored 862 nest attempts, of which only 172 (27%) fledged any offspring. Of 2,549 eggs laid during this period (mean ± S.D. clutch size = 3.5 ± 0.6), only 333 (13%) fledged, and the mean (± S.D.) proportion of eggs fledging per nest was 0.12 ± 0.29. The high nest failure rate leads to extremely low average lifetime reproductive success for those individuals that attempt to breed: the mean (± S.D.) lifetime reproductive success for females was 2.0 ± 3.0 offspring fledged (range = 0–13; *N* = 55 females through 2012), and for males was 2.0 ± 3.2 (range = 0–17; *N* = 41 males through 2012). Nests fail due to abandonment, starvation, and predation, but failure is primarily attributable to the latter, as 92% of complete nest failure is due to predation. Diurnal predators include birds, baboons, snakes, and squirrels and nocturnal predators include genets, mice, and snakes. During the nestling stage, starvation remains an important source of nest failure, particularly during the beginning of the season when some pairs nest before the true onset of the rainy season, and the end of the breeding season when the rains begin to taper off.

Social behavior

Kinship

The male-biased dispersal pattern of superb starlings results in kin structure within a social group that is higher among males (mean $r = 0.12$) than among females (mean $r = 0.07$) (Table 11.1). Male kin structure in particular varies greatly among groups, ranging from $r = 0$ to 0.26. The group with the lowest average relatedness among males surrounds the Mpala Research Centre where food and water are available year-round. This group is also the largest and has the most transient birds that are banded during the dry season and never seen again, as well as many birds that are only seen in the group for a short period of time.

Although the overall kin structure in most groups is relatively low, this is likely the result of having large groups with multiple unrelated breeding females and a mix of related and unrelated breeding males. Kinship among breeders and helpers has not yet been formally assessed, but the majority of helpers are offspring of the breeding pair or other close relatives. Thus, within the larger, plural breeding group exists smaller subgroups organized around the family unit. So, although the overall mean relatedness among males in the group is relatively low, high pairwise relatedness among many members of the group suggests that kin selection is likely to play an important role in the evolution or maintenance of superb starling societies.

Given the range of kinship values in superb starling groups, individual must have a mechanism to recognize relatives. In at least some cooperatively breeding birds, kinship is assessed through vocalizations (Sharp et al. 2005; McDonald and Wright 2011; Akçay et al. 2013) (see also Chapters 2, 3, and 10). In other species, vocalizations also have been shown to signal group membership (Tyack 2008) or individual identity (Stoddard 1996). Superb starlings make short, stereotyped vocalizations, or flight calls, when approaching conspecifics. Immigrant females are able to learn these flight calls as adults after joining a new social group (Keen et al. 2013). A combination of acoustic recording analyses and playback experiments were used to show that superb starling flight calls are more similar within than among groups, and that individuals respond differently to playbacks from their own group versus those from other groups (Keen et al. 2013). Call similarity was not correlated with genetic relatedness, however, indicating that flight calls are learned and reflect social association and individual identity rather than kinship. Thus, in complex societies with both kin and nonkin group members, signaling individuality and group association, and not just kinship, may be an important mechanism that facilitates cooperation.

Offspring care and nest defense

Superb starlings are apparently obligate cooperative breeders, with >90% of nests having at least one helper feeding nestlings (Rubenstein 2006). Determining whether all nests have helpers – the definition of an obligate cooperative breeder – is a difficult task because nest predation rates are high in this population and the number of attendants at a nest increases with nestling age (Rubenstein 2006). Most of the nests where helpers were not observed were depredated early in the hatchling period, and it is likely that helpers would have been observed feeding nestlings had the nest survived longer. In any case, helping is very important and increases parental fitness; nests where chicks starve have approximately 50% fewer helper visits and provisioning trips per hour than nests where chicks do not starve (Rubenstein 2007c). Only breeding females incubate eggs (and there is no observational or genetic evidence of egg dumping), but once the eggs hatch, social fathers and helpers aide in provisioning offspring. Mothers contribute >50% of the nestling provisioning, while social fathers and helpers split the rest equally. As many as 14 helpers have been observed provisioning at a single nest, but the mean (± S.D.) number of helpers at a nest is 3.3 ± 2.7 ($N = 222$ nests from 2001 to 2014).

Nestling provisioning and helping behavior is extremely complex. Although most nests are attended by helpers that are previous offspring of the breeding pair, helpers can assist at multiple nests simultaneously, and breeders occasionally provision at others' nests after their own nests have failed. Cases of breeders helping at others' nests often involve brother – brother and father – son relationships, but they can also involve less related individuals. In a few cases, one of the breeding individuals that was observed helping at another pair's nest was observed to be paired with one of the other breeders the following breeding season.

Patterns of nestling provisioning vary both in time and space. For example, the proportion of nestling provisioning done by helpers – but not mothers or social fathers – varies among years and is related to the amount of pre-breeding rainfall (Rubenstein 2006). Helpers contribute a greater proportion of the provisioning following dry pre-breeding periods, and a lower proportion following wetter pre-breeding periods. In contrast, the proportion of provisioning done by mothers – but not helpers or social fathers – varies among groups and is related to territory quality. Mothers do a greater proportion of nestling provisioning on lower-quality territories and a lower proportion of provisioning on higher-quality territories (Rubenstein 2006). This result is somewhat surprising and suggests that further study of the temporal and spatial patterns of nestling provisioning is needed.

Superb starlings use a loose sentinel system to protect nests from predators. When parents are actively feeding chicks, at least one group member often perches on the top of a tree within 30 m of the nest. Both helpers and nonbreeder/nonhelpers act as sentinels that will actively alarm call if a potential predator approaches the nest. In experiments involving model predators, mothers were always the first to attack models, but eventually helpers and nonbreeder/nonhelpers attacked models more collectively than either the mother or social father alone (Rubenstein 2006). Thus, although nonbreeder/nonhelpers do not provision nestlings, they appear to play an important role in the group given that nest predation rates are so high. This could at least partially explain why superb starling groups are so large and why birds that neither breed nor provision nestlings are allowed to remain in the group.

Mating system

Superb starlings are socially monogamous with an average of 10% of offspring and 17% of nests resulting from extra-pair fertilizations. Extra-pair paternity is higher in the long rains breeding season (12% of offspring and 19% of nests) than in the short rains breeding season (8% of offspring and 14% of nests). Moreover, extra-pair paternity varies across years, ranging from 0% to 24% of offspring and 0% to 45% of nests. Between 2001 and 2013, molecular analyses also indicated that at least 22% of socially breeding females and 17% of socially breeding males engaged in extra-pair fertilizations at least once.

Although extra-pair paternity is low overall, there is high variation among groups, ranging from 4% to 32% of offspring and 7% to 60% of nests (Rubenstein 2007d). This variation in extra-pair paternity – most of which involves males from outside of the group – is unrelated to group size, genetic relatedness within groups, and pre-breeding rainfall. Instead, rates are correlated with territory quality (as estimated by grasshopper abundance and grass cover) such that extra-pair paternity is highest on low-quality territories with little grass cover and few insects (Rubenstein 2007d). This pattern likely reflects differences in the effectiveness of mate-guarding by males on territories of different quality. Preliminary observations and radio telemetry data suggest that females on lower quality territories forage further from the nest and central glade, indicating that they may have increased opportunity to mate with extra-group males. Thus, territory quality may influence a male's ability to guard his mate, and a female's ability to escape this mate-guarding and seek extra-pair fertilizations from outside the group.

Females exhibit two distinct extra-pair mating strategies: half of females that had extra-pair offspring in their nest (7% of all extra-pair offspring from 2001 to 2005) copulated with extra-pair sires from inside the group, and half (also 7% of all extra-pair offspring) copulated with extra-pair sires from outside the group (Rubenstein 2007a). Females that choose extra-pair mates from inside the group tend to be first-time breeders or those that had few surviving offspring from previous years (Rubenstein 2007a). Because these females have few potential kin helpers, they target unrelated subordinate (i.e., nonsocially paired) males that could potentially help at their nests (Rubenstein 2007a). In nests that survived to hatching, many of these subordinate sires did indeed act as helpers.

In contrast, females that choose extra-pair males from outside the group are able to increase the genetic diversity of their offspring. Offspring produced from extra-group males were more heterozygous – in terms of standardized heterozygosity and internal relatedness – at microsatellite loci than offspring produced by the social mate (Rubenstein 2007a). Females that sought out these extra-group males are those paired to mates that were relatively less heterozygous than themselves. Thus, females can potentially gain both direct benefits, in the form of increased alloparental care, and indirect benefits, in the form of increased offspring genetic diversity, by being promiscuous.

Extra-pair fertilizations are not the only strategy that birds use to make secondary mate choice decisions. Birds can mate-switch, or divorce, if the pair bond is inadequate (Botero and Rubenstein 2012). Mate switching is extremely common in superb starlings, with 45% of breeders of both sexes switching mates at some point during their breeding tenure; between 2001 and 2013, 231 pairs – involving 143 males and 151 females – attempted to breed in the population. Although most of the mate-switching occurs between breeding seasons, 10 cases of divorce within a breeding season have been observed. It is not yet clear why birds divorce within- or among-years, but in nearly all cases both birds remain in the group, and often, both the male and female will re-mate at some point in the future.

Not all pairs are quick to divorce, however, and some remain faithful despite being unsuccessful at breeding. The maximum number of failed breeding attempts in a season by a faithful pair is four, and the maximum breeding tenure for a pair without ever fledging offspring is four years (up to eight breeding attempts). In contrast, the maximum breeding tenure for birds that have bred together successfully is six years. Further work is clearly needed to understand how pairs form and why some end in divorce while others do not.

Synthesizing the social lives of starlings

Social and sexual competition in cooperative breeders

Intense social and sexual competition for breeding opportunities, as is evident in many cooperative breeders (Rubenstein 2012; Young and Bennett 2013), suggests that both males and females may benefit by the use of armaments to compete with same-sex individuals or ornaments to attract mates (Lyon and Montgomerie 2012). Comparative work in the entire group of African starlings has shown that cooperatively breeding species are less sexually dimorphic in plumage and body size than noncooperatively breeding species (Rubenstein and Lovette 2009). This reduced sexual dimorphism occurs in cooperative species because females are more similarly ornamented to the males of their species rather than vice versa. Moreover, females tend to be larger and more ornamented than the females of noncooperatively breeding species. Thus, selection – be it natural, sexual, or social – on traits used in intrasexual competition may be particularly intense in females in cooperatively breeding species, ultimately resulting in trait elaboration in both sexes.

Starling coloration is particularly vivid and appears to be under intense sexual selection. African starlings are the only monophyletic avian group to display all four of the structural color-producing melanosome morphotypes identified in birds (Durrer 1970). The mechanisms of color production have evolved directionally in this group from simple to more complex, resulting in faster color evolution, the occupation of novel regions of color space with new and brighter colors, and accelerated diversification via sexual selection (Maia et al. 2013). Some of the most colorful plumage and complex melanosome morphotypes occur in the *Lamprotornis* group where cooperative breeding behavior is particularly common.

Superb starlings are sexually monomorphic not only in plumage coloration, but also in other socially or sexually selected traits. Adults sing complex and diverse songs with as many as 82 distinct motifs, including all of the motifs used in flight calls (Keen et al. 2013). Although the function of superb starling song is unknown, males and females both sing during the breeding and nonbreeding seasons and there appears to be no differences in the number of motifs that each sex sings, with males producing an average (±S.D.) of 56.1 ± 1.6 motifs (range = 47–64) and females 54.7 ± 1.9 (range = 47–61) (Pilowsky and Rubenstein 2013). Moreover, there were no measurable differences in the structure of male and female songs. Breeder song differs in structure from nonbreeder (both helper and nonbreeder/nonhelper) song, however, with breeders producing songs with a higher proportion of unique motifs per bout than nonbreeders. Additionally, individuals singing in groups produce songs that are more continuous and have longer bouts than those singing alone. Thus, although the function of superb starling song is still unclear, it may be a signal used by both sexes to establish dominance rank or signal breeding status. Song could also be used to attract mates, but further work on this topic is needed.

As a plural breeding species, superb starlings have relatively low reproductive skew compared to singular breeding species characterized by a single breeding pair because more than one individual of each sex breeds in the group. Since social groups are typically so large, only about 25% of the birds in the group form pairs and breed socially despite the fact that nearly all groups in all years contain nonbreeding immigrant females and (unrelated) philopatric males of breeding age that could presumably pair and breed. Therefore, competition for dominance rank and reproductive conflict over breeding roles and mating opportunities appears to be quite high.

It is not yet clear how dominance status – or for that matter, how mate choice – is achieved in superb starlings, but it is likely that there are separate male and female dominance hierarchies. Observations made at baited feeding platforms have indicated that breeders are dominant to nonbreeder/nonhelpers which are dominant to helpers (Rubenstein 2006). Age likely plays a central role in dominance status, as breeders tend to be older than nonbreeder/nonhelpers, which tend to be older than helpers. Both sexes are aggressive and females often supplant subordinate males at the feeding platforms. Comparisons of glucocorticoid stress hormones in individuals with different breeding roles suggest that aggressive interactions and social suppression of breeding by dominants increases in drier years (Rubenstein 2007b; Rubenstein and Shen 2009). Aggressive interactions – most of which occur in flight – at the end of the pre-breeding period and beginning of the long rains breeding season are also apparently higher in drier years. Thus, environmental factors appear to interact with social factors to influence aggressive interactions, dominance rank, and ultimately breeding roles in superb starling social groups.

The opportunity for multiple pairs to breed in superb starlings social groups – that is, low reproductive skew – sets the stage for strong competition for social rank and high potential reproductive conflict over breeding roles and mating opportunities in both sexes (Rubenstein 2012). This not only influences social structure and creates tension over which birds get to breed and which help, but the similarly high potential for intense reproductive conflict within groups may help explain the monomorphic plumage (Rubenstein and Lovette 2009) and complex but similar vocalizations of males and females (Pilowsky and Rubenstein 2013). Further work is needed to explore signal evolution and maintenance in this and other cooperative breeders, particularly in species or populations where reproductive skew varies among groups.

Environmental uncertainty and the evolution of cooperative breeding

Ecological constraints on dispersal have long been thought to influence the incidence of cooperative breeding behavior in birds. Most barriers to independent breeding, such as a shortage of vacant breeding territories, the costs of dispersal, and difficulties in finding a mate (Hatchwell and Komdeur 2000) are the result of living in a spatially heterogeneous landscape where suitable territories are limiting (Emlen 1982; Koenig et al. 1992). Spatial constraints on dispersal are not the only environmental factor that can influence cooperative breeding behavior, however, as temporal variation in the environment may also be important (Emlen 1982). Comparative analysis in the African starlings (Rubenstein and Lovette 2007), later extended to all terrestrial birds (Jetz and Rubenstein 2011), suggest that cooperative breeders are found more commonly in temporally variable environments where precipitation varies unpredictably from year-to-year. One hypothesis for this relationship is that helpers at the nest may buffer groups against harsh conditions when food becomes limiting (Rubenstein and Lovette 2007).

Contrary to this hypothesis, recent work in hornbills (family Bucerotidae) suggests that cooperative breeders are found in less, not more, variable environments (Gonzalez et al. 2013). Similarly, in acorn woodpeckers (*Melanerpes formicivorus*), having helpers increases fitness only during environmentally favorable years, not in environmentally harsh years (Koenig et al. 2011; Chapter 13). These discrepancies in the role of environmental variability in favoring cooperation may simply be a taxonomic issue, however, since in Jetz and Rubenstein's (2011) global analysis, cooperative breeding behavior was predicted by rainfall variation in passerines (such as starlings), but not in nonpasserines (including hornbills and woodpeckers). Instead, temperature variation, which is indicative of a latitudinal signal, predicted sociality in nonpasserines. Nonetheless, for African starlings, environmental uncertainty in the form of interannual rainfall variation appears to be important in shaping the evolution and maintenance of cooperative breeding behavior.

In superb starlings, nearly all components of their social behavior and breeding life history are related to among-year variation in rainfall. The most climatically variable period of the year occurs during the pre-breeding dry season, when the coefficient of variation in mean monthly rainfall is highest (Figure 11.1c). Pre-breeding rainfall impacts a variety of physiological mediators, including glucocorticoid stress hormones (Rubenstein 2007b) and immune function (Rubenstein et al. 2008). Baseline and stress-induced corticosterone levels are correlated with pre-breeding rainfall in subordinate birds that become helpers but not in the more dominant individuals that become breeders or nonbreeder/nonhelpers during the following breeding season (Rubenstein 2007b). The elevated levels of stress hormones in helpers during the driest years are most consistent with the hypothesis that environmental conditions influence the relative costs of dominance behavior. These rank-related costs in turn affect the degree and intensity of social interactions, and ultimately reproductive decisions and breeding roles (Rubenstein 2007b; Rubenstein and Shen 2009). In contrast to levels of corticosterone, immune function – measured as the capacity for innate immunity in plasma to kill Gram-negative, nonpathogenic bacteria – was lowest in years with dry pre-breeding periods, but did not differ significantly among birds of different breeding roles (Rubenstein et al. 2008).

Annual variation in pre-breeding rainfall has a number of carryover effects to the breeding season. Rainfall variation directly influences maternal body condition, which later impacts offspring sex ratio (Rubenstein 2007c). Mothers in poor body condition during the

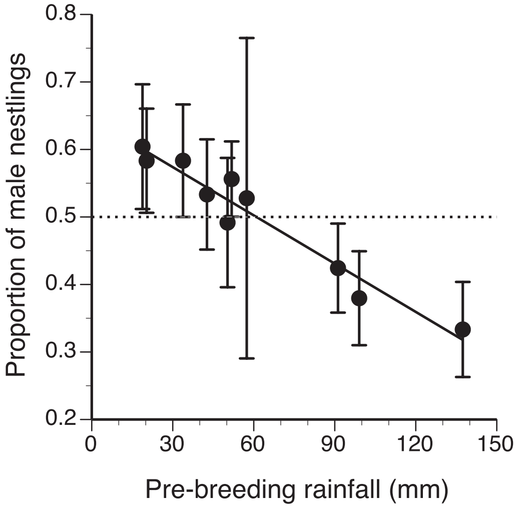

Figure 11.2. Pre-breeding rainfall predicts offspring sex ratio in superb starlings. Females overproduce male offspring in dry years and female offspring in wet years. This figure extends data published in Rubenstein (2007c) through 2013. Only nests where three or four nestlings survived to day 7 after hatching were used in the original analysis and graphed here. Each point is the mean (± S.E.) proportion of male nestlings per nest in a given long rains breeding season. Only years in which three or more nests were sampled were included. The year 2010 was excluded because it was an El Niño year where continuous rainfall meant that there was not a pre-breeding dry season. The total sample size was 80 nests over 11 breeding seasons (range = 3–14 nests per year). The dotted line represents an even 50:50 sex ratio.

pre-breeding period overproduce male offspring when pre-breeding rainfall is low, but overproduce female offspring when rainfall is high (Figure 11.2). Although this pattern appears to contradict the Trivers-Willard hypothesis (Trivers and Willard 1973), it does not because female superb starlings – like most cooperatively breeding birds (Hauber and Lacey 2005) – have a higher variance in reproductive success than males (Rubenstein 2007c). Thus, in accord with the Trivers-Willard hypothesis, mothers should be expected to overproduce female offspring when conditions are best, as is observed in superb starlings.

Pre-breeding rainfall also influences demography and reproductive behavior. Group sizes are larger in years with wetter pre-breeding periods (Figure 11.3), which may be due to greater offspring production, enhanced survival, and/or reduced dispersal. Additionally, the number and proportion of birds that breed for the first time is greater following wetter pre-breeding periods, suggesting that reduced dispersal in high quality years could at least partially influence the group size pattern (Rubenstein 2007b).

Since superb starling physiology, behavior, and life history are affected by among-year variation in rainfall, environmental uncertainty is also likely to influence fitness. Although mean reproductive success for breeding pairs in a group does not appear to be impacted by either temporal (rainfall) or spatial (territorial quality) environmental variation, variance in reproductive success is correlated with among-year variation in rainfall and among-territory variation in grass cover. That is, the standardized variance in reproductive success declines with increasing environmental quality (both rainfall and territory quality), as well as with increasing group size (a proxy for the potential for cooperation and the number of helpers in the group) (Rubenstein 2011). Specifically, in drier years, differences in territory quality are amplified and variance in reproductive success among groups is higher. Thus, environmental uncertainty influences variance in superb starling fitness, but not mean fitness, suggesting that cooperative breeding behavior may itself be a risk-averse strategy that groups use to reduce environmentally induced fecundity variance. Although environmental variation may be the primary force reducing variance in reproductive success in superb starlings, this "bet-hedging hypothesis" applies to any selection pressure that could influence variation in fitness, such as predation and brood parasitism (Rubenstein 2011).

The logic underlying the bet-hedging hypothesis is relatively straightforward. If having helpers in the group reduces the variance in reproductive success across years by limiting complete nest failure in some years, perhaps by preventing nestling starvation in harsh years or by successfully defending a clutch from a nest predator, then selection should favor having helpers in the group even if doing so reduces the mean reproductive output of the group and the mean per capita reproductive success of the breeders. Such declines in mean

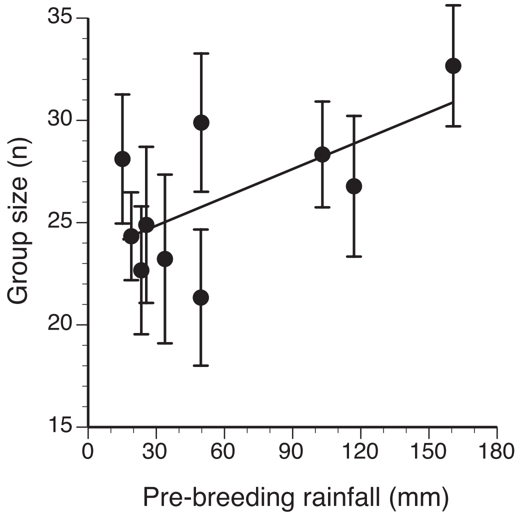

Figure 11.3. Superb starling group size varied with pre-breeding rainfall from 2002 to 2012. Groups were larger in years when more rainfall fell during the pre-breeding period ($F_{1,80} = 14.6$, $P < 0.001$; GLMM includes social group as a random effect to account for repeated measures across years). This pattern may result from increased offspring production, increased survival, and/or decreased dispersal in years with more rainfall during the pre-breeding dry season. The year 2010 was excluded because it was an El Niño year where continuous rainfall meant that there was not a pre-breeding dry season.

per capita reproductive success with increasing group size are common in cooperatively breeding vertebrates. Moreover, similar patterns of declining offspring production with increasing colony size are observed in eusocial insects, where the phenomenon is called Michener's paradox (Michener 1964). Of course, reducing years of complete nest failure will inevitably lead to a slight increase in the mean in addition to a reduction in the variance. This may explain why in superb starlings there is no relationship between group size and mean reproductive success (Rubenstein 2011), rather than a negative relationship.

If having helpers is a form of insurance that breeders use to minimize fecundity variance, then we expect the bet-hedging hypothesis to be most relevant to species living in large social groups. Of course, as group size increases with the retention of more subordinate individuals, reproductive conflict over breeding opportunities is likely to increase (Shen et al. 2014). One way for breeders to reduce this potential conflict may be to allow others in the group to breed, and thus, plural breeding could evolve. This scenario predicts that plural breeding is more likely to be found in systems where among-year variation in fecundity is high. Although this prediction has not been explored in detail, most plural breeding birds are found in semi-arid environments similar to those of the superb starling (Brown 1987).

Clearly more data from superb starlings and other cooperatively breeding species are needed to test the bet-hedging hypothesis. In general, the bet-hedging hypothesis should be tested in plural cooperatively breeding species where some but not all females in a social group reproduce. For species with variation in social structure among groups or populations, groups with helpers would be predicted to have a higher geometric mean fitness but not arithmetic mean fitness than groups without helpers. Moreover, for closely related species with different social systems living in similar environments, cooperative and noncooperative breeders should show different relationships in mean and variance in fitness with environmental and demographic parameters. Ultimately, researchers must consider how selection on variance in fitness, rather than on mean fitness alone, might influence cooperation and conflict in cooperatively breeding species.

At broad geographic and taxonomic scales, the degree of among-year variation in precipitation influences the incidence of cooperative breeding behavior in African starlings (Rubenstein and Lovette 2007) and more generally in all terrestrial birds, at least in the passerine lineage (Jetz and Rubenstein 2011). This temporal variability hypothesis suggests that living in kin-structured family groups and having helpers-at-the-nest allows birds to buffer environmental conditions when they are harsh and take greater advantage of conditions when they are good (Rubenstein and Lovette 2007). This appears to be the case for the plural breeding superb starling, where pre-breeding rainfall influences stress hormones, immune function, maternal body condition, and sex allocation, as well as the adoption of different breeding roles, levels of parental care, the intensity of reproductive conflict within groups, and demographic structure. Although mean reproductive success in groups is not directly influenced by rainfall variation, variance in reproductive success is related to pre-breeding rainfall. Cooperative breeding in superb starlings, specifically having large, plural breeding groups with many potential helpers, may therefore be an adaptation to reduce complete nest failure by buffering groups against environmental uncertainty and protecting nests against predators.

In summary, superb starlings appear to be able to reduce environmentally induced fecundity variance in both time and space by living in complex, plural breeding groups. Having a stable pool of subordinate individuals available to act as helpers to feed nestlings appears essential in this obligate cooperative breeder because poor quality years occur frequently and unpredictably. Indeed, when females lack access to potential helpers, they are willing to recruit helpers through extra-pair fertilizations with subordinate males within the group (Rubenstein 2007a). Moreover, subordinate individuals also play an important role in nest defense. When the mean lifetime reproductive success for both males and females is only two offspring fledged, preventing even a single nest predation event could more than double an individual's reproductive output. Thus, nearly all aspects of the superb starling's social life, including the evolution and maintenance of its complex plural cooperatively breeding social system, are influenced by the climatically variable savanna ecosystem in which they live. Superb starlings, however, are a cosmopolitan and wide-ranging East African species that can also be found occasionally in more mesic and more xeric environments. It will be interesting to compare the behavior, life history, and physiology of superb starlings living in deserts and forests to those in the savanna.

Conclusion

Superb starlings are endemic to the savannas of East Africa and have one of the most complicated lifestyles of any cooperatively breeding bird. They are an obligately cooperative species, with nearly all nests having helpers that provision nestlings. Group sizes are among the largest of any cooperatively breeding bird studied, and each group has multiple breeding pairs that can be assisted in caring for offspring by more than a dozen helpers. Superb starlings have a female-biased dispersal pattern, which results in higher genetic relatedness among males than among females. These sex-biased patterns of dispersal and philopatry result in a patriarchal society, and although both sexes help, males do more of the nest provisioning than females.

Although nearly all breeding females immigrate into the group, surprisingly, nearly half of the breeding males also appear to be immigrants. This likely explains the relatively low overall relatedness among males and among females. Both sexes of superb starlings also compete intensively for breeding opportunities, which may have implications for the evolution of sexually or socially selected traits like plumage coloration and song in this species. Breeding positions are constantly in flux, and divorce is frequent in this population. However, pairs are generally faithful and extra-pair paternity is on average quite low (10% of offspring and 17% of nests), even though promiscuous females can gain a variety of direct fitness benefits, such as helper recruitment, and indirect fitness benefits, such as increased offspring genetic diversity. Despite low overall promiscuity, extra-pair paternity varies greatly among groups and is influenced by territory quality, with higher rates on lower quality territories with reduced grass cover and lower insect abundance. This pattern is likely the result of females escaping mate-guarding on the lower quality territories where all individuals need to forage further from the nest and the central glade.

Superb starlings live in a variable environment where the amount of rainfall and duration of the rainy season varies unpredictably from year-to-year. Annual variation in precipitation during the most variable period of the annual cycle, the pre-breeding dry season, influences all aspects of life for superb starlings, including breeding roles, stress physiology, immune function, helping behavior, reproductive conflict, and demographic structure. Moreover, cooperative breeding itself may be an adaptation to this uncertain climate, as allowing subordinate helpers to remain in the group may be a risk-averse strategy used by dominant breeders to minimize environmentally induced fecundity variance. Ultimately, the complicated lifestyle of the superb starling, and the degree of cooperation and conflict within their complex societies, is tied directly to the spatially and temporally variable savanna environments in which this plural breeder lives.

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