DOMINATRICKS

Reproductive conflict between female Southern Pied Babblers

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Conflict among individuals is an overt and often costly behaviour that can provide interesting insights into the complex nature of avian societies. With research techniques becoming ever more detailed, unique opportunities to understand the causes and outcomes of such conflict are now possible. **Mandy Ridley** and **Alex Thompson** take a detailed look into the sex lives of the cooperatively breeding Southern Pied Babbler and reveal fierce battles between females for males, infanticide, and the huge cost of conflict to both the group and the females involved.

The sweltering sands and sun-baked riverbeds of the Kalahari are home to the Southern Pied Babbler *Turdoides bicolor*, an intensely territorial species that forages in groups of between three and 15 adults. These vociferous and long-lived birds are cooperative in the strictest sense, with genetic studies revealing that only the dominant pair breed successfully, while the remaining group members help to raise the young produced by the dominant pair. Each group maintains an exclusive territory that it defends aggressively against both neighbouring groups and individuals prospecting for breeding opportunities.

Groups are very tightly knit: the individuals are in constant close association (rarely more than 20 metres apart) and they forage together throughout the day. While the rest of the group is searching for food, the birds take turns to act as sentinel, perching in exposed positions in the tree-tops and using alarm calls to warn the foraging group of any approaching predators. Dominance within the group is very stable and is maintained by aggressive behaviour, which can be both physical and vocal. It includes jumping on subordinates, pecking, displaying (during which the dominant bird approaches the subordinate with primary feathers splayed and down feathers puffed up, thus appearing twice as large as normal), and 'over-marking', or drowning out, the calls of subordinates.

Southern Pied Babblers are long lived and because dominant individuals can remain in power for up to eight years, breeding vacancies are rare and subordinates may have to wait a long time for a breeding opportunity. Genetic analyses have revealed that dominants are very good at monopolising all breeding activity, but they cannot show us the constant attempts by subordinates to usurp the dominant's position and take control. Parentage in this species is not always the result of a straightforward monogamous pairing. Instead, intense battles between the dominant birds and determined subordinates often precede the breeding attempt and, in many cases, delay successful breeding until the conflict is resolved. Any weakness in a dominant individual (such as injury, sickness or age) may act as a signal for subordinates to try their luck, and the prolonged battles that ensue can be overt and extremely costly to the entire group. An example of this type of conflict recently occurred in one of our long-term research groups, The Crusaders.

Play-fighting among group mates appears to be good practice for the real thing. Adult females engage in lengthy and aggressive fights in their quest for absolute dominance.

A typical pied babbler group, The Crusaders comprise four adults: a dominant pair and two subordinates. The dominant male, Lomax, immigrated to the group following the death of the resident male and instantly caused competition between the group's two females. Following the death of her father, the subordinate female, Comix, was now freed from incest avoidance and could mate with Lomax. The only thing preventing her from doing so was the aggressive behaviour of the dominant female, Mopbop.

At the end of a long, dry Kalahari winter, Mopbop severely injured her left leg. This could not have come at a worse time: with such a severe handicap her foraging efficiency was reduced and, despite the abundant insect life available after the early summer rains, her weight did not increase and she was unable to reach breeding condition. It took all of her effort simply to keep up with the group as they moved between foraging sites, and she spent much of her day simply resting in the shade rather than building up fat reserves. With the breeding season under way and Mopbop's injury preventing her from effectively asserting dominance, Comix seized her chance.

Together with Lomax she spent several hours a day building a nest of twigs and grass in a tall riverbed acacia. With Mopbop unable to prevent the union, Comix mated with Lomax and started to lay her first clutch. This was a severe blow for Mopbop: as chicks remain ▷

The Southern Pied Babbler research population is based in the southern Kalahari on a private game reserve. All groups are fully habituated and individually identifiable by means of coloured rings, and long-term life-history data have been collected on all birds in the population for the past seven years.

As a result of high levels of habituation, we are able to accompany the group throughout the day at a distance of one to three metres without causing the birds any distress. They become so used to our presence that they display 'relaxed' behaviour more often associated with mammals than birds. This includes prolonged bouts of play-fighting, which can take several different forms, such as wrestling on the ground, chasing about a bush and hide-and-seek ambushes. The whole group (including the dominant pair) may invest in such 'play behaviour' for several hours a day. An additional benefit of habituation is that we can entice each babbler to jump onto a weighing scale in exchange for a small food reward. This allows us to monitor body mass on a daily basis, which is very important when trying to assess the cost of fighting between females and the body mass gain required prior to egg-laying.

The pied babblers are also very relaxed about our presence at their nesting sites and allow us to put up cameras to monitor activity at the nest. Because pied babblers' nests are often five to 10 metres up a tree, their behaviour in them would remain unknown to us without the use of these cameras. Before we installed our first nest camera in 2006, we didn't suspect infanticide as a form of female–female competition in pied babblers. This new technology and our ability to monitor group behaviour on a daily basis have allowed us to unravel the complex story of reproductive conflict within this species.

nutritionally dependent on adults for several months after fledging, this meant that even if she recovered condition, Lomax would not be willing to start another breeding attempt until the current brood was nearly independent. The only option Mopbop had to prevent Comix from breeding was infanticide.

No sooner had Comix laid her first egg than Mopbop, in her emaciated state, ate it, using the nutrition that Comix had deposited for her offspring to help her regain her own health. After two consecutive days of this egg-eating behaviour, Comix abandoned the nest. At no point did she challenge Mopbop and try to prevent her from eating the eggs, despite having invested several days in building the nest and a week of intense foraging in order to gain sufficient weight to lay her eggs. Notwithstanding the extra nutrition, Mopbop's injury did not heal. Comix, on the other hand, quickly regained her pre-breeding weight. Mopbop's condition continued to deteriorate and she made no effort to begin nest-building with Lomax. Several days after abandoning the nest, Lomax and Comix went through the strenuous task of building a second nest, only for history to repeat itself as Mopbop once again ate the eggs.

During the next couple of weeks Mopbop regained the use of her leg and built up the reserves needed for the expensive production of eggs. Her recovery coincided with the next set of rains, which brought much-needed water and insect life to the Kalahari, but also an unexpected threat. Hundreds of Wattled Starlings had followed the rains and were noisily courting and building their nests in the riverbed acacias. The huge flocks of starlings were constant companions to The Crusaders as they foraged in the food-rich soils along the riverbed.

Back to full health and weight, Mopbop was now able to exert her influence over the upstart Comix. She exercised her dominance in many forms, ranging from aggressive physical attacks to the more subtle 'duet-calling' with Lomax. Soon Lomax was chasing Mopbop in aerial courtship displays and performing the 'invitation walk', in which the male picks up a stick, puffs out his down feathers and waddles towards a female, presenting the stick while giving a low, purring call. After the laborious task of building her first nest and laying her first egg of the season, Mopbop briefly left the nest to forage. On her return she found the shattered remains of her egg at the base of the nest tree.

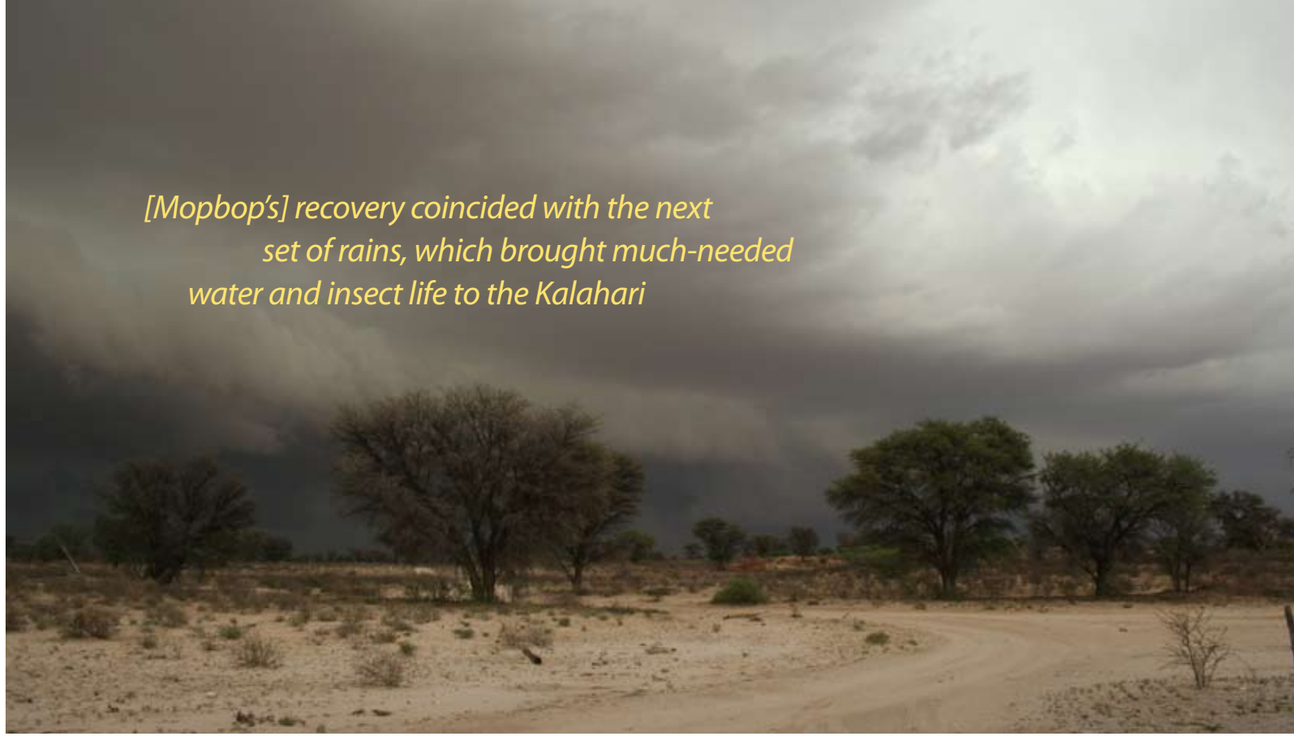
A well-placed nest camera reveals the cost of reproductive conflict: a dominant babbler female is eating the egg of a subordinate to prevent her from breeding successfully.

The culprit? A Wattled Starling. The evidence of this destruction, like the previous infanticide events, was captured on a nest camera. Such predation came as a surprise as Wattled Starlings were not expected to threaten babbler nests. The reason for the destruction was not evident as, after ejecting the egg from the nest, the starling made no attempt to consume the contents for nutrition. The most likely explanation appears to have been competition between Wattled Starlings and Southern Pied Babblers for nesting sites and limited food sources. By destroying the babblers' breeding attempt, the Wattled Starling may have been reducing competition for food when raising its own brood.

In addition to the Wattled Starlings, the rain brought an abundance of insect life and this allowed The Crusaders to embark on their fourth breeding attempt of the season. With all the group members fat from the invertebrate bonanza, the nest was rarely left unattended and the mistake that cost The Crusaders their third nest was not repeated. After brooding her clutch for 15 days, Mopbop was rewarded with the sight of her first chick of the season. Over three consecutive days, all three eggs hatched. Despite her injury at the start of the season, Mopbop invested heavily in the brood, as did her competitor Comix and the rest of the group. Soon the gaping mouths of three large, healthy nestlings could be seen each time the adults returned with food.

Then, despite all the group's efforts, four days before the brood was due to fledge a predator took them during the night and we discovered the remains of the nestlings at the base of the nest tree. It was not clear from the remains what predator had been responsible for the killing. While we have recorded several instances of Southern Yellow-billed Hornbills taking nestlings, usually they take them whole. The fact that the remains were dismembered in so many pieces and that the nestlings' deaths occurred overnight suggests that a nocturnal mammalian predator, such as a genet, was the culprit.

Now two-thirds of the way through the breeding season and having expended a lot of energy on four consecutive nests, The Crusaders ▷



Above *Torrential summer storms are the lifeblood of the Kalahari, bringing much-needed plant growth and insect emergences.*

Below *Feeding young requires a lot of effort by adults, involving the excavation of nutritious larvae in a parched habitat.*

Opposite, below *Being able to measure the birds' body mass on a daily basis gives researchers a remarkable insight into the health and status of all members of the population.*

Stills from nest-camera footage reveal a Wattled Starling ejecting eggs from an unattended babbler nest. This was an unexpected and previously undocumented event.

were both without offspring (in contrast to all the neighbouring groups) and in poor body condition. It was a critical situation. The conflict between the two females had cost them dearly and they urgently needed to raise offspring that could be recruited into their party to help prevent surrounding groups from invading their territory. Comix regained her condition quickly and, subsequent to the death of the dominant female in a neighbouring group (which created a vacant breeding position), she left her own group, preventing any further conflict between the two females. The race was now on for The Crusaders to rear a brood before winter, when food would be scarce and raising chicks would be more difficult.

Fledglings require an extended period of care, representing a massive investment by adults. These young Crusaders birds will require several more months of nurturing before they are fully independent.

Without the competition with Comix to delay matters, Mopbop and Lomax managed to build their nest in only two days and Mopbop was able to forage more intensively. Less than a week after Comix had left, Mopbop laid her first egg. Two weeks later, the fifth clutch of the season hatched. With the help of Lomax and the subordinate male Mexico, Mopbop was able to raise her brood to fledging age and, after five months of continuous intensive effort, The Crusaders recruited three healthy fledglings into their group.

But the struggle was not yet over: young birds require prolonged post-fledging care. They would only start to forage independently after two to three months and would still require some assistance from the adults for up to five months. With winter fast approaching and the abundance of insects declining rapidly, The Crusaders had a lot of hard work ahead of them. However, if they successfully recruited all three fledglings into the adult population, the group would be able to defend its territory borders and assure its future.

Having the two females competing for reproduction had been very damaging to the group; through infanticide and overt aggression its reproductive output was greatly reduced. Groups that have no reproductive conflict can raise multiple broods and may recruit up to eight fledglings per season. The only way that The Crusaders could breed successfully was for one female to be in complete control. Now, with her own son and daughters in the group, Mopbop will not be challenged for breeding status and thus her future as the dominant female is secure.

After a season of disorder, conflict and debilitating injury, and with three new recruits to help raise next season's broods, the future finally looks bright for Mopbop and The Crusaders. □

Read more about Southern Pied Babblers in Africa – Birds & Birding *11(3): 50–57 and 12(5): 56–59.*