



New Director Issue

This month is one of change; we say a warm goodbye to Margaret Kinnaird, Mpala's Director of seven years, and wave hello to incoming Director Dino Martins.

read more





Costs of Reproduction

Sarah Guindre-Parker discusses her PhD research on superb starling behavior and reproduction.

read more

Leaving the Pack

Wild dog dispersal, tracked with GPS collars, is critical to maintaining genetic diversity in the species.

read more





With a Little Help From Their Friends

Ant-acacia mutualism is a highly important relationship in the Kenyan bush. Kirsten Prior explains her lab's research on this topic.

read more

Secrets of Survival on the Savannah

Yi-Ru Cheng writes about the complex social behavior, specifically cooperative breeding, of the grey-capped social weaver. read more



Time To Say Goodbye...

Margaret Kinnaird

It's time to say goodbye to Mpala. The years have been rich -- full of challenges and achievements, a few heartaches and much joy. I have had the great pleasure of helping Mpala double in size and budget, significantly expand infrastructure, make the centre substantially more 'green', and vastly improve the lives of our staff. I have enjoyed deepening relationships and expanding partnerships, and have had the pleasure of overseeing a large increase in Kenyan involvement at Mpala by providing internships, scholarships and other educational opportunities for young students and scholars. It has been a thrill to host top-notch researchers from around the world and share in their discoveries. And it has been equally satisfying doing whatever I could to move private lands conservation forward in Kenya.

There is much I will miss upon leaving. I will miss the expansive, immeasurable beauty of the Laikipia landscape. I will miss the sights and sounds of elephants – especially the leathery slap of ears and tummy rumbles of the families that frequent my saltlick. I will miss the plucky hornbills that awaken me every morning with insistent taps on the bedroom window. I will miss the hundreds of hyraxes draped in seductive poses on the rock walls. I will miss my family of dwarf mongooses, squeaking with delight over a handful of peanuts. I will miss the little dik-diks trying to act big during mock fights. I will miss the coughs, whoops and roars that make me stir in the night. Most of all I will miss my staff, their dedication, their wonderfully uninhibited laughs, their complicated handshakes and their enthusiastic two-armed waves. I will even miss their salutes. Most of all, I will miss the people behind them.

Good-bye to all and thank you for enriching my life. •



return to title page

MPALA MEMOS July 2015

...And Hello

Dino J. Martins



As Mpala bids farewell to Director Dr. Margaret Kinnaird, we welcome incoming Director Dr. Dino Martins. Dr. Martins is one of Kenya's leading entomologists. He was previously the Academic Field Director for the Turkana Basin Institute Field School and is an Assistant Professor at Stony Brook University in New York. He holds a PhD in Organismic and Evolutionary Biology from Harvard University. Dr. Martins' current research is focused on the interactions between insects and plants, specifically ants and plants, and pollinators and flowers. He recently published a pocket guide to insects of East Africa, and previously published a handbook on pollinator diversity in East Africa.

Dear students, scientists, friends and the wider Mpala community,

I am deeply honoured and humbled to have been selected to serve as the director of the Mpala Research Centre. I thank the Search Committee, Board of Trustees, National Museums of Kenya, Kenya Wildlife Service, scientists and Laikipia community for their support and feedback during this process. This is a very exciting time to be a scientist in Kenya and I look forward to meeting, talking and exploring how we can work together to sustain, grow and celebrate science and education at Mpala.

Firstly, I would like to salute the tenure of Dr. Margaret Kinnaird who has ably served the students, scientists and staff of the research centre for the last eight years. Dr Kinnaird leaves an outstanding legacy that is evident in the cutting-edge, world-class science accomplished here. She has forged a dynamic team, instituted systems in management and infrastructure and built important links with local and international institutions. Dr. Kinnaird's accomplishments have brought an energy and optimism that is palpable at Mpala today. Therefore, we all owe her our thanks and gratitude for her thoughtful and dedicated leadership.

Mpala is one of the world's leading field research centres and as part of the greater Laikipia ecosystem offers students, scientists and visitors the opportunity to explore one of the most beautiful and interesting parts of the world. From termites to elephants, hornbills to hippos, livestock to public health, the potential for exploration of new ideas and questions here is almost limitless. And the potential links between these questions, synergies and opportunities are themselves myriad like the many links between species in this ecosystem.

This is also a challenging time for Kenya as a country. It is without a doubt a time of great change. Social, political and environmental changes are rapidly sweeping through our world, and Laikipia is no exception. Mpala offers us a tantalising glimpse of life on the planet carrying on its evolutionary dance to an ecological drumbeat. The future presents both challenges and opportunities to link this deep understanding of the world around us with practical knowledge to make a difference in the lives of people in Laikipia, Kenya and beyond.

return to title page



I very much look forward to exploring new ideas and projects, building on Mpala's strengths and connecting students and scientists with opportunities that will have a broader impact across the Horn of Africa. I would also like to let you all know that I would be happy to listen to questions, concerns or ideas that you might have related to Mpala or research in Kenya. I will continue to communicate regularly with you, and my door will always be open to all of you at Mpala – so please feel free to stop by, even if it's just to say 'Habari!'.

I would also like you all to welcome our new Princeton in Africa Fellow, Danielle Martin who will be joining us in July and thank our out-going fellow, Sally Goodman, who has been a wonderful part of the Mpala team for the past year.

Looking forward to working with you and moving Mpala forward,

Kind regards, Dino J. Martins (dmartins@princeton.edu)



A storm lights up the sky above the research centre during the final days of this year's long rains.

return to title page

MPALA MEMOS July 2015

Costs of Reproduction

Sarah Guindre-Parker

All sexually reproducing organisms are faced with a fundamental decision: to invest valuable time, energy, and resources in reproduction or in their own survival. This trade-off between fertility and longevity is called the 'cost of reproduction' and has been documented across a diverse range of animals including humans, small mammals, birds, and fish.

The costs of reproduction are thought to underlie a number of behaviors in the animal kingdom, including the evolution of many mating and social systems. For example, cooperative breeding – when three or more individuals raise young together – is a behavior widely assumed to result from costly parental care. In theory cooperative breeding animals are unable or unwilling to raise young as a mother/father pair and need additional help to successfully raise their young. However, the costs of reproduction in cooperatively breeding species have rarely been studied. For my PhD dissertation, I have been studying the costs of reproduction in a free-living population of cooperatively breeding superb starlings (Lamprotornis superbus). My research goals include determining whether animals living and reproducing in social groups experience costs of reproduction, and whether cooperative breeding can help to lower the costs of reproduction.

My research focuses on a population of >1000 superb starlings that has been monitored continuously since 2001 at the Mpala Research Centre. Superb starlings live in year-round territorial groups of 20-45 individuals, and an individual may live up to 12 years in the wild. Within each group, multiple mother/father pairs can breed at any given time. In addition to the parents, all nests have between one and ten birds that bring food for the young. Superb starling chicks are mainly fed insects, thus these birds breed during the long (March to June) and short (November-December) rainy seasons when insects are most abundant.



An active superb starling nest in an acacia tree, containing two blue eggs.

Each breeding season, adult superb starlings adopt one of three social roles: 1) breeders (i.e. the parents), 2) helpers (i.e. individuals contributing to offspring provisioning), or 3) non-breeders/non-helpers (i.e. non-breeding birds that do not contribute to raising the offspring). The parents care for their chicks to the greatest extent, while the helpers provide some food for the young (although to a lesser degree); both these groups should have some costs of reproduction in doing so. Conversely non-breeder/non-helper birds should not have any costs of reproduction because they spend all their time, energy and resources on themselves.

return to title page



To determine whether the costs of reproduction lead to differences in lifespan based on breeding role, I used a long-term dataset of observations. Individuals born in or immigrating into our study population are trapped and color-banded with a unique combination of bands on their legs. These allow our team to observe and track individuals throughout their lives. Specifically, we determine breeding roles every rainy season by performing a series of observations at active nests (i.e. nests with eggs or chicks). Because birds typically immigrate into a group when they are young, and stay in the same group until they die, we can estimate the minimum lifespan of a bird based on when they arrive in a group and when they are no longer observed in that same group.



Two young superb starlings approaching a ground trap baited with papaya. These birds will be caught and color banded.

My research has shown that individuals' lifespan varies in relation to social role (i.e. the primary social role adopted throughout an individual's life), and thus how much time and energy they allocate to feeding young. Breeding individuals, who care for young to the greatest extent, have significantly shorter lifespans than non-breeding/non-helping individuals who do not contribute any care for the young. Helpers, who care for young to a lesser extent than breeders, lead longer lives than breeders, but shorter lives than non-breeders/non-helpers.

An adult superb starling collecting insects to bring back to the nest to feed chicks.



return to title page

These results show that superb starlings do experience costs of reproduction. These costs of reproduction vary from bird to bird, such that individuals providing greater care for young experience greater declines in survival. Ultimately, being a breeder rather than a non-breeder/nonhelper can reduce lifespan by an average of two years. This is a rare example of how reproducing can alter lifespan in a wild population. My future research will expand upon these findings in two ways: 1) I will determine whether having a greater number of helpers at a nest can reduce the cost of reproduction for breeders, and 2) I will determine whether having less food available during reproduction (linked to rainfall) can increase the cost of reproduction. •

Leaving the Pack



Stefanie Strebel & Helen O'Neill

African Wild Dog packs are formed when a group of females meets a group of unrelated males. During the formation of the pack, one male and one female will become dominant over their brothers and sisters and become the pack's alpha male and female. Wild dog packs are centered on the alpha male and female, they are normally the only individuals who reproduce; the other founder members help them raise their pups but usually don't produce any themselves. Each year's pups will stay with the pack to help raise the next year's pups, meaning packs will often increase in size each year. The more the pack grows, the better it becomes at growing as there are more individuals helping to hunt and care for the pups. However, for any individuals other than the alphas, there is very little opportunity to breed! In order to get a chance to breed themselves, young adults split off from their natal pack, usually in single sex groups, in search of other wild dogs with whom they can form their own pack. This behavior is called dispersal, and enables the formation of new packs and prevents inbreeding.

Wild dogs, as one of the widest-ranging members of Africa's large carnivore guild, cover huge distances when dispersing that can expose them to tremendous risk if they move out of wildlife-friendly landscapes into areas less tolerant to the presence of predators. Human-dominated areas can pose a significant survival threat to dispersing wild dogs, particularly if the wild dogs attack livestock. Even if such events occur infrequently, the dogs are at great risk of being targeted for retaliatory killings. There are also risks from contact with domestic animals, which can expose wild dogs to potentially fatal diseases such as rabies. However, dispersal is crucial for wild dog populations because it enables the gene flow required to keep populations robust and healthy.

The Kenya Rangelands Wild Dog & Cheetah Project is working to promote landscape connectivity for wild dogs and cheetahs by identifying corridors and landscape features that aid connectivity between different areas, as well as features that may disrupt landscape level connectivity. GPS collars are crucial to achieving this objective as they provide detailed location data on the daily movements of our study animals and allow us to detect land use types and geographical features that facilitate or inhibit movement. They are particularly invaluable in recording the movements of dispersing wild dogs - it would be impossible to keep up with those individuals otherwise.



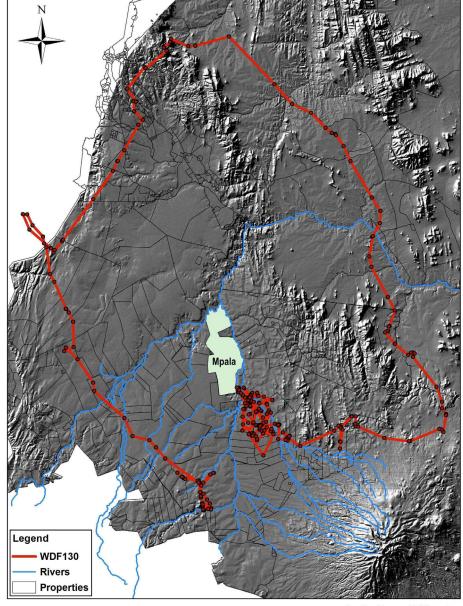
A pack of wild dogs spends the day resting in the shade.

return to title page



An example of the amazing data we can collect from these collars came from a young wild dog earlier this year. In mid-March, one of the project's GPS-collared wild dogs, a yearling female (WDF130), dispersed from her natal pack - the Ol Pejeta Pack. Together with her two sisters, she travelled over 500 km in one month in search of other wild dogs and new territory. Their voyage took them in a huge loop (see Map), passing near Lake Baringo to the west and crossing the Karisia mountains, then turning back south and skirting Lewa before spending some time around Ol Jogi, El Karama and Mogwooni. Interestingly, while other wild dogs have tended to concentrate their activities in hilly areas, WDF130 mainly skirted around hills in her movements. This might reflect her upbringing on Ol Pejeta, which is more open and less hilly than other parts of our study area. We are waiting to see if she decides to settle near southern Ol Jogi, of if the group continues their search for mates.

WDF130 (OI Pejeta Pack disperser) Movements 12 March - 15 April 2015



© Kenya Rangelands Wild Dog & Cheetah Project

0 5 10 20 Kilometers

WDF130's dispersal track is just one of the movement da-

tasets that the project is continuing to collect from dispersing wild dogs and cheetahs in Laikipia. Combined, all this data will enable us to evaluate the degree to which landscapes are still connected, vital information for the conservation of these two wide-ranging species. •

Acacias Get By With a Little Help From Their Friends

Kirsten Prior

Life in the Kenyan bush may seem to be dominated by the struggle among organisms: predation, herbivory, and competition. However, cooperation among organisms, or mutualism, also plays a critical role in structuring the communities and ecosystems here at Mpala. A great example of a keystone mutualism is the interaction between the whistling thorn acacia, Acacia drepanolobium, and the several species of symbiotic ants it hosts. In black cotton soil, whistling thorn acacia occurs at high densities as an overstory monoculture. The overwhelming dominance of these trees is due largely to the protection provided by the ants from megaherbivores like elephants. Previous work indicates the potential for drastic changes to this ecosystem if the ant-plant mutualism is lost or altered. Uncovering the mechanisms driving this mutualism is important, given its key role in this ecosystem.

Mutualistic interactions are unstable from an evolutionary and a population dynamic standpoint. Evolutionary theory, for example, suggests that mutualisms should be unstable because the temptation for a partner to "cheat" is high. That is, it would be advantageous for a partner to gain fitness benefits without providing rewards back to its partner, especially if rewards are costly. Understanding how mutualisms have arisen and are maintained in nature is an open question in biology. To this end, ecologists measure costs and benefits of species interactions. To accurately do so, it is essential to measure costs and benefits in realistic ecological settings, such as in the context of other community members and environmental heterogeneity. The ability to conduct large-scale manipulative experiments in an intact ecological community is one of the reasons that Mpala is such an ideal place to study the



Acacia-ants protect trees from mega-herbivores like elephants.

evolutionary ecology of mutualisms.

We already know quite a lot about the cost and benefit story for this ant-plant mutualism. The benefits of the mutualism to symbiotic ants from the plants seem obvious. Acacia drepanolobium provides housing in the form of swollen thorns (domatia) and carbohydrate resources in the form of extra floral nectaries (EFN). From previous work, we know that there is a cost to the plant of producing these resources for ants. Trees housing some species of symbiotic ants grow more slowly than trees free of ants, and these resources for ants

return to title page

are relaxed when ants are not needed (i.e., in the absence of herbivores). Despite the high cost of housing ants, they provide a net benefit to the tree. The ants protect trees from large herbivores – mainly elephants that can catastrophically damage trees. Elephants avoid trees that have highly active ant colonies, and remov ing ants from trees can cause trees to experience major damage by elephants, with trees often being knocked over or completely uprooted.

As I alluded to above, these ants and trees do not interact in isolation. There is another mutualistic partner that might play an integral role in this mutualism. The most common and arguably the "best" mutualist ant, Crematogaster mimosae (RRB), tend honeydew-producing scale insects. Mutualisms between honeydew-producing insects and ants are common in nature. Scales provide a carbohy-drate-rich resource to ants and ants tend scales, providing them with several services, including protection from predators and pathogens. Scales are sap-sucking insects that are costly to the tree. We are interested in how the interaction between ants, scales, and the tree play into this mutualism story. If the scales are costly to the tree, why do ants tend scales? Do scales provide a benefit to the ants, and in turn the tree? This question of why ants tend scales is especially curious in this ant-plant system given that, unlike many other cases in which ants tend scales, direct carbohydrate resources are also provided to the ants by the tree in the form of EFN.



Ants get carbohydrate resources from two sources: (left) from extra floral nectaries (EFN), and (right) from tending honeydew-producing scale insects.

Our team is currently examining the role of scale insects in this mutualism. Generally, we observe that trees with highly active ant colonies also have more scales. From these observations alone, we don't know what the cause and effect of this relationship is. Is the higher abundance of scales on trees with more ants just a function of more ants? Or, do the scales also benefit the ant by increasing their colony growth and activity? To untangle this relationship, we set up a manipulative experiment, where we reduced resources to ants (domatia, EFN, and scales). We examined ant colony growth,

return to title page

continued on page 11

MPALA MEMOS July 2015

and the ability of ant colonies to resist competition from neighboring ant colonies and to protect trees from herbivores. We are finding that scales seem to be pretty important. We know from previous work that trees with larger colonies are better at resisting attacks by elephants. We found that scales influence ant colony size and population growth by increasing the production of reproductive ants, and by enabling more ants to pack inside domatia (likely via the production of "carton" material produced from waste and debris that provides extra living space for ants). Scales also influence the ability of ant colonies to protect trees from herbivores and takeovers. Trees with scales were more resistant to takeovers by neighboring ant colonies, and also had less damage from elephants. Crematogaster mimosae tends scales, while most of the other symbiotic ant species don't (or at least not to this level). Perhaps this carbohydrate boost contributes to the ecological dominance of this ant species in the community and its ability to be the highest-quality partner – or protector of the tree.

Still the question remains, why tend scales if ants can obtain carbohydrates from EFN? Do scales as a resource have any advantage over EFN? Well, EFN production is largely under the control of the plant. When new shoots are produced, new EFN are produced. In contrast, scales are likely largely under control by the ants. When ants spend more time tending scales, scales on trees likely increase.

Perhaps scales play an important role in this system by buffering ant colonies from low-carbohydrate scenarios, such as under stressful conditions, when new shoot and EFN production is low. When EFN production is low, and the ants can't increase the production of carbohydrates from this source, perhaps they regulate their carbohydrate source by increasing scale tending. In fact, in our experiment, we found more scales on trees in which EFN were reduced. We are interested in pursuing this question regarding the context dependency of this "tripartite" (three partner) mutualism in more depth. That is, is the relationship between scales, ants, and trees particularly strong under stressful environmental conditions? •

Undergraduate researcher in the Palmer Lab, Jess Gunson, and research assistants Stephen Kesiyo and John Lemboi, set up an experiment to see if scales become more important to ants when trees are stressed. Jess is stressing trees by applying simulated elephant damage.



Secrets of Survival on the Savannah



Yi-Ru Cheng

The grey-capped social weaver faces many challenges living on the savannah. The ecosystem here is known for unpredictable rainfall, which means unstable food resources for raising young. Moreover, nest predation is extremely high (>80%), and roaming elephants often destroy weaver colony trees (Fig. 1). Despite the great environmental pressures, the population of the grey-capped social weaver is abundant, which leads one to wonder about their survival strategy. A unique feature of this species is their complex social behavior, as their name implies. These weavers prefer living in a colony and breeding as a cooperative group in which more than two individuals par-



Fig 1. Half of the colony trees are destroyed by elephants each year.

ticipate in the parental care. The Weaver Project at Mpala aims to understand the social structure and cooperative behavior of grey-capped social weavers and investigate how their social networks change with environmental conditions.

The social dynamics in a complex system are often difficult to observe. We use PIT (passive inte-



grated transponder) tags on birds to automatically record their movement among different nests and construct the social networks (Fig. 2). Preliminary data show that the birds move between different nests and even colonies through the rainy season. In general, social networks are more stable during the breeding stage than nonbreeding stage. While a pair of birds often maintains two nests at a time.

Figure 2. Equipment set-up for collecting social network data.

return to title page



some birds slept in up to five different nests through the sampling period. This joint-sleeping behavior might be a way of maintaining the social bonds. How these findings relate to the fluctuation of rainfall across years awaits more analysis.

A colony of grey-capped social weavers is composed of multiple family groups. Birds that build their nests nearby to one another are generally relatives, according to the results of genetic testing. Offspring, particularly males, tend to stay close by and form breeding groups with their parents. When conditions are favorable and predation is low, they act as breeders; however, when the nests fail, either due to predation or food shortage, they become helpers and feed the nestlings of their relatives (usually their parents). In some cases, older members of the colony will even help feed their 'grandchildren'. The social bonds of the family members allow the birds to maintain flexibility between being a breeder or helper, and increase the probability of passing on their genes in a highrisk environment.

As mentioned previously, nest predation, particularly during the egg stage, is extremely high for the grey-capped social weaver. Over 90% of nest predation is due to the common egg-eater snake (*Dasypeltis scabra*) (Fig. 3), a specialized egg-eating machine. We found that the birds have developed an anti-predation strategy of tossing out their last-laid egg in the clutch when they find their eggs to be missing. Destroying one's own egg seems odd at first, but makes sense for a bird that lives a long life and can breed multiple times in one rainy season. In other words, when the expectation of future



Figure 3. The common egg-eater (Dasypeltis scabra) is the main nest predator of grey-capped social weaver.

reward is low, they stop investing in the market and bet on the next investment.

Throughout the world, only about nine percent of bird species are cooperative breeders. Most of these species are found in semiarid environments like the African savannah. We hope our findings on the grey-capped social weaver will provide insight on surviving in this harsh environment and explain why the cooperative breeding strategy is prevalent for African birds. •

Mpala At A Glance



Seventeen undergraduate students from Michigan State University stayed at Mpala for three days in May as part of a summer course in Kenya on Behavioral Ecology of African Mammals.

Seven University of Florida undergraduate students came to Mpala in late May for a 2.5-week field course on East African Ecology.

On May 30, thirty-one form one students from Daraja Academy visited the Research Centre for Daraja Day. They learn about opportunities for careers in science and conservation and about the research that takes place at Mpala. The students spent the morning participating in fieldwork with researchers. Kenna Lehmann

Michigan State students discuss their work at Mpala's River Camp.

The Koobi Fora Field School, run by the National Museums of Kenya and George Washington

University's Center for the Advanced Study of Human Paleobiology, held a one-week program at Mpala during a six-week field course in paleoanthropology, the study of human origins.

The MWF Board of Trustees held its annual meeting at Mpala from June 20 to 22.

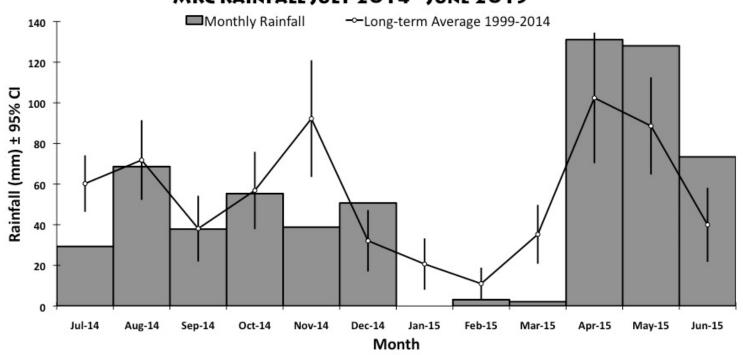
PhD student Sarah Guindre-Parker points out a superb starling nest during Mpala's Daraja Day.

University of Florida students pose for a photo.









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