Behavioral Ecology: The Evolution of Lion Cooperation and African Conservation

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Abstract

Lions (*Panthera leo*) are the only true social cat species in the world, living in prides of varying sizes and, to one degree or another, displaying cooperation to ensure survival and the passing on of genes to future generations of offspring. But does a greater knowledge of the evolution of lion cooperation as a survival response to evolutionary pressures promote a better understanding of these apex predators that will effectively champion sound conservation policies? By examining evolutionary biology and cooperation within an evolutionary context, how it plays out in lion society, and briefly analyzing how such discoveries outline the need for appropriate habitat conservation and genetic preservation in the literature review, this argumentative essay will stress continued field investigations into the evolution of lion cooperation, a necessary preface to determining effectual *in situ* and *ex situ* management strategies. Doing so will successfully protect these charismatic megafauna, associated predator and prey species, and the remaining biodiversity of the ecosystems they inhabit.

Pair of juvenile lions (*Panthera leo*) in Uganda's Murchison Falls National Park. Photo by Michael Schwartz.

Introduction

Despite their dwindling wild population, lions (*Panthera leo*) continue to fascinate people from all walks of life. From the majestic and phenotypically varied manes adorned by males that serve as signals of virility to females (West & Packer, 2002) to a pride of lionesses toppling large prey species such as cape buffalo (*Syncerus caffer*), these apex predators exist not only against the terrestrial backdrops of kopje-dotted plains and open woodlands, but also in a plethora of nature documentaries, movies, sports logos, and other lion iconography (Schwartz, 2017).

What arguably captivates people most about lions, however, is that they are the only truly social felines of all 36 species of wild cat (Antunes et al., 2008). While other species such as the tiger (*Panthera tigris*), leopard (*Panthera pardus*), jaguar (*Panthera onca*), mountain lion (*Puma concolor*), and cheetah (*Acinonyx jubatus*) occasionally come together as mating pairs within their respective species, and although all feline mothers are known to care for, nurture, and rear cubs up until their sub adult years, it is only lions that maintain larger groupings. Sisters, mothers, daughters, grandmothers, fathers, sons, uncles, brothers, and unrelated males will live, hunt, play, reproduce, rear cubs, and defend one another from danger, including their gravest of natural threats: nomadic lions and/or lionesses from different prides. To reiterate, no other species of wild cat is known to exist in such high intraspecific numbers or cooperate to such a degree as to ensure fitness and the survival of a bloodline.

Yet for all that cooperation has afforded them, lions are becoming ever more an endangered species, with defaunation largely resulting from habitat loss and human-wildlife conflict, a lack of prey resulting from bushmeat poaching, and unsustainable hunting. From what was once a population of 200,000 lions across the African continent roughly a century ago, there are now estimated to be no more than 20,000 extant individuals (Rust, 2018).

Considering all that has been discovered about the evolution of cooperation and the evolutionary construct of cooperation as it relates to African lions, would continued research inform sound conservation policies that can aid conservationists and policymakers in protecting lions from ever increasing anthropogenic threats?

To answer such a question, it is imperative to first analyze and compare earlier studies of cooperation as a byproduct of evolution vis-à-vis natural selection, followed by a look into the previous research of the evolutionary aspects of cooperation in lion society to gain a better understanding of population genetics, pride structures, and identifying populations as evolutionary significant units (McGowan, Kesler, & Ryan, 2010).

Literature Review

Gardner et al. (2009) define cooperation as, “any adaptation that has evolved, at least in part, to increase the reproductive success of the actor's social partners.” Within the context of cooperation as a product of evolutionary biology is a theory developed in 1964 by the late English evolutionary biologist, W.D. Hamilton. Coined inclusive fitness, it, “describes how well an organism transmits copies of its genes to future generations."

According to Gardner et al., inclusive fitness is owed to either mutual cooperation (also known as direct fitness benefits) or altruistic cooperation (also known as indirect fitness benefits). A more concrete description of direct and indirect fitness is given by Gardner et al. in the following:

> This theory is based upon the understanding that adaptations function for the purpose of transmitting the underlying genes to future generations, and that this can be achieved by either (1) increasing the reproductive success of the individual ('direct fitness' benefits); or else (2) increasing the reproductive success of other individuals who carry copies of the same genes ('indirect fitness' benefits).

Gardner et al. classify inclusive fitness theory into four types of social behaviors. The previously mentioned notion of altruism incurs a cost to the actor while benefiting the recipient.

The other aforementioned concept of mutualism (also known as mutual benefit) is beneficial for both actor and recipient. Selfishness, meanwhile, benefits the actor while incurring cost to the recipient. Lastly, spite is viewed as the behavior that incurs cost to both actor and recipient (Gardner et al., 2009; Hamilton, 1964, 1970; West et al., 2007a, b), though this can hardly be deemed cooperation with the intent to increase reproductive success.

Regarding the subject matter at hand, direct fitness benefits and its association with mutualism bears closer examination. A portion of the Gardner et al. study specifically draws attention to a much smaller African mammal, the omnivorous meerkat (*Suricata suricatta*). By living and cooperating in large groups, meerkat members benefit through an increase in success variables such as overall survival, substantial foraging, and, in similar fashion to lion cooperation, winning intraspecific battles (Gardner et al., 2009), which will be briefly touched upon later.

Meerkat cooperation also includes the communal rearing of offspring, which lionesses likewise share in what is known as a crèche (University of Minnesota, n.d.). But to reiterate, the greatest benefit derived from this level of cooperation is the enhancement of genetic fitness in association with survival and reproduction.

Recall that Darwin posited that evolution by natural selection is dependent on, "success in leaving progeny," while at the same time recognizing that success can, at times, be achieved through dependency. Accordingly, and in order to better relate this to macro-level cooperation in lion society, it is imperative to dig down to the genetic level. Denison and Muller (2016) demonstrate this by calling attention to eukaryotic cells, which are multicellular, found in plants, animals, and fungi, and share a division of labor (Darwin, 1859; Denison & Miller, 2016; Zhang et al., 2016).

Their brief description of cooperation through division of labor notwithstanding, Denison and

Muller elaborate by describing how these cells contain mitochondria, used in the generation of energy through respiration. As descendants of symbiotic bacteria, "surrounded by their own membranes and containing their own DNA," mitochondria eventually integrated with their host cells, and have since lost an excess amount of genes, so much so that they would be unable to survive and reproduce apart from the host cells, thereby demonstrating symbiotic cooperation (Denison & Muller, 2016).

Such similarities, according to Denison and Muller, suggest that plants, animals, and fungi, "evolved from a one-time origin of this ancestral symbiosis between two microbial species," stressing the ease with which cooperation can evolve among genetically identical cells (Denison & Muller, 2016).

As such, multicellular organisms like eukaryotic cells provide a wonderful illustration of cellular cooperation through this division of labor, collectively working in a number of capacities to form the tissues and organs of complex organisms (Denison & Muller, 2016) like meerkats and lions. Moreover, Denison and Muller attribute the evolution of these systems to the notion that every cell that comprises a multicellular individual carries, "an identical (or nearly identical) genome."

Denison and Muller also write that, "genetic similarity among multicellular individuals...plays a major role in the evolution of cooperation on the macro level," and that, "close relatives are more likely to share genes, including genes for cooperation," thus concluding that kin selection will favor cooperation. This echoes the example illustrated by Gardner et al. regarding familial meerkat cooperation, though it is noteworthy to mention that despite the majority of meerkats being related, there are sometimes individuals that are not necessarily blood relatives. This, too, is mirrored in lion units.

Turning back to cooperation among African lion intra-groups (prides), Packer questioned togetherness as an evolutionary construct when weighing it against the evolutionary understanding that if an animal is too generous, others might benefit at its expense. This renders cooperation a bit puzzling, especially in a world where success is determined by, "a lifetime production of surviving offspring" (Packer & Pusey, 1997). Yet Packer, Gilbert, Pusey, and O'Brien shined some much-needed light on this inquiry by performing a molecular genetic analysis of lions in Tanzania's Serengeti and Ngorongoro Crater ecosystems that Denison and Muller's statement on kinship and cooperation retroactively corroborates.

Aptly named, *A molecular genetic analysis of kinship and cooperation in African lions*, Packer et al. (1991) utilized DNA fingerprinting to highlight the complex but necessary kinship structure of lion prides. Their findings indicated that, "female companions are always closely related...male companions are either closely related or unrelated...and mating partners are usually unrelated."

A paternity analysis revealed that the success of male reproduction is altered as male coalition size increases (Packer et al., 1991). In other words, the inclination to form male coalitions with non-relatives is reduced as coalition sizes grow larger. Hence, Packer et al. discovered that certain intra-group males will only act as, “non reproductive ‘helpers’,” if the coalition chiefly consists of close relatives. This, according to Packer et al, clearly demonstrates kin selection, since male lions acting as helpers are decreasing their own chance of survival and reproduction but increasing that of male relatives who share their genes.

It must be emphasized, however, that despite their own lack of reproductive success, these ‘helper’ males are still ensuring the passing on of their own genetic representation as it relates to their kin siring offspring, thus affirming the enhancement of personal fitness associated with cooperation between relatives under the auspices of natural selection. For Packer et al. (1997), this means that, “their presence increases the reproductive success of their companions,” by virtue of a coalition’s strength in numbers. In short, a male’s reproductive success largely depends on how well his coalition can withstand challenges from outsiders.

Recalling the Gardner et al. observation of meerkats, cooperative success can be measured by the ability of family groups - related and unrelated - to repel outside meerkat groups. Likewise, lions exhibit similar behavior, as male coalitions will roar in unison (Packer & Pusey, 1997) to ward off any outside lion that would threaten to encroach on their collectively-owned territory, not to mention physically protect one another from interlopers and marauding nomads should it come to that.

While not all males will take part in reproduction if the coalition is larger and more closely related, smaller coalitions of unrelated males share more reproductive responsibilities as further elucidated:

> Previous explanations for cooperation among male lions did not require kinship to maintain the behaviour. Each male was assumed erroneously to father an equal proportion of offspring in all coalition sizes, and therefore to gain equally as per capita reproductive success increased with coalition size. But it is now clear that this is only true for small coalitions, kinship is essential for the maintenance of larger coalitions where reproduction is highly skewed (Packer et al., 1991).

This thorough understanding of the social hierarchy and cooperation of lions by Packer et al. stresses the need for conserving reasonably large habitats on the African continent in order that lion intra-groups can avoid inbreeding and potential extinction, as inbreeding would lower intraspecific variation and therefore fitness, causing the next generation of offspring to be less likely to survive and reproduce; this would express itself through an increasing number of genetic disorders resulting from more frequent occurrences of incestuous matings (McGowan et al., 2010; Gillespie, 1998).

It is no surprise, then, to see large swathes of wilderness such as the Serengeti National Park in Tanzania set aside to accommodate such cooperative behavior and protect lions as an evolutionary significant unit, which is defined by criteria such as geographic separation, genetic monitoring, and, "locally adapted phenotypic traits caused by differences in selection" (Smith, 2004). It should be added that despite the fact that the Serengeti boundary was demarcated prior to this study, these findings reinforce the argument against calls for park fragmentation, which has become the subject of contentious debate in recent years (Blanton, 2014).

Though kin selection was found to be one evolutionary component of lion cooperation, another key discovery made was mutualism exhibited in male coalitions, which Grinnell, Packer, and Pusey (1995) uncovered in a different field study. In order to determine if male cooperation was based on the evolutionary models of kinship, reciprocity, or mutualism, Grinnell et al. utilized recorded playbacks of manufactured lion "roars" for a study population of 200 lions in Tanzania's Serengeti ecosystem (Grinnell, Packer, & Pusey, 1995; Schwartz, 2018).

Under mutualism, individuals from separate or same-species groups will benefit from their interaction, though such behavior does not include altruism (Landry, 2010). The Grinnell et al. study, *Cooperation in male lions: kinship, reciprocity or mutualism?*, confirmed mutualism as lion coalitions would collectively rush, "to investigate the manufactured roars generated by 'intruding' males in preparation to defend their territories" (Grinnell et al., 1995; Schwartz, 2018). Grinnell et al. (1995) detail this profound discovery in the following selected portion of their study:

> Males did not appear to condition their cooperation on either the relatedness or the behaviour of their companions. Kinship did not influence the speed with which companions reached the speaker, the extent to which males monitored each other's behaviour or the degree to which males spread out while approaching the speaker. Similarly, males did not appear to base their responses on the behaviour of their companions.

Moreover, the Grinnell et al. findings confirmed not only mutualism, but Packer's hypothesis that male cooperation removes the temptation for an individual lion to defect if an outside challenge occurs, primarily since a male's, "ability to repel intruders and maintain pride leadership would be reduced if his partner(s) were killed or wounded," thereby ending individual male reproductive success (Packer et al., 1988; Packer et al., 1991; Grinnell et al., 1995; Schwartz, 2018).

Once again, such a profound understanding of lion cooperation under the aegis of evolutionary biology helps underscore why adequate space is paramount to prevent a genetic bottleneck as recapitulated in the following:

> When there are too few individuals in a population, cousins or siblings may be forced to mate with each other. Genetic drift, or random changes in the genetic makeup of a population, can result in the increased prevalence of dangerous genetic disorders simply by chance in small populations (Gillespie, 1998).

Taking the environment into further consideration, the ecosystem coupled with genetics plays a huge role in the evolution of lion cooperation. More recently, researchers Mosser, Kosmala, and Packer (2015) hypothesized that, "group territoriality may be an emergent property, which evolves due to synergistic interactions of landscape structure, population density, and behavior."

In essence, they posited that lion sociality likely evolved from typical feline patterns of solitary territoriality when two different conditions converged on one another: an environment that was productive and, "heterogeneous at the appropriate scale," and individuals carrying a predisposition toward cooperative defense of territory resulting from genetic inheritance (Mosser, Kosmala, & Packer, 2015).

From an environmental perspective, a lioness's reproductive success and individual fitness is largely dependent on river confluence access - Mosser et al. (2009) refer to these localities as "hot spots" - which provides water, food, and shelter. As for inheritance, all individual lions possess either a solitary or social genotype (Mosser et al., 2015). By utilizing existing empirical evidence related to African lions, and through the creation of a spatially explicit and stochastic simulation, Mosser et al. demonstrated that upon reaching maturity, solitary individuals will leave the natal group and live alone, while social individuals will either remain in the natal group or leave depending on what natal territory is available and the degree to which it will support them as adults (Mosser et al., 2015).

As lion social groups primarily consist of related individuals, Mosser et al. (2015) showcase how kin selection is implicit in their model through varying territorial inheritance by, "either requiring social offspring to leave their natal group with their cohort at maturity (no inheritance) or allowing social offspring to remain in the natal group (inheritance)." As the results show:

> Group territoriality is more likely to be the favored strategy (>50% of the final population) as total landscape value increases, depending on landscape structure...The effect of landscape value is nearly absent in homogenous landscapes, where the social genotype is never favored. In landscapes with randomly distributed hot spots...increasing landscape values and increasingly heterogeneous landscapes consistently predict a higher proportion of social individuals. Where hot spots are clustered...the effect of landscape value interacts with landscape heterogeneity. These patterns are consistent throughout the sensitivity analyses...Although the simulations consistently showed that a high landscape value supports high lion population density...population density alone did not determine the prevalence of social individuals (Mosser et al., 2015).

Indeed, habitat and habitat availability were (and are) critical for the evolution of cooperation in lion behavior. Yet it must be stressed that genetics (variation) play just as crucial of a role, a concept highlighted throughout the above-mentioned literature. Therefore, continued field investigations into the genetically and environmentally generated evolution - past, present, and future - of lion cooperation is critical for aiding future ecologists, wildlife biologists, and policy experts in advocating policies that will successfully preserve lions.

On an interesting sidenote, researchers have often pondered as to why leopards (*P. pardus*), who share the same habitats as lions, did not evolve similar cooperative behavior. Being the smaller of the two felids (mesopredators), leopards suffer from what is known as, "significant interference competition from lions" (Balme et al. 2009, 2013; Packer et al. 2009). Naturally, any attempt by a group of leopards to occupy a hot spot already dominated by, "sympatric lions," would be met with what is referred to as considerable disruption, supporting the notion that lions themselves only dominated savanna ecosystems after the disappearance of saber-tooth cats (Weredelin et al., 2010; Mosser et al., 2015).

Argument

As skepticism arguably remains at the core of many a research-oriented vocation, there may be those who question the value of an in-depth understanding of evolutionary biology and its place in modern-day conservation practices. In this instance, they may even go so far as to question why and how knowing the evolution of cooperation - from the genetic level to inclusive fitness, mutualism, altruism, kin selection, etc. - and its specific application to lion biology and ecology is relevant to any concomitant *in situ* and/or *ex situ* conservation measure created with an intent to preserve *P. leo* at the species level within (or outside) its naturally occurring habitats.

To best answer such a hypothetical query, it is necessary to paint a hypothetical picture. For argument's sake, say none of the previous research of lion cooperation had ever taken place. What if mammalogist, George Schaller, never ventured to Tanzania in 1966 to study lion behavior for the next three years in the Serengeti National Park? What if he never documented his findings, nor ever published them in his seminal work, *The Serengeti Lion: A Study of Predator-Prey Relations* (Schaller, 1972)? Imagine if his successor and founder of the Serengeti Lion Project, Craig Packer (Packer & Pusey, 1997) and his fellow research associates, never performed a molecular analysis of lions or any other DNA tests to learn more about the evolution of lion cooperation? How would lion conservation look today if they hadn't spent years of laborious field research with the aim of contributing a better understanding of this evolutionary construct?

Taking this forlorn picture into serious consideration, one can safely conclude that it is precisely because of this historical mosaic of monumental research that any responsible efforts to protect lions were even considered, let alone established in a number of wild corners of the African continent. Not only that, but the work done by Schaller, Packer, Grinnell, Pusey, Mosser, and others is all the more important to remember and revisit often as the increasing threat of anthropogenic extinction for lions (and other wildlife) looms like a menacingly dark cloud over the remaining protected plains, deltas, semiarid and arid deserts, and woodlands of Africa.

On a more fundamental level, Darwin wanted to understand why animals in different places were, in fact, different (Usborne, 2010). Fast forward to today and evolutionary biologists, conservation biologists, and restorative ecologists are continually stressing the need to quantify these different, vulnerable, threatened, and endangered population sizes in light of the fact that any further reduction in their numbers will inevitably result in two particular biological dangers: inbreeding depression and a loss of genetic variation, which will inevitably lead to extinction.

Without the research done by evolutionary biologists to highlight such perils, no one would be taking active steps to counteract them. Ergo, and considering the litany of obstacles that threatened species like lions are facing, evolutionary theory suggests that in order to secure their long-term survival, conservationists need to focus not only on individual members of the species, but also their, "ability to evolve in the face of changing environmental variables," meaning focusing conservation efforts on the preservation of genetic variation itself (University of California, Berkeley, n.d.; Gillespie, 1998). Sufficient genetic variation ensures protection from erratic climate conditions, landscape alterations, and harmful pathogens, both naturally occurring, and emanating from domestic animals living within and outside of protected areas.

As the research clearly demonstrates, genetic variation in lion populations exhibiting cooperation in intraspecific numbers averaging ≥ 13 members (African Lion & Environmental Research Trust, n.d.) heavily depends on the availability of ideal-sized habitats in order to avoid low numbers, which to reiterate, would lead to inbreeding depression and low genetic variation.

Throughout Africa, lion censusing is not merely performed to provide an estimated total population or number within a given protected area (national park, game reserve, conservancy), but also to determine whether or not the species is below, at, or exceeding carrying capacity wherever it resides. Additionally, this is done to assess whether or not the size of a protected area is sufficient enough to support any proposed lion reintroduction plan, while determining how many lions prime habitat could conceivably host.

All of this, however, would have been for naught had there been no pioneering research into the evolution of cooperation, which establishes a baseline template for deciphering lion social hierarchies, the nature of different forms of intraspecific cooperation, and lion population dispersal, among other variables. Once again, this effort has charged conservationists with developing proper *in situ* management strategies, consequently ensuring genetic variation throughout remaining populations of wild lions.

If a good understanding of genetic variation in relation to habitat helps establish healthy populations, then balancing appropriate lion populations means calculating a minimum viable population (Holsinger, 2007) within their respective environments, or alternatively, choosing appropriately-sized habitats to host a suitable number of lions that can interbreed successfully and subsequently produce offspring with adequate variation.

Without this knowledge, conservationists simply would not be able to assess source-sink dynamics, top-down trophic cascades and the ecological consequences of cascade effects and/or mesopredator release, adequate population regulations, and its association with disease prevalence and disease prevention (Pulliam, 1988; African Lion & Environmental Research Trust, n.d.; Fraser, 2011; Packer, 2015).

Recall the early 1990s overreaction to the Feline Immunodeficiency Virus (FIV) in lion populations throughout the Serengeti and Ngorongoro Crater ecosystem (Packer, 2015). It was erroneously assumed that there would be imminent extinction if the virus wasn't dealt with immediately. However, previous studies related to cooperation and genetics in lion populations by Packer et al. in collaboration with the National Cancer Institute confirmed that all adult lions in the Serengeti and Ngorongoro Crater had been FIV positive for, "twenty years (and genetic studies suggested they'd been infected for thousands of years), yet the populations were doing just fine" (Packer, 2015).

While FIV turned out to be a non-issue, such an overreaction still confirms the need for these types of studies; the conservation community must be well prepared when facing pitfalls
such as genetic stochasticity, demographic stochasticity, environmental stochasticity, and natural catastrophes (Holsinger, 2007), and they should look to evolutionary biology as a necessary tool in the conservation kit. Focusing on the genetic component, Fox and Wolf (2007) draw attention to the fact that it must be highly prioritized in species preservation:

> There is a need for a better integration of genetics into conservation biology, particularly by using population viability analyses (stochastic computer projections)...It will be especially important for understanding the fate of fragmented populations, as there are so many variables affecting such populations that they are difficult to study in the wild.

Though the focus of this argument mainly centers around *in situ* conservation, it is noteworthy to add that one successful way that genetics are being well utilized for lion (and other animal species) protection is an *ex situ* method incorporated by all Association of Zoos and Aquariums accredited zoological institutions in the United States through the use of captive breeding techniques and appropriate record keeping in what is known as studbooks.

These, "collective histories...are known as the population's genetic and demographic identity and are valuable tools to track and manage each individual [animal]," in order to assure a healthy, captive population in the event of extinction in the wild (Association of Zoos and Aquariums, n.d.). Though this is not a direct result of the evolutionary study of cooperation or the research involved with the evolution of *P. leo* cooperation, the case can certainly be made that previous genetic studies within lion cooperation research can be indirectly attributed to this effective system of genetic mapping for the purposes of *ex situ* species survival.

Conclusion

Lions are obligate carnivores, social felids, and a keystone species under which a diverse range of other species live and depend on for the survival of an ecologically intact food web. As socially cooperative creatures, Packer states that, "the king of beasts above all exemplifies the evolutionary crucible in which a cooperative society is forged" (Packer & Pusey, 1997). It is the lion's environment and its genetic diversity, then, that must be successfully preserved in order that this remarkably cooperative biological taxon be given the opportunity to continue along its ecological and evolutionary trajectory.

Bearing this in mind, this phenomena - that which comprises intraspecific cooperation - would never have been understood to the extent that it is today without the relentless, indeed, self-sacrificing research undertaken by those within the scientific community who wanted to

better understand its origins. By taking hold of the origins of cooperation on the genetic level, how that plays out within the lion social hierarchy, and the degree to which the environment and genetics determined its ancient path, conservationists from a range of scientific fields are now better able to map out protection strategies that will promote biodiversity and hopefully secure a future for lions throughout their remaining sub-Saharan strongholds.

Continued research is therefore paramount in determining present and future conservation approaches, proposals to various conservation bodies and government institutions, and sound wildlife management policies at the ground level. Failure to do so would not only be scientifically incurious, but dangerous in a conservation sense for remaining lion populations in Africa as well as other species that depend on the existence of lions for their own survival in the food web. One only hopes that many more of these critical questions are asked, and that many a scientific inquiry will follow.

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