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Cooperation in Male Lion Coalitions: Evolutionary Evidence Of Mutualism?

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A coalition of male lions in Tanzania's Serengeti National Park. Photo Courtesy of National Geographic photographer Nick Nichols.

When considering mutualism as one form of cooperation, its success is measured chiefly to the extent that it enhances the inclusive fitness of the participating species (Leigh, 2010). Despite the fact that mutualism is often described with examples involving interspecific beneficial interactions, there are cases of intraspecific groups exhibiting cooperation in a world predominantly driven by competition and the never ending struggle to survive (Hoeksema & Bruna, 2000; Herron & Freeman, 2005).

Between 1987 and 1990, Grinnell, Packer, and Pusey (1995) embarked on an intensive field experiment involving a study population of 200 lions in Tanzania's Serengeti ecosystem and recorded

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playbacks of lion “roars” to determine if male cooperation was based on the evolutionary models of kinship, reciprocity, or mutualism.

As natural selection is the byproduct of inter- and intraspecific competition in an effort to survive and produce more offspring, it cannot be stressed enough that male lion coalitions exhibit fierce competition with other coalitions, and that coalition and pride success in terms of well established territories, offspring sired, and offspring safety up until they are evicted from the pride—subadult males in particular—is largely dependent on the strength of male coalitions (Grinnell et al., 1995). As such, is their cooperation based on the evolution-based cooperative concepts of kinship, reciprocity, or mutualism? This is the key question that Grinnel et al. set out to answer.

Grinnell et al. demonstrate sound scientific reasoning by first outlining their understanding of cooperative behavior vis-à-vis the three aforementioned methods, followed shortly thereafter by stressing the need to better understand animal behavior within this cooperative context; they posit that male lions, in particular, can provide an invaluable opportunity to test these three ecological modes of cooperation (Grinnell et al., 1995).

It is, therefore, important for readers to have a solid understanding of cooperation under the auspices of ecology and evolution, not to mention its byproducts. While Grinnell et al. do not explicitly summarize all tenants of cooperation—they do so generally, likely expecting that those within the same (or similar) research circles are already well-grounded in it—they do spend time briefly examining three different modalities that may or may not be applied. Specifically, what is kinship? What is reciprocity? And what is mutualism? To deliver a better scope concerning this review, the following two paragraphs give short, concise definitions of each.

Kinship (kin selection) is an ecological and evolutionary strategy favoring the reproductive success of an organism’s relatives, even at a cost to that organism’s own survival and chances of future reproduction (“Kin selection,” n.d). Herron and Freeman (2005) define reciprocity as fitness benefits exchange, temporally separated, between two individuals with a net gain result for both parties. Grinnell et al. explore this concept further by providing a short comparative-contrastive analysis of prisoner’s dilemma (game theory) as it relates to male lion behavior.

Lastly, species, whether they be inter- or intraspecific, involved in mutualism will benefit from the interaction, though they do not necessarily behave in altruistic fashion (Landry, 2010).

Grinnell et. al do not appear to showcase any assumptions prior to their experiment and subsequent findings and analysis, though they do display a thorough understanding of male lion behavior, likely acquired through previous field research and other modes of research. This may well have yielded some initial assumptions prior to testing and results, but if this indeed was the case, it was not disclosed or inferred at any point in the published article.

As previously mentioned, their study population included roughly 200 lions living in 20 prides in an area roughly 2000~km² of Serengeti National Park, Tanzania (Packer et al., 1988). From July, 1987 to

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July, 1990, Grinnell et al. (1995) performed a total of 40 playback experiments on 15 male lion coalitions of varying sizes, recorded on still evenings, facing the microphone at a maximum 30 meter distance, and each playback occurring approximately 20 minutes before dusk.

In order to maintain sampling accuracy, the researchers utilized the following methods while in the field with their electronic gear (recording devices) and safari vehicles (Lions were habituated to the presence of vehicles and made no known association between the vehicles and the recordings.):

We played back choruses of one, two and three roaring males to groups of one to four resident coalition males. All playbacks were performed while the residents were well inside their normal pride range. We used 13 recordings of 10 coalitions in the experiments: five three-male, four two-male and four single-male roars. Within these size categories, we chose recordings according to geographic location of the subjects (e.g. a recording of lions resident in the north would only be played to lions in the south) and how often each recording had been played to a certain coalition or in the study as a whole; care was taken to intersperse recordings both within and between male groups as appropriate (Grinnell et al., 1995).

These methods clearly demonstrate the meticulous nature of Grinnell, Packer, and Pusey in effectively maintaining sampling accuracy. Moreover, they scrupulously collected data that is relatively easy to comprehend, relevant to the study, and most importantly, as scientifically accurate as possible. As such, there do not appear to be any procedural errors, nor is there a need for further methodology recommendations within geographical confines.

However, as this investigation was species-specific to sub-Saharan Africa, it would have been interesting had the researchers repeated this field study somewhere in addition to Serengeti National Park in order to verify their results. Would a different sample population in a different lionscape (Botswana, Kenya, South Africa, Uganda, Zambia, Zimbabwe, etc.) have yielded the same, similar, or different cooperative results? It would have certainly been worth it had this experiment been repeated in one or more different countries, not to mention one or more different ecological biomes. Of course, one must acknowledge time, financial, and other constraints, but hypothetically, it could have either potentially strengthened or altered initial findings.

Ultimately, male lion behavioral ecology validated both cooperation and mutualism as evolutionary constructs; coalitions collectively rushed to investigate the manufactured roars generated by “intruding” males in preparation to defend their territories. Even if a male within a coalition lagged behind, or if approaching walked side-by-side or in tandem, it did not deter them from forming an offensive by which they were prepared to fight their would-be interlopers. The results confirm an evolutionary basis of male lion cooperation as elucidated by Grinnell et al. in the following summary:

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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.

The only caveat to these findings was male coalition sizes in relation to the electronically recorded number of intruders and the availability of cover, or lack thereof. In other words, outnumbered lion coalitions would cooperatively retreat to safety if rival roars appeared to outnumber their own outfit, thus demonstrating the ability of lions to count, a remarkable risk assessment strategy (Grinnell et al., 1995) when confronted with a real, or in this case, fabricated threat.

As far as consequences and implications are concerned, Grinnell, Packer, and Pusey were able to successfully validate a previous field investigation led by McComb who, along with Packer and Pusey, performed similar previous playback recordings in an effort to better understand the differences between male-led and female-led intraspecific competition.

Whereas female cooperation was found to be largely dependent on the number of pride members—related females, cubs, and subadults—males confronting male nomads were found not to be dependent on the size of their respective pride size, including the number of females, cubs, and subadults (McComb, Packer, & Pusey, 1994). Their only concern was their own coalition size in comparison with that of rival nomads, thus further validating the significant degree of mutualism and unconditional self-interest (Grinnell et al., 1995) when it comes to protecting and maintaining their own reproductive success.

In an earlier study, Packer et al. (1988) calculated that every additional coalition member will increase reproductive success by 0-64 surviving cubs per male. As such, the 1995 study confirms that cooperation removes temptation for any male lion to defect when an outside challenge occurs since a male's ability to repel intruders and maintain pride leadership would be reduced if his partner(s) were killed or wounded (Packer et al., 1988). This, according to Packer, could end a male's reproductive success, a critical essence of natural selection.

The perspective of each contributing author is scientific in nature, primarily since it is objective, logical, rigorous, and experimental in lieu of being purely theoretical or biased in any way (Raman, 1951). While it is unknown if these particular authors had differing points of view or assumptions prior to their findings, one can safely assume that their collective approach to problem-solving and seeking validation as it pertained to hypotheses was dialectic in nature, this being further evidence of having an objective, scientific point of view.

Lastly, this investigation could have been done with a deeper look at the role genetics plays in cooperation between this particular species. But again, it must be stressed that spatial and temporal limiting factors almost always prevent scientists from obtaining additional information during the course of research.

This is why the scientific method of research is, for all intents and purposes, an eternal challenge. It is only through continued testing, validation, more testing, and more validation that a greater understanding of the natural world can be successfully achieved.

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