

The articles in this bibliography are organized chronologically under primary and secondary article headings. This is because much of the research in the topic of lion group territoriality and roaring behaviour builds off of each other, with many newer papers referencing older papers. Prominent papers in this field are also published by a consistent set of researchers, adding to the chronological progression.

#### Primary articles:

**McComb, K., Packer, C., & Pusey, A. (1994). Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. *Animal Behaviour*, 47(2), 379–387. <https://doi.org/10.1006/anbe.1994.1052>**

**Summary:** Previous research involving aggressive animal encounters, or animal contests, have largely focused on disputes between single individuals. However, these contests differ greatly from contests between social groups, which have not nearly been studied as extensively. This article investigated how female lions assess other lion prides when in contest. Specifically, McComb et al. (1994) tested whether group size plays a role in these encounters and how agonistic behaviour would subsequently be adjusted. To explore this question, free-ranging lion populations in Tanzania were studied. Artificial contests were created using playbacks of unfamiliar lion roars to simulate the presence of intruders within pride territories. Two major findings were recorded from this study. First, it was observed that as the number of intruders increased, lion defenders were more reluctant to approach the intruders, and took a longer period of time to do so. Secondly, it was determined that as the number of defenders increased, the likelihood of approaching intruders increased. This study was significant as it was one of the first studies to look at numerical assessment in lions and provided an important foundation regarding lion territorial defence for many other research articles. It also provided evidence for the hypothesis that lions assess their success rate in territorial disputes through assessment of relative group sizes. Additionally, this study confirmed both lion numerical assessment abilities and lion roaring in the coordination of defence activities. However, this study exclusively looked at female lion contests. Additional research could focus on males, or a mix of both to provide a more wholistic perspective.

**Contribution:** This article was one of the first to study numerical assessment in African lion when engaging in territorial contests. The research in the article confirmed previous hypotheses regarding lion territorial defence and provided important information from which subsequent articles built off of. Overall, this work provided generalized evidence which allowed for many potential follow-up questions and studies to be conducted.

**Grinnell, J., Packer, C., & Pusey, A. (1995). Cooperation in male lions: Kinship, reciprocity or mutualism? *Animal Behaviour*, 49(1), 95–105. [https://doi.org/10.1016/0003-3472\(95\)80157-X](https://doi.org/10.1016/0003-3472(95)80157-X)**

**Summary:** Intruder male lion roars are seen as serious threats by resident males. In these situations, resident males will collectively approach the intruder. This is beneficial in that it lessens the risk of

injury individually and defends the reproductive potential of the entire lion group. This article investigated the cooperative territorial responses by male lion groups and tested evidence of kin-based cooperation. To explore this question, playback experiments were conducted. In this study, playback experiments are experiments where lion intruders were simulated by playing foreign lion roars from a digital audio recorder.\* The roars of various resident male groups were subsequently recorded and analyzed. The behaviour of the groups was also observed when presented with intruder lion roars. Three major findings were recorded from this study. First, it was observed that resident males were slower at approaching larger amounts of intruder roars. Secondly, it was determined that males walk side by side or in tandem during the approach. Lastly, Grinnell et al. (1995) found that lion resident males approached the intruders at different times, suggesting some sort of hierarchy or system of approach. This study was significant as it provided information on lion territorial approach behaviour and confirmed evidence of numerical assessment. As one of the first papers on lion territorial defense, specifically approach behaviour, this article provided a framework and knowledge foundation to build subsequent questions from. It also provides valuable general information on lion territorial behaviour.

**Contribution:** This article provides new, quantifiable insight into how exactly male African lions approach territorial intruders. The research in the article advances overall knowledge of lion territorial behaviour, which has previously been limited. This is important for subsequently understanding the role vocalizations or roars have in this territorial behaviour. This work also provides various potential follow-up questions regarding how lions assess intruders from their roars and how they assess numerical situations.

**Grinnell, J., & McComb, K. (2001). Roaring and social communication in African lions: The limitations imposed by listeners. *Animal Behaviour*, 62(1), 93–98.**  
<https://doi.org/10.1006/anbe.2001.1735>

**Summary:** Vocal signals serve a variety of different functions in many different species, including African lions. However, these signals can create costly risks for nomadic lions when exploring unowned territory. The main objectives investigated in this study were three-fold; they wanted to determine whether nomadic males roar at lower rates than resident males, whether roaring behaviour indicates a willingness to escalate in a contest with other males and whether roaring behaviour can be affected by temporal changes in residence status. To explore these objectives, a combination of observation and playback experiments\* were used. Radiocollared male lions were visually followed and the contexts and behaviours associated with bouts of roaring were recorded. Recordings of lion roar sequences were also taken and analyzed. Three major findings were recorded from this study. First, it was observed that only resident, male lions roar within the studied territory. Secondly, it was determined that roaring in male lions occurs when they are prepared to escalate. Lastly, it was found that escalation by resident males only occur when the males is on the territory where they were resident. This study was significant as it provides information on African lion vocal signals in relation to territorial ownership. This has not been studied previously, providing

novel results. This study also provides insight into what long-distance acoustic signalling is likely like in other social species, in which eavesdropping occurs.

**Contribution:** This article provides novel, evidence-based insight into when African lions decide to vocalize in relation to territorial ownership. It furthers previous research on animal communication and its involvement of signallers and receivers. Overall, the research in the article advances knowledge of lion vocalization behaviour in regard to territoriality, which has previously been limited, and opens a set of further research questions to be explored.

**Mosser, A., & Packer, C. (2009). Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behaviour*, 78(2), 359–370. <https://doi.org/10.1016/j.anbehav.2009.04.024>**

**Summary:** In animals that socially group, such as African lions, numerical advantage in intergroup competition may be highly advantageous. However, the trade-off between group size and access to a limited number of resources has never been formally tested. This article tested five hypotheses, all of which examined the role of group size in territorial competition. To test these hypotheses, pride territories were mapped, and the quality of each territory was determined based off of landscape characteristics such as distance to rivers, vegetation type and prey density, which have all been previously correlated with reproductive success. The interactions between neighbouring prides were subsequently observed for aggressive encounters. Two major findings were recorded from this study. First, it was determined that female African lion reproductive success is significantly affected by intergroup competition. This suggests that in intergroup competition, larger prides do indeed have a competitive advantage. Secondly, it was determined that in risky or dangerous areas with high intergroup competition, prides that were larger and had more adult females had higher rates of reproductive success. This study was significant as it was the first comprehensive analysis examining the role of group size in territorial competition. It also provides quantifiable evidence of the advantages of sociality in African lions. Lastly, this study scientifically confirmed the benefits of having a numerical advantage in African lion intergroup competition, which had never been formally tested. However, this study was limited in the number of prides tested and therefore did not produce reliable evidence regarding the trade-off between group size and access to a limited number of resources. Additional research needs to be conducted to explore this trade-off in more detail, using this study as a foundation.

**Contribution:** This article provides new, quantifiable insight into the role group size plays in territorial competition, highlighting important benefits from having a numerical advantage in intergroup competition. The research in the article advances overall knowledge surrounding group size and access to a limited number of resources, which has never been formally tested. This serves extremely important for understanding African lion group dynamics on a broad scale, and how intergroup territoriality affects this.

**Mosser, A., Kosmala, M., & Packer, C. (2015). Landscape heterogeneity and behavioral traits drive the evolution of lion group territoriality. *Behavioral Ecology*, 26(4), 1051–1059. <https://doi-org.ezproxy.lib.ucalgary.ca/10.1093/beheco/arv046>**

**Summary:** Group territoriality is a comparatively rare form of sociality, which suggests that it evolved under a restricted set of conditions. However, past work has only focused on ecological drivers of evolution. This article investigated how the evolution of group territoriality in African lions may have been influenced by landscape heterogeneity and population density. In this study, Mosser et al. (2015) explore the fitness benefits of solitary versus social territoriality in regard to different individual behaviors and patterns of landscape structure. To explore these questions, an agent-based simulation model was created. This simulation model is computer-based and simulates a population of female lions through time. It was designed by incorporating existing empirical data on lions, particularly the population dynamics observed from current continuous research studies. Different simulations were carried out, with three behavioral traits—cooperative territorial defense, territorial expansion, and territorial inheritance—either present or absent. Solitary individuals and social individuals were placed in these simulations and tested against each other. The major finding concluded in this study was that lion sociality arose likely due to various environmental factors. This includes a productive, heterogeneous environment, an environment with high-quality patches, and an individual behavioral predisposition favouring cooperative territorial defense. This study was significant as it provided information on the evolution of group territoriality in African lions, and the likely environmental requirements leading to this, which had not been previously studied. This study also provides insight into how group territoriality may have arisen in other social species by providing insight into the complexity of group dynamics.

**Contribution:** This article provides new, model-based insight into how group territoriality evolved in African lions. The research in the article advances previous knowledge of African lion group territoriality evolution. This ultimately helps in the understanding of lion vocal behaviour in territorial defence.

**Gray, S. M., Montgomery, R. A., Millspaugh, J. J., & Hayward, M. W. (2017). Spatiotemporal variation in African lion roaring in relation to a dominance shift. *Journal of Mammalogy*, 98(4), 1088–1095. <https://doi.org/10.1093/jmammal/gyx020>**

**Summary:** Given the social and behavioral complexity of lions, vocal communication is incredibly important in defending territory, maintaining social cohesion, and gathering information about conspecifics. Specifically, roaring helps defend pride resources, deter rivals, and increase opportunities of siring cubs in neighboring prides. However, whether a lion roars or not can depend on location, dominance hierarchies, and many other factors. This article investigated the configuration of lion roaring at the home-range scale and how this can be altered through spatiotemporal changes and social rank. To explore this, GPS-fitted collars were first used to track lion movement and roaring behaviour. The social rank of the male coalitions were subsequently calculated using an index of social dominance. Roaring locations were analyzed. The major finding of

this study was that male lions change their roaring behaviour and frequency depending on their location within their home range and their social rank. Males have a tendency to roar less when they are near the periphery of their home range as opposed to the core, and also when they are in subordinate social ranks. This study was significant as it provided novel information assessing territorial behaviors relative to changes in social hierarchy, something that has not been studied before. It also investigated how spatiotemporal factors can affect where and when lions roar. This study presents many further questions to be studied. It suggests that reintroduced lions may behave differently from wild conspecifics, and that much is yet to be learned on how this behavior differs. By learning this information, it can aid in population health assessment in managed reserves, which was one of the main purposes of this study.

**Contribution:** This article provides new insight into how exactly territorial behaviors relative to changes in social hierarchy and spatiotemporal factors can be altered. The research in the article advances overall knowledge of lion vocalization behaviour. This is important not only for interpreting species ecology, but also for benefiting species conservation in managed reserves where reintroductions are common. This work also provides various potential follow-up questions regarding how reintroduced lions may behave differently from wild conspecifics.

**Wijers, M., Trethowan, P., Du Preez, B., Chamailé-Jammes, S., Loveridge, A. J., Macdonald, D. W., & Markham, A. (2020). Vocal discrimination of African lions and its potential for collar-free tracking. *Bioacoustics*, 30(5), 575–593. <https://doi.org/10.1080/09524622.2020.1829050>**

**Summary:** Long-distance signalling is essential to lion communication. It helps build group cohesion and helps coordinate the defence of territorial boundaries. It also helps in allowing conspecifics to identify other individuals. However, little is known about how lions convey their individual identity in their call structure and whether there are consistent differences between the call structure of individual lions. This article investigated how calls from individual lions differ based on the fundamental frequency of their roars. To explore these questions, acoustic and accelerometer biologgers were utilized to locate and record separate lion roar events. GPS collars were also used to determine the home range of the studied coalitions. Lion roar events were then analyzed for structure using spectrograms. The major finding from this study was that the fundamental frequency of lion roars varied between lions originating from different locations. This suggests that temporal patterns, such as fundamental frequency, may be a mechanism for lion vocal identification in lion roars. This study was significant as it provided novel information on how lion call structure differs between individual lions, allowing for individual identification. This had not previously been studied, likely due to the difficulty of gathering sufficient samples of lion roar recordings from known individuals in the wild. This study also presents a novel methodology of studying lion vocalizations using acoustic and accelerometer biologgers. However, this study did have some limitations, which provides opportunities for further research. One such limitation is the age-related variations in individual lion roars. Since this study was conducted over a short time period, the effect age has on lion roars remains unknown.

**Contribution:** This article provides novel, quantifiable insight into how call structures in individual lions vary, allowing for individual identification. This had not been previously studied. Knowing how the transmission of information relating to identity occurs in lions is crucial in understanding how communication plays a role in mechanisms such as territorial defence. This study also presents a contemporary methodology of obtaining lion roars: through the use of biologgers and modern technology. The efficiency of this methodology will likely dictate how future studies are conducted.

**Wijers, M., Trethowan, P., Du Preez, B., Chamailé-Jammes, S., Loveridge, A. J., Macdonald, D. W., & Markham, A. (2021). The influence of spatial features and atmospheric conditions on African lion vocal behaviour. *Animal Behaviour*, 174, 63–76.**  
<https://doi.org/10.1016/j.anbehav.2021.01.027>

**Summary:** Little is known about how lion vocal behaviour may be affected by spatial and temporal variations in the costs and benefits of communication. This article investigated the influence spatial features and atmospheric conditions have on African lion vocal behaviour. In this study, Wijers et al. (2021) aimed to investigate the role spatial preferences and atmospheric conditions had on lion vocalizations. To explore these questions, eight adult lions were fitted with biologgers attached to GPS satellite collars that recorded audio and locomotion data. A portable weather station was situated in the study site to record weather data. Three major findings were recorded from this study. First, it was observed that lion vocalizations occurred predominantly during the night, with the highest rate being just before dawn. Secondly, it was determined that as wind speed and temperature increased, the odds of vocalization decreased, while as humidity increased, the odds of vocalization increased. Lastly, Wijers et al. (2021) found that lions strongly avoided vocalizing outside their home range. This study was significant as it provided information on lion vocal behaviour with simultaneous location information, which has been limited in the past due to inherent data collection challenges. It also introduces the methodology of monitoring continuous animal movement through biologgers, which is a new technology that overcomes many of the challenges associated with direct observation. Since this study only investigated the influence spatial features and atmospheric conditions have on African lion vocal behaviour, additional research needs to be conducted to explore other factors that may influence vocalization. This includes social factors, an individual's proximity to its pride members and various others.

**Contribution:** This article provides new, quantifiable insight into how exactly spatial features and atmospheric conditions influence African lion vocal behaviour. The research in the article advances overall knowledge of lion vocalization behaviour, which has previously been limited due to challenges in obtaining this data. This is important not only for interpreting species ecology, but also for benefiting species conservation through passive acoustic monitoring. This work also provides various potential follow-up questions regarding how lions sense optimal environmental conditions, what other factors are at play and overall how this complex behaviour evolved.

Secondary articles:

**Larom, D., Garstang, M., Payne, K., Raspet, R., & Lindeque, M. (1997). The influence of surface atmospheric conditions on the range and area reached by animal vocalizations. *Journal of Experimental Biology*, 200(3), 421–431. <https://doi.org/10.1242/jeb.200.3.421>**

**Summary:** Long-range calls are used by many animal species to communicate and establish relationships with individuals of the same and different species. Many factors affect these long-range calls, including both environmental and genetic factors. However, determining the effect each factor has separately poses a complex challenge. This determination is made easier when studying animals living in flat savanna environments. Because of this, long-range calls in such animals have been extensively studied. This article reviews research that describes and explores the factors that can affect the calling range and area of various animals with low-frequency and long-range calls. It also presents an efficient method used for estimating sound propagation during field studies. In lions, roars are used to find and avoid conspecifics over large distances spanning several kilometres. Lion roars also function in territoriality. This suggests that a relationship exists between territory size and calling area. This helps explain why lions almost exclusively roar at night: to maximize the calling area of their roars under optimal conditions. Accompanying this, lions utilize long-range calls to avoid, contact, join and inform conspecifics. When deciding when to call, lions consider how atmospheric conditions may influence their calls and preferentially call during periods of optimal transmission. Factors that have been found to influence lion calls include topography, regional weather patterns, seasonality and climate variation. These factors indicate potential selective pressures that have historically shaped lion nocturnal calling behaviour.

**Contribution:** This article summarizes the understandings of long-range calls, particularly for animals living in flat savanna environments and provides an overview of existing research. It explores how long-range calls are affected by atmospheric factors and makes suggestions on when optimal conditions for each animal occurs. Given the broadness of the topic, many unanswered questions can be the focus of future works. This includes diving deeper into how certain factors may have shaped lion vocal patterns. This article is helpful in finding related articles regarding lion vocalization behaviour and learning more about the ultimate effects that may have influenced vocalizations.

**Benson-Amram, S., Gilfillan, G., & McComb, K. (2018). Numerical assessment in the wild: Insights from social carnivores. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1740), 20160508. <https://doi.org/10.1098/rstb.2016.0508>**

**Summary:** Number assessment plays an essential role in animals, helping with foraging, predation, reproduction and others. Because of this, numerical ability has been intensely studied in many animals. This article reviews research that describes and explores the numerical abilities of most animals, in both captive and wild, and how this can affect activities such as feeding, territorial defense and individual recognition. In lions, the territorial defense behaviour and the associated

roaring behaviour varies depending on the number of defending adults and the number of individual intruders. The probability of approach by defenders increases as the number of defending adults and subadults increases. The probability of approach decreases as the number of intruders increases. Accompanying this, the amount of time defending lions take to both approach intruders and reach a loud roaring level is longer if more intruders are present. This suggests that in social carnivores, numeric information presented in visual and auditory modalities is integrated during decision-making, specifically in territorial defense. The only exception is in environments of high competition for resources, where the assessment of numerical advantages may not alter territorial defense behaviour. A hierarchical and rank system may also exist in territorial defense behaviour, as some defenders consistently approach intruders first, while other defenders consistently lag behind.

Wild carnivores, such as lions, living in complex societies may possess the ability to distinguish between individual group members and unfamiliar conspecifics based off of roars. Defending lions spend more time moving and looking in the direction of a roar when the roar is from an individual from a different group versus an individual from the same group. Defending lions also display more indicative behaviours of social stress when the roar is from an individual from a different group. This suggests that lions have cognitively rich multimodal representations for different individuals.

**Contribution:** This article summarizes understanding of numerical abilities of captive and wild animals, providing an in-depth overview of existing research. It explores how numerical ability of animals may play a role in feeding, territorial defense and individual recognition. Given the broadness of the topic, many unanswered questions can be the focus of future works. This includes identifying the cognitive mechanisms used by social carnivores to assess numerical advantage and focusing on a more diverse set of species. As a review, this article is a helpful resource in finding related articles regarding lions and their territorial defense behaviour.