

Territoriality in a pride of semi-wild lions, *Panthera leo*

Internship report - Master of Veterinary Medicine

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Abstract

The African lion, *Panthera leo*, is a powerful symbol in Africa but the lion numbers are declining rapidly. Once, the African lion lived across the entire continent, except for the Sahara Desert and rainforests. Nowadays they occur in less than a quarter of their historic range (Nowell *et al.*, 2012). Conservation programs are necessary to keep the African lion from further declining. One of the ways of conservation is releasing captive bred animals into the wild. Before releasing captive bred lions it is necessary to assess their capability to survive in the wild. One of the skills for survival is the ability to successfully defend a pride's territory against intruders and competitors for food. This study in Antelope Park, Zimbabwe, assesses whether captive bred lions released in a semi-wild environment react similar as wild lions do to intruders in their territory. The reactions of the pride members are tested by means of playbacks (McComb *et al.*, 1994). The lions of the semi-wild pride show similar behavior as wild lions and are more willing to approach intruders when they outnumber them.

Background

Sociality of lions

Lions are the only felids that live in social groups, called a pride. A pride of African lions, consists of 2-18 related females, their cubs and weaned juveniles up to 42 months of age, and one to nine males that are unrelated to the females (Schaller, 1972). Some of the benefits of living in a pride are that female lions hunt together, share their food and nurse each other's cubs. Perhaps the most important reason why lions live in social groups is group defense of the pride's territory against other females and infanticidal males. A territory is crucial for reproduction of the pride and a single female is not able to defend her territory and protect her cubs alone (Packer *et al.*, 1990). Fighting provides a risk of injury and death, especially for solitary animals and small prides. Two females is the minimum pride size (Schaller, 1972; Packer *et al.*, 1990). The young males of a pride disperse at the age of two to four years and they will remain solo or forming a coalition with other males, commonly with their cohort mates (Pusey and Packer, 1987). After a period of a nomadic lifestyle they eventually take over a new pride. On the other hand, females usually stay in their natal pride. Juvenile lionesses are weaned at 8 months of age and reach sexual maturity at 42 months of age. During this development, cubs develop and become less reliant on adult females territorial defense and food (Heinsohn *et al.*, 1996).

A pride's territory

A territory is essential for resources of the pride, which is necessary for individual reproductive success (Grinnell, 2001). The resources for which males and females defend their prides are different. Males form coalitions with other males to compete against each other and take over a female pride.

This is necessary for male reproduction. Females defend a territory for the resources for raising cubs and keeping the cubs alive (Grinnell, 2001). These resources include secure denning sites, dry season water base and prey availability (Packer, 1986). Therefore, defending a territory is crucial for the survival of the pride mates. Increasing reproductive success is achieved by communal care of the cubs in the pride and the protection of the pride males. Nomadic lionesses give birth to cubs as often as lionesses in a pride but they fail to raise the same number of cubs because of the lack of communal care and protection (Schaller, 1972). Territorial behaviour is also a powerful mechanism for effective use of the area (Schaller, 1972). The number of animals that hunt in a particular area which permits a uniform and socially less disruptive use of food resources is limited. This is in contrast to the situation where most of the lion population is competing for prey in a few places (Schaller, 1972). The success of a lion's pride cooperative hunt is also increased if they have detailed knowledge of the location of ambush places, river crossings and waterholes. Hence, confidentiality in the environment is crucial for efficient hunts.

Territorial contests

A lion pride defends its territory through scent marking, patrolling, roaring and direct aggressive encounters. Lions can distinguish their pride mates from intruders through their roaring (McComb *et al.*, 1994). By listening to their roars they are able to compare the number of defenders with the number of intruders. Based on this comparison they assess the odds of approaching the intruders and winning a territorial contest. Only if they outnumber the intruders they will approach them (McComb *et al.*, 1994). Juvenile lions are also capable of weighing the odds of winning a territorial contest and will only approach if these odds are in their favor (Heinsohn *et al.*, 1996). Juveniles display this trait first probably to judge their own safety when staying close to the adults in territorial conflicts.

Adult lionesses display a variety of behaviors in group territorial defense. Most females cooperate unconditionally, but some only contribute when their help is most needed and the chance of winning would otherwise be low (Heinsohn and Packer, 1995). Other females let their pride mates bear the risks of fighting the intruders by lagging constantly behind. A few even lag further behind when their help is most needed (McComb *et al.*, 1994). These position preferences are consistent within individuals and appear in their juvenile phase (Heinsohn *et al.*, 1996).

Territorial playbacks

Territorial behavior of prides can be stimulated by simulating territorial intrusions using playbacks of recorded lions (McComb *et al.*, 1994; Heinsohn *et al.*, 1996). Female lions can respond to the playback in three ways: looking intently in the direction of the playback from their original position, retreat in the opposite direction or approaching the speaker (McComb *et al.*, 1994). In previous studies the effect of the number of intruders was tested by playing back the roars of a single intruder or three intruders roaring together. Female lions reached the loudspeaker slower, looked back at their pride mates and paused more often when approaching the playback of three intruders (McComb *et al.*, 1994). Furthermore, adult females were more likely to approach if the number of defenders increased. The likelihood of approach also increased when the pride contained more subadults, and when they had cubs (McComb *et al.*, 1994). These results show that adult lionesses can distinguish members of their pride from strangers and weigh the odds of winning a contest by comparing the number of defenders with the number of intruders and only approach the defenders

when they outnumber them (McComb *et al.*, 1994). Male lions only roar when they are resident in a pride. Therefore, resident male lions treat playbacks of male lion roars as a serious threat (Grinnell *et al.*, 1995). The resident defenders approached the loudspeaker in practically every opportunity and the probability of approach was only slightly reduced when they were outnumbered by 1 to 3 (Grinnell *et al.*, 1995). Heinsohn *et al.* (1996) showed that juvenile lionesses, between 8 and 42 months, participate more in group territorial defense with age. Their approach was dependent on the number of intruders and the number of adults in their own pride. The probability of approach of juvenile lionesses was higher with a lower number of intruders and higher with more adults in their own pride (Heinsohn *et al.*, 1996). As adult females show position preferences in group-territorial defense so do juvenile females. The leading and lagging behavior of juveniles appear to be consistent over long periods of their juvenile phase. However, juvenile males respond in a different way than juvenile females to intrusion playbacks. Males do not play a bigger role in territorial defense with age as females do. Moreover, they tend to be at the back of the group response when they show a response (Heinsohn *et al.*, 1996).

Spotted hyenas and their relationship with lions

Spotted hyenas (*Crocuta crocuta*) live in clans of 10 to 60 or more hyenas of both sexes and all ages. The clan is a fission-fusion society in which members are not always together but forage alone or in subgroups (Watts and Holekamp, 2007). The size of the clan is adapted to availability and vulnerability of food as there are more hyenas needed to hunt zebra but less for scavenging lion kills (Schaller, 1972). As lions do, hyenas also spend a large part of the day resting, about 20 hours. Hunting occurs usually at night, particularly early in the evening and morning (Schaller, 1972). Hyenas usually hunt alone but once a prey is captured group members join the feeding at the carcass (Watts and Holekamp, 2007). They often live and hunt in an open habitat where competitors as lions can notice their killed prey. Therefore clan members should group in order to protect their carcasses (Watts and Holekamp, 2007). Spotted hyenas and lions are competitors and have a dietary overlap of 58.6% (Hayward, 2006). Lions frequently steal kills from hyenas because they are bigger and have more power (Schaller, 1972). However, if enough group members are present, spotted hyenas are also capable of stealing kills from lions, although in a lesser extent than lions from hyenas. They are also efficient scavengers because they have the capacity to eat and digest parts of the carcass that lions discard, like bones (Kruuk, 1972). Scavenge opportunities of prey killed by lions are important for spotted hyenas. Therefore hyenas do not systematically avoid lions, only under some circumstances, as shown by playback experiments of lion roars (Watts *et al.*, 2008). On the other hand, lions are less likely to approach playbacks of spotted hyena whoops, depending on gender of the group of lions (Webster *et al.*, 2010). Lion groups including an adult male lion were very likely to approach the hyena whoops but lion groups without a male did not approach. This shows that an accompanying adult male lion in the group influences the willingness of the females to initiate an interaction (Webster *et al.*, 2010).

Relevance of the study

The African lion is a powerful symbol in Africa but the lion numbers are declining rapidly. Once, the African lion lived across the entire continent, except for the Sahara Desert and rainforests. Nowadays they occur in less than a quarter of their historic range (Nowell *et al.*, 2012). Myers (1975) stated that the lion numbers may have been halved, perhaps even to a number as low as 200.000 since 1950.

According to the IUCN (2012) the African lion is a vulnerable species with a population reduction of 30% over the past two decades. This corresponds to approximately three lion generations. The lions in West Africa are classified as endangered in the Red List (Bauer and Nowell, 2004). The IUCN (2006a, b) reported an estimated lion population of approximately 33,000 lions. Riggio *et al.* (2013) showed that over 30,000 lions remain in approximately 3,000,000 km² of sub-Saharan Africa, distributed across 27 countries. Five countries have already lost their lions since 2002 (Riggio *et al.*, 2013).

Many lions live in small isolated lion populations which can easily become extinct in these regions. A lion population needs to have a long-term viability in order to sustain the lion population or even increase the number of lions. There are some criteria which lead to long-term viability of lion populations. The lion area which meets these criteria is called a lion stronghold. According to Riggio *et al.* (2013): “ For a lion area to qualify as a stronghold, it must satisfy three qualifications: (1) contain at least 500 individuals, (2) be within protected areas or designated hunting areas, and (3) the numbers of lions must be stable or increasing as assessed by the IUCN Cat Specialist Group (IUCN 2006a, b)”. Across entire Africa there are 10 lion strongholds which contain approximately 24,000 lions. Another 4,000 lions are in potential strongholds, area's with less than 250 lions which do not meet criteria (2) or (3). However, over 6,000 lions are not certain of long-term viability. Especially the lion populations in West and Central Africa which are threatened through local extinctions, even in protected areas (Riggio *et al.*, 2013).

Conservation programs are necessary to keep the African lion from further declining. One of the ways of conservation is releasing captive bred animals into the wild. In order for captive bred lions to survive in the wild it is necessary to have all the skills and to behave like wild lions do. One of these skills is the ability to form stable prides and to defend successfully the pride's territory against intruders and competitors for food. The object of this study is to assess whether captive bred lions in a semi-wild environment behave similarly to wild born lions when it comes to territorial behavior. If those captive bred lions show similar territorial behavior as wild lions there is a good chance that they will pass those skills on to their cubs.

Antelope park & ALERT

The African Lion & Environmental Research Trust (ALERT) at Antelope Park promotes and facilitates the development of lion conservation management plans and also educates local communities about maintaining biodiversity and conserving nature. The “African Lion Rehabilitation and Release into the Wild program”, founded at Antelope Park, is a four stage program to reintroduce captive bred lions into the wild. The study was done within this reintroduction program of the African lion. Antelope park has a stage one and a stage two site at the park.

In stage one the cubs are born in the breeding center and taken away from their mother at 3 weeks old. The park staff members act as the dominant pride members and take the cubs out for walks in the bush. These walks are very beneficial to their development because their prey instincts develop and they learn how to hunt. From 18 months old it is not safe for humans to walk with them anymore and they move on to the next phase of stage one, the Night Encounters. During Night Encounters the lions walk besides a car through the bush and improve their hunting skills by stalking, hunting and even killing prey.

After their Night Encounter phase the project manager looks back at the data that have been collected for several months on the lions about their characteristics, behaviors and hunting success.

On the basis of these data and assessments a pride is created of a few females and one or two males and they are released into a semi-wild fenced off area, stage two. This site contains prey species so the pride members can hunt for themselves but they are the only lions in this area without competitive predators. Now they have to form a stable pride, there is no human contact anymore. Meanwhile, research is conducted at the stage two site on all topics of lion behavior. Once the stage two pride is self-sustaining they will be relocated into a larger area with competitive predatory species. In stage three the lions give birth to cubs and raise them on their own. When the cubs born in stage three are old enough they will be joined with other stage three cubs to form a pride. This pride will be released in stage four, into areas across Africa with low populations or where lion activity is needed. The stage two pride of Antelope Park has given birth to cubs before they were transferred to a stage three area. Therefore research has been performed on both the adults and their cubs.

Materials & Method

Study area and animals

The study was conducted during the period between October 2012 and January 2013 in Antelope Park (19°28'S, 29°09'E), Zimbabwe, upon a semi-wild pride in a 403 acres fenced off release site. Antelope Park is a private game park of 3000 acres, located in the Zimbabwean Midlands, 10 km from Gweru. The semi-wild "Ngamo" pride consists of 1 male (codename MI), 6 females (codenames AS, KE, KW, NL, NR and PH) and 5 cubs (codenames AT1, KE3, KE4, AS4 and AS5). All the adults are captive born lions and have had human contact before they were released in the site on the 1st of September 2010. The cubs in the release site are all wild born in the site by the pride. The oldest female cub (AT1) was born on 20 January 2011 by AT who was taken away from the pride because of problematic behavior. The 2 female sibling cubs of KE (KE3 & KE4) were born on the 4th of October 2011 and the male and female sibling cubs of AS (AS4 & AS5) were born on the 4th of November 2011. PH is the alpha female of the pride. KE and KW are siblings, as well as NL and NR.

Lion and hyena playbacks

Several numbers of lion intruders were used to play back at the Ngamo pride. The roars of 1 female, 3 females, 5 females and 12 females were played back. Also the roars of a group of 1 male and 2 females and a group of 8 mixed lions were used. The different recordings were randomizing played. All the intruder lions on the recordings were unfamiliar to the Ngamo pride.

Two different types of hyena vocalizations were used, laughing and whooping. Whooping is used for long-distance interactions to signal separated individuals (Webster *et al.*, 2010). Laughing, "giggle calls", are mainly used when hyenas are feeding together on a prey (Kruuk, 1972). The recordings used were 6 laughing, 24 laughing, 6 whooping and 24 whooping hyenas. Most hyena playbacks were performed with and without the pride male being present in the group.

The number of defenders was not always the same as some members of the pride were not always present at every playback experiment.

Playback experiments

The playback experiments were performed using a Superman P.M.P.O. 18000W Professional Speaker, an ECOO 12V battery and a Solar Africa 12V DC to 230V AC inverter. The playback recordings were played from a USB stick connected to the speakers, with the battery and the speakers both connected to the inverter. The speakers were placed outside the fence of the release site, hiding behind bushes, approximately 200m away from the lions. Playbacks were performed during morning sessions (between 7 and 8am) or afternoon sessions (between 5 and 6pm), as roars are rare before 5pm and after 8am (Schaller, 1972). The responses of the lions were monitored for 1h from the onset of playback using field notes and a camera. The playback was repeated after 5 min if there was no reaction from the lions. Reactions from the lions were classified in 7 classes: retreating from playback fast paced (-2), retreating from playback slow paced (-1), no reaction (0), vigilant to/looks in direction of playback (1), approaches playback slow paced (2), approaches playback fast paced (3) and roars in response to playback (4) (see also Appendix I – Territorial behaviour data sheet). The order of approach was also recorded on the data sheet. A note was made of the lead lion in an approach to the loudspeaker and the number of pauses and look backs. Cub response was classified by their position in the group during an approach: front, middle or back of the group. If the pride male (Milo) was present a note was made if he showed territorial behaviour (rubbing, spraying or scraping) during the 1h observation after the playback. Weather conditions (cloud cover, temperature, rain and wind) and direction of the playback were also recorded. Lion roar playbacks were performed once in every 8 days and hyena playbacks once in every 10 days.

Analysis

Chi square and log linear analysis were used to examine each independent variable on the binary dependent variable approach = 1 and no approach = 0. Three types of independent variables were used: type of sound (small group of 1 female, 1 male/2 females, 3 females or 5 females = 0; and a big group of 8 mixed lions or 12 females = 1), type of lion (adult females = 1, alpha female = 2, male = 3 and cubs = 4) and male on playback sound (yes = 1 and no = 0). No statistical analysis was performed on the hyena playbacks.

Results

In total, 15 lion and 5 hyena playbacks were performed to the Ngamo pride. It was necessary to exclude two lion playback sessions of 3 roaring females because the playback sounds were not loud enough due to problems with the speakers.

Effect of the background of the pride to playbacks

The adult females of the Ngamo pride showed in all cases reactions to the playbacks comparable to those of lions in the wild. They looked in the direction of the playback or approached the loudspeaker whenever they heard the sound of roaring intruders.

In the approaches to the playback sound there were different individuals who took the lead in the group response. In 2 out of 9 approaches the alpha female was the first one to move off in the direction of the loudspeaker. In 2 other approaches the oldest cub (AT1) was the leader of the group.

Effect of number of intruders

Also the number of intruders on the playback affected the willingness from the defenders to approach. The odds of approach to a small group of intruders is 3,5 times bigger than to a big group of intruders on the playback. There is an association between the approach of the defenders and the group size of the intruders on the playback (Pearson Chi-square = 13,319, $p = 0,000$).

The odds of approach of the alpha female (PH) is 9 times bigger than the odds of the other adult females. However, there was no association found between an approach and the type of lion (alpha female, adult females, male or cubs).

The odds of approach of the defenders to a playback sound with a male on it is 0,79 times bigger than to a playback sound without a male on it. However, there was no association found between an approach of the defenders and a male on the playback sound.

Juveniles' reaction and position

The odds of approach of the cubs is 1,36 times bigger than the approach of the females to the playback sound. The oldest cub (AT1) was even the first one of the whole pride to move off to the playback sound in two playback sessions. In those cases the playbacks concerned 1 female and 12 females. Moreover, AT1 was always the first one of the cubs to move off to the playback sound. The male cub (AS5) was always the last one of the cubs to follow in an approach.

Reaction to hyena playbacks

In 2 out of 5 hyena playbacks the Ngamo pride reacted with an approach to the direction of the loudspeaker. Those playbacks concerned 6 whooping and 24 laughing hyenas. In the third playback of 6 laughing hyenas, only 2 adult females set off for an approach. The following 24 whooping hyena's playback didn't elicit an approach of the pride at all. The last playback of 6 whooping hyena's made 8 out of the 10 present pride members look in the direction of the loudspeaker.

Discussion

McComb *et al.* (1994) have shown that adult lionesses assess the odds of winning a contest by comparing the number of female intruders with the number of their own pride. They only approach intruders if they outnumber them. The semi-wild pride of Antelope Park reacted in the same way. The pride members were more likely to approach the sound of the playback when a small group of intruders (<6) were played back. However, the first playback to the pride was of 8 mixed lions and set off an approach, the alpha female leading, almost immediately after the pride heard the sound. In general, the alpha female was more willing to approach a playback sound than the rest of the adult females but there was no association found between an approach and type of lion, because of the small number of observations.

The females of the Ngamo pride were more willing to approach the loudspeaker when a playback without a male lion on the sound was played. However, because of the small number of observations there was no association found between an approach and a male lion on the playback sound.

The male (MI) of the Ngamo pride approached the loudspeaker on every occasion, except once, when the rest of the pride also moved off to the loudspeaker. Besides that, he roared in response to the playback sound of 1 male and 2 females. One time the male lion roared in response to the playback sound of 1 female and aggressively charged the fence while he previously was eating from a carcass. According to Grinnell *et al.* (1995) resident male lions approach the loudspeaker almost every opportunity and the probability of approach is slightly reduced when they are outnumbered by 1 to 3. Grinnell and McComb (2001) showed that male lions in the Serengeti and the Ngorongoro crater only roar when they are prepared to escalate. An attack will be provoked by roaring whilst in the territory of resident males. When sounds of unfamiliar males were played the resident males both roared and approached the loudspeaker aggressively. The Ngamo pride's male reacted similar as wild lions do. No playbacks were performed with more than one male lion on the sound which would have given more insights into the ability of the pride's male in assessing the odds of winning a contest.

Heinsohn *et al.* (1996) showed that juvenile females were more likely to lead and males were more likely to lag. The juveniles of the pride followed the females every time in an approach to the loudspeaker, with the juvenile male being the last juvenile to follow. The oldest cub (21 months old when the experiment started) was always the first one of the juveniles to approach the loudspeaker. Juvenile females from 6-42 months old show position preferences during group territorial responses (Heinsohn *et al.*, 1996). Besides the oldest and the male juvenile, the other juvenile females didn't show a position preference in an approach to the loudspeaker. The juveniles of the Ngamo pride showed almost similar behavior as wild juveniles.

Webster *et al.* (2010) showed that lion groups with an accompanying adult male lion were very likely to approach the hyena whooping playbacks. Lion groups without a male did not approach hyena playbacks. The two times the hyena playbacks set off an approach of the Ngamo pride only one of the times the adult male lion was present in the group. The other time the male lion was later seen at the fence line not far from where the playback was played. During the third playback some difficulties with the loudspeakers occurred and the playback had to be played three times because the volume could not be set up to maximum. Due to this the sound was heard very softly and only the lions that were resting but not asleep gave a reaction. Just before the fourth playback was performed to the pride they killed a wildebeest and were all feeding. They did not show any interest to the 24 whooping hyena sound. It is perfectly possible that the pride didn't even hear the playback sound because they were all growling very loud over the carcass. The last playback performed of 6 whooping hyenas made 9 of the 12 pride members vigilant to the playback sound and the adult male stood up but didn't approach the loudspeaker.

Conclusion

This study has shown that semi-wild lions react the same way as wild-borne lions to a group of lion intruders. Captive born lions assess the likelihood of winning a contest on the basis of relative group size, just as wild lions do. This is a positive result for the chances of captive born cubs to learn from their parents required behavior for living in the wild.

Overall, the results should be interpreted cautiously because the same pride members were measured several times which makes the observations dependent of each other. Because of the

limited length of the study the several playback sounds were tested only a few times which makes it difficult to get to significant results.

Further research is required in order to see if the observations found are statistically significant. In this study it was not possible to place the loudspeaker inside the release area and to keep the distance between the pride and the speakers in all cases the same. The distance varied between 50m and 250m which may have had some influence on the results. The sound intensity of the playbacks differed with the difference in distance kept between speakers and pride. In a next study it would be necessary to keep the distance always fixed.

Lion playbacks were performed every 8 days and hyena playbacks approximately every 10 days because of the limited period in which the study had to be performed. This may cause habituation to the occurrence of the playbacks which might disturb the reactions of the pride. For this reason, in a next study, there should be much more time between two successive playbacks.

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References

- Bauer, H. and Nowell, K. (2004). Endangered classification for West African lions. *Cat News* **41**: 35-36.
- Grinnell, J., Packer, C. and Pusey, A.E. (1995). Cooperation in male lions: kinship, reciprocity or mutualism? *Animal Behaviour* **49**: 95-105.
- Grinnell, J. (2001). Modes of cooperation during territorial defense by African lions. *Human Nature* **13**: No. 1, pp. 85–104.
- Hayward, M.W. (2006). Prey preferences of the spotted hyaena (*Crocuta crocuta*) and degree of dietary overlap with the lion (*Panthera leo*). *Journal of Zoology* **270**: 606—614.
- Heinsohn, R. and Packer, C. (1995). Complex cooperative strategies in group-territorial African lions. *Science* **269**: 1260-1262.
- Heinsohn, R., Packer, C. and Pusey, A.E. (1996). Development of cooperative territoriality in juvenile lions. *Proceedings of the Royal Society London Biology Sciences* **263**: 475-479.
- IUCN (2006a). Conservation strategy for the lion in West and Central Africa. Yaounde, Cameroon.
- IUCN (2006b). Regional conservation strategy for the lion *Panthera leo* in Eastern and Southern Africa.
- Kruuk, H. (1972). *The Spotted Hyena: A Study of Predation and Social behavior*. University of Chicago Press, Chicago.
- McComb, K., Packer, C. and Pusey, A.E. (1994). Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. *Animal Behaviour* **47**: 379-387.
- Myers, N. (1975). The silent savannahs. *International Wildlife* **5**: 5-10.
- Nowell, K., Breitenmoser-Wursten, C., Breitenmoser, U. and Hoffmann M. (2012). "Panthera leo". IUCN Red List of Threatened Species. Version 2012.2. International Union for Conservation of Nature.
- Packer, C. (1986). The ecology of sociality in felids. In: Rubenstein, D.I. and Wrangham, R.W. (eds.), *Ecological Aspects of Social Evolution*, Princeton University Press, Princeton, New Jersey, pp. 429-451.
- Packer, C., Scheel, D. and Pusey, A.E. (1990). Why lions form groups: food is not enough. *The American Naturalist* **136**: 1-19.
- Pusey, A.E. and Packer, C. (1987). The evolution of sex-biased dispersal in lions. *Behaviour* **101**: 275-310.
- Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., Funston, P., Groom, R., Henschel, P., de longh, H., Lichtenfeld, L. and Pimm, S. (2013). The size of savannah Africa: a lion's (*Panthera leo*) view. *Biodiversity and Conservation* **22**: 17-35.
- Schaller, G.B. (1972). *The Serengeti lion: a study of predator-prey relations*. University of Chicago Press.

Watts, H.E. and Holekamp, K.E. (2007). Hyena societies. *Current biology* **17**: No. 16.

Watts, H.E., Blankenship, L.M., Dawes, S.E. and Holekamp, K.E. (2010). Responses of Spotted Hyenas to Lions Reflect Individual Differences in Behavior. *Ethology* **116**: 1199-1209.

Webster, H. , McNutt, J.W. and McComb, K. (2010). Eavesdropping and Risk Assessment Between Lions, Spotted Hyenas and African Wild Dogs. *Ethology* **116**: 233-239.

Appendix I – Territorial data sheet

Territorial Behaviour

Lion

Reaction to playback

Date	Time	GPS S	GPS E	AT1	AS	KE	KW	NL	NR	PH	MI	AS4	AS5	KE3	KE4	Playback Type

Rank of reaction:

-2 retreating from playback fast paced

-1 retreating from playback slow paced

0 no reaction

1 vigilant to/looks in direction of playback

2 approaches playback slow paced

3 approaches playback fast paced

4 roars in response to playback

Order of approach

Time of playback	Time of approach from onset (secs)	AT1	AS	KE	KW	NL	NR	PH	MI	AS4	AS5	KE3	KE4	DNF	NP

Leaders response

Date	Time	Leader	Pauses	Looks back	Notes

Cub response – group position

Date	AT1	AS4	AS5	KE3	KE4

Cub response:

Front of the group (F)

Middle of the group (M)

Back of the group (B)

Direction of playback

Date	Time	Direction of playback	Position of lions in release site

Weather condition

Date	Cloud cover	Temperature	Wind	Rain

Notes

Date	Notes