

Reintroduction of Social Carnivores

Effect of composition on cooperation and hunting success in lion hunting groups



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July 2011



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Summary

Reintroduction of endangered species is important in conservation biology. An additional aspect in social carnivores is forming a social bond to increase their fitness. Lions form social prides to hunt cooperatively on larger prey and become more efficient hunters. This study was within a reintroduction project in Zambia, where captive-bred lions learn to hunt and form a social pride in a four stage program. The main question was what the effect is of mixing lion hunting groups on their cooperative behavior and which composition is the most effective. Composition of groups was changed, by putting lions together which did not hunt together before. The results show no difference in cooperation among different group compositions. However cooperation decreases when hunting groups change every encounter. Another result is the lightest lion starts the stalk, while the heaviest lion makes the kill. Just like wild lions they are able to cooperate by a division of labor based on body size. But towards the end of the study, the lions decided to hunt more solitary instead of cooperatively, meaning the experimental setup had a negative influence on lion's cooperative behavior. Lions do not need to be together from young age, to cooperate during hunting. They still cooperate in new group compositions. This study adds to the knowledge how to successfully introduce social carnivores into the wild. Often the causes of reintroduction failure are unknown, which underlines the importance of researching the used methods.

1. Introduction

1.1 Problem Statement

Reintroduction of animals is a hot topic by conservation biologists to save endangered species. Especially carnivores get much attention, because of their large influence on herbivores and other carnivores (Creel & Creel, 1996; Larivière et al., 2000; Mills, 1991). Carnivores need sufficient prey, but can also unbalance the prey population, when the carnivores are overpopulated. There are already many problems related to solitary carnivores, but with social animals there's one additional aspect. Those carnivores will suffer from lower reproductive success, when being released on their own. They need a social group to increase cub survival and increase hunting efficiency (Caraco & Wolf, 1975). The problem in this study is related to hunting behavior, a more detailed look is taken at the cooperation in lion groups within a reintroduction project. This is to understand the social behavior related to hunting and how this can be improved to increase reintroduction success. Sociality is needed when hunting, because hunting success increases when lions cooperate during a hunt (Stander & Albon, 1993).

1.2 Relevance

The lion is declining (Sunquist & Sunquist, 2002), so that is why a good conservation program is needed to prevent further declining of the species. One of the ways is to reintroduce captive bred animals back into the wild. This study is done within a reintroduction program of the lion. One of the objects of the study is to look if further improving of the used methods is possible. The influence of group composition will be investigated and its impact on the different hunting groups will be analyzed. This way there could come a better understanding of how to improve conservation strategies. Also hardly any research has been done with the focus on group composition, so this study might contribute to more knowledge about this part of hunting behavior in lions. The focus in most articles is about the group size, or the environmental variables affecting the hunting success (Caraco & Wolf, 1975; Funston et al., 2001). Because the lions will be assigned to a certain group, solitary hunting is also a possibility. In this study lions could refuse to cooperate in certain group compositions.

1.3 Lion Encounter

This study was done within a reintroduction program of the African Lion at Lion Encounter, which is part of African Lion and Environmental Research Trust (ALERT). ALERT promotes and facilitates the development of lion conservation management plans and also educate the local communities how to maintain biodiversity and conserve nature. The "African Lion Rehabilitation & Release into the Wild Program" is a four stage program to reintroduce captive bred lions into the wild (Fig. 1).

In stage one the cubs are taken away at an age of three weeks old from their mother in the breeding centre. The people act as the dominant members of the pride and take the cubs on walks. From the age of 18 months they are able to stalk and kill small prey species by themselves. After 18 months it is not safe anymore to walk besides them, and from this age they are placed in the next phase of stage one. This is the Night Encounter program, in which phase the research was done. The Night Encounters are hunting sessions for the lions, where they are taken out of their enclosure and can walk freely around within the hunting site. The lions can chose to walk behind the vehicle or in front of the vehicle. Goal of the Night Encounter stage is to improve their hunting skills.

When having their hunting skills developed to sustain themselves, they are released in stage two, where they have to hunt for themselves, and the lions are not fed anymore. In stage two all human contact is removed and the lions are able to form their own social pride. The lions are radio-collared to check their movements. In stage three those lions give birth to young cubs, and raise them on their own. These cubs have not been in contact with humans and are replaced into reserves and national parks in stage four of the program.

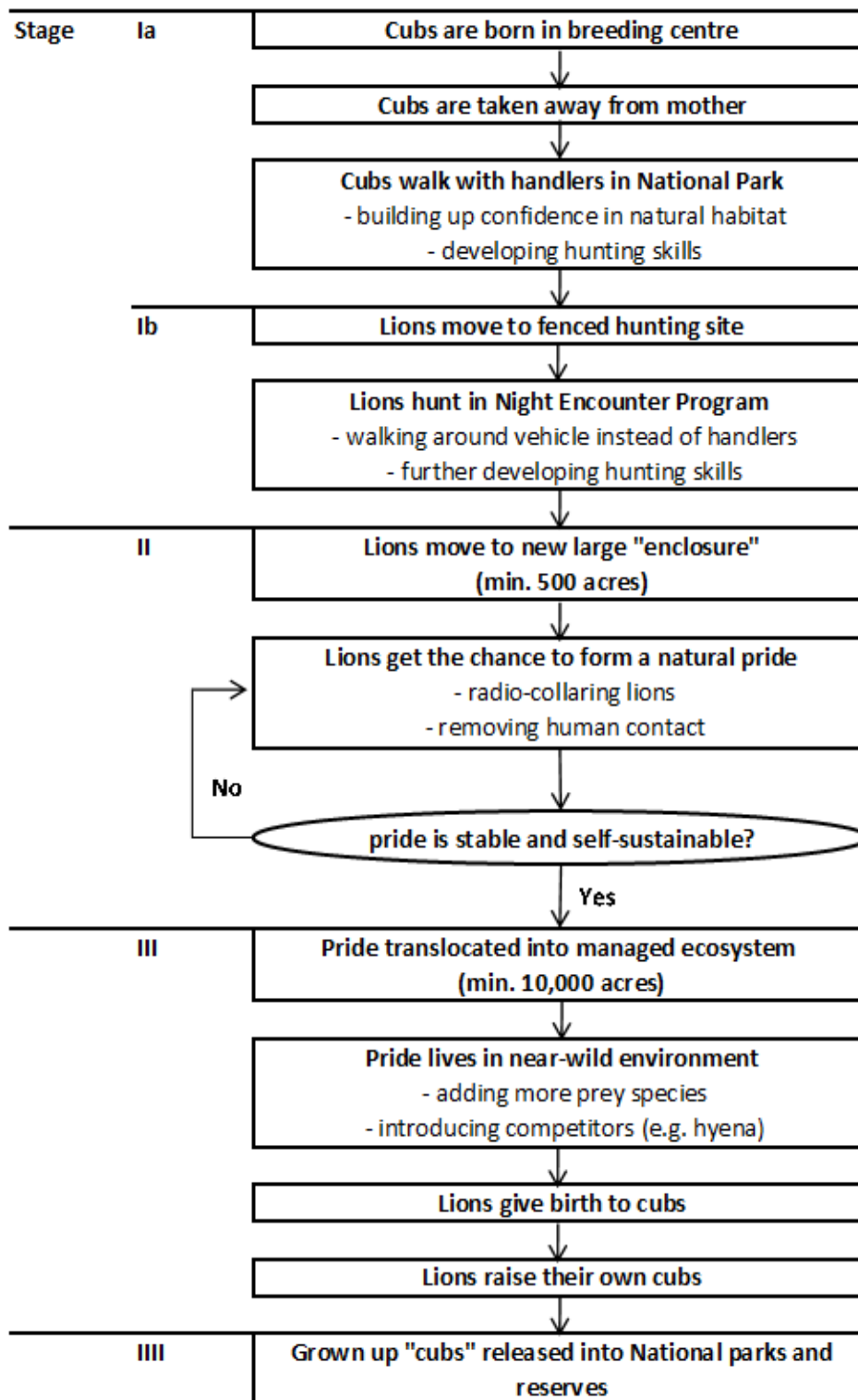


Figure 1. The four stages of the African Lion Rehabilitation & Release into the Wild Program

2. Research questions & objectives

2.1 Objectives

For this study several objectives were formulated related to the reintroduction project and the lions behavior:

- Getting insight in the importance of group composition on the level of cooperation in a lion group
- To investigate whether there are differences among different group compositions, whereby lions who hunted together previously to the Night Encounter program, will be mixed into new group combinations
- Investigating the individual lion's behavior regarding the position they take during a hunt
- Investigating if the lions in the reintroduction program show behavior like wild lions
- Investigating whether the lions can learn to hunt effectively

2.2 Questions

For this study the main questions are:

Does changing group composition of lion hunting groups affect their cooperative hunting behavior?
What group compositions result in best hunting success?

To answer these questions a few questions need to be answered for each observed hunt, namely:

- What does the composition look like? Which lions were in the same group before the Night Encounter program?
- What prey species does the group attempt to hunt?
- What is the level of cooperation?
- Who stalks first? Who chases first? Who makes the kill?

When the above questions for each group are answered a comparison between lion hunting groups can be made resulting in two part questions:

- What are the differences in level of cooperation among the different hunting group combinations?
- What are the differences regarding individual hunting behavior?
- How can these differences be explained?

2.3 Hypotheses

- I expect a higher level of cooperation in group compositions, where more lions of the same "old" group are together. Old groups are lions which hunted together before the study (this is explained in more detail in M&M). Those lions have more experience hunting with each other, taking certain roles in the group. Stander (1992a) reported that lion groups in which female lions occupied their preferred role had a higher hunting success. I assume because the lack of experience hunting with each other, there will be less cooperative attacks in "new" groups.
- Regarding individual behavior, I think the lions are able to adapt to new roles in a new hunting group. Stander (1992a) stated their preferred role leads to higher hunting success, but also that lions are able to adapt and occupy new roles within a group. So I assume lions will be observed in different positions in new group compositions.

3. Background information

3.1 Problems with reintroductions

Species are declining because of habitat destruction and fragmentation, which result in isolation of populations. Also overhunting is a threat to species survival (Kramer-Schadt et al. 2005; Sjöåsen, 1996). Reintroduction of endangered animals is one way to prevent species go extinct. Often those reintroductions are unsuccessful, and there is no proper indication on the causes (Gusset et al. 2006). The factors affecting success are not well understood (Hunter, 1998).

For carnivores, projects are costly, lengthy and complex, and need to become more efficient (Kramer-Schadt et al., 2005). For several species there are already reintroduction programs, like the European Lynx (*Lynx lynx*), African Lion, European otter (*Lutra lutra*), Grey wolf (*Canis lupus*), and African wild dog (*Lycaon pictus*, Kramer-Schadt et al. 2005; Sjöåsen, 1996; Larivière et al., 2000; Gusset et al., 2006). One difference in reintroduction projects, is in the way of releasing. In a soft release, the animals stay in a fenced area before the real release, they stay in captivity for a while (Hunter, 1998). Contrary in a hard-release the animals are put into a new area, without getting used to the area for a certain period.

In social animals, the social bonds seem important for a successful reintroduction (Gusset et al. 2006; Hunter, 1998). An additional problem with social animals is the group structure. For example dogs live in packs with related dogs, which is not good for preventing inbreeding (Frantzen et al., 2001).

Also there is the option to release captive bred or wild caught animals for reintroductions, where the latter can better be defined as a translocation of animals.

3.2 Cooperation in lions

Group hunting by terrestrial carnivores like the lion is thought to reduce problems of finding and subduing prey, and to improve killing efficiency. Group hunting seems an attempt at maximizing food intake per capita by improving foraging success (Scheel, 1993). This is important in open terrain, when a high influence of scavengers and widely dispersed prey is present. Lions are the only social felids which hunt in groups (Funston et al., 2001; Stander & Albon, 1993).

There is already a lot of research about hunting behavior of lions, but most is related to the effects on foraging or hunting success caused by environmental variables, group size of the lion or the prey species. However, group composition is not taken into account and no details are given as to why it could be important. Stander (1992a) suggests that hunting success can increase when lions are in their preferred role within the group. He compares a lion group with a football team, with centers and wings. The wings are the lions which mostly start the chase, while the centers capture the prey in an ambush position. This is an example of division of labor, where some lions initiate the attack, and others ambush the prey. In addition Stander & Albon (1993) state that coordinated group attacks have a higher probability of making a kill. They compare different prides and their attack coordination. Both studies, mentioned above, observe lions in the wild, having no control of the composition of the lion hunting groups. The first study focuses on the individual lion in a group, only looking at its role, and does not take other lions into account.

3.3 Prey and lion variables affecting the hunt

The vulnerability of prey is determined by its abundance, size, temporal and spatial distribution, defenses and anti-predatory tactics (Hayward & Kerley 2005). Lions have an initial acceleration advantage, but this is lost within the first few seconds, after which the Thomson's gazelle rapidly outpaces them, followed by the zebra and the wildebeest which are only fractionally faster than the lion. The buffalo also has a slight speed advantage, while the warthog is relatively slow compared to the ungulates (Hayward & Kerley 2005; Schaller, 1972). Hayward & Kerley (2005) suggest a strong correlation between body mass of the prey and injury risks for a predator, because larger prey are able to inflict more damage on lions than smaller prey.

Features of the predator that affect hunting success are hunting group size and composition, and hunting method (Hayward & Kerley 2005). Coordinated group hunts and lioness group size are the two most important variables in determining the success of hunts (Stander & Albon, 1993).

When looking at the observed group sizes, it seems that in the Etosha N.P. (Namibia) the lions prefer to hunt in pairs. Success rates of a solitary lion are 2.3-2.6% and this is lower than in other national parks, where success rates are at least five times higher (Stander, 1992). Because the individual success rates are this low, the highest benefit in Etosha is hunting in pairs when success can increase to 27% (Stander, 1992). Pairs do have the highest intake rate, but their hunting success on larger prey is much lower than larger groups. During the dry season, the intake for pairs is 12 kg compared to 10 kg for larger groups, but the hunting success rate is 10%, while groups of six have a success rate of 34,2% (Sunquist & Sunquist, 2002). Thus pairs do have a higher intake, but have to spend more time and energy to get their food intake.

In the Serengeti, Schaller observed group sizes of 2-5 lions on gazelle and 3-5 lions on wildebeest and zebra (Schaller, 1972). Large groups of five lions also take small prey, which has no higher efficiency when looking at the hunting success rates which are almost the same for larger groups on gazelle. It might be the case that the opportunistic behavior of the lion is the reason for this, and also small prey are captured (Stander & Albon, 1993). The highest efficiency for a solitary lion is when it kills small prey and for a group of five lionesses highest efficiency is gained by killing buffalo. Groups of 2-4 lionesses do not kill buffalos, but stick to medium sized prey (Packer et al., 1990).

In Kruger N.P. only pairs have a lower intake and benefits start already from three lions and higher. Solitary lions have advantages here compared to pairs, but have a lower intake compared to groups of 3-4 lions (Funston et al., 2001). Hunting groups are seldom larger than seven lions, it seems lions prefer a smaller group size of five and hunt mostly with a group up to five (Schaller, 1972).

3.4 Environmental variables effecting the hunt

The most important environmental factors are cover, time of the day, moon presence and habitat (Scheel & Packer, 1991; Stander & Albon, 1993). The difference between day and night is especially important, because darkness decreases the visibility of the lion. During daytimes the amount of cover is important, and grass height from 0.4 meter up to 0.8 meter affects hunting success positively (Hayward & Kerley 2005). Darkness is important as well, the presence of the moon affects hunting success negatively. The interaction between day/night and cover has an effect on the probability a hunt is successful (Stander & Albon, 1993).

4. Material and Methods

4.1 Study area

Dambwa Forest (S17.45;47.3,E025.47;15.2) shares a 4 kilometer border with Mosi-oa-Tunya National Park (Livingstone, Zambia), but is classed as a separate area of land. The forest is about 108 km², and is 3 kilometers away from the Zambezi River. 900 acres of the forest is used for the hunting site. The hunting site is surrounded by a fence, so lions will not be able to get out by themselves. At the edge of the hunting site are the enclosures for the lions, in which the lions stay when they are not out for a Day or Night encounter. The main vegetation in this area is Munga woodland and Miombo woodland. Also there is riverine vegetation, mixed woodland, thicket and mopane woodland. Game has been released in the hunting area, which consist of 41 impala (*Aepyceros melampus*), 15 puku (*Kobus vardonii*), 44 wildebeest (*Connochaetes taurinus*), 5 zebra (*Equus burchelli*). The fence prevents most animals from coming in, however some small animals still manage to get in the hunting site. Other animals spotted are duiker (*Sylvicapra grimmia*), Chacma baboon (*Papio ursinus*), Kori Bustard (*Ardeotis kori*) and other birds, springhare (*Pedetes capensis*), and rabbits. The exact numbers of these animals in the hunting site are unknown, and could change over time. Within the hunting site, the lions are the only large predators. Thus there is no competition for prey animals.



Figure 2. Map of area Livingstone (Zambia), hunting site at Dambwa Forest enlarged

4.2 Lion hunting groups

In this study ten captive bred lions were followed, eight females and two males. Since the age of one year, they are together living in the same enclosure. During this study, they were between 18 and 27 months old. In the first stage of the reintroduction program, four different groups were taken out for walking, which did not change until the Night Encounter program. These different groups walked and hunted together in these group compositions, and did not hunt with any of the other lions till the start of this study. The groups were as follows (Table 1):

- 1) three females, 2KLs
- 2) one female and two males, LZTs
- 3) two females, 2Rs
- 4) two females, 2Ts

As part of this study, in the Night Encounter program these four groups were mixed into new combinations to investigate whether there were any differences in hunting behavior. Thus the lions in the four old groups, mentioned above, were mixed to create new groups. For example the 2KLs got an addition lion from the LZTs in their group. Also new groups were created by taking one lion from each group. The new groups had two up to five members.

In the program there was full control of the lions. They were not all the time walking around freely. The time they got released into their hunting area could be managed, and also which and the number of lions. The lion's enclosure was in the hunting site near the boundary and it consist of several sections. The lions could be separated with the help of three management gates, and a group could be released by opening the main gate to the hunting site. There were two large enclosures and two small ones, which were about ten percent of the large enclosures. The lions which were not on an encounter, were put in one of the smaller enclosures, or in the larger one. After the observation period the lions followed the handlers back to their enclosure. Lion Encounter asks permissions from the Zambia Wildlife Authority (ZAWA), and will not do anything without approval. The methods used in the program are approved by the ZAWA.

Table 1. Composition old and examples of new lion hunting groups

Old groups					
<i>Names</i>	<i>Gender</i>	<i>Abbreviation</i>	<i>Names</i>	<i>Gender</i>	<i>Abbreviation</i>
Kela	F		Leya	F	
Kwandi	F	2KLs	Zulu	M	LZTs
Loma	F		Toka	M	
Rundi	F		Temi	F	
Rusha	F	2Rs	Tswana	F	2Ts
Examples new groups					
<i>Additional lion</i>			<i>One of each group</i>		
Kela			Toka		
Kwandi			Kela		
Loma			Rundi		
+ Leya			Temi		

4.3 Instruments

During the observations the lions were followed from a vehicle, a Land Rover with place for twelve people including the driver. The distance between the vehicle and the lions was between 10-50 meters and increased to 100 meters when prey were spotted to prevent warning the prey of the presence of the lions. The lions were used to humans nearby, because of their captive bred history. Lions are nocturnal animals, so part of the observations were done during the night, which resulted that extra tools to improve vision were needed. Spot lights with a red filter over the top were used to watch from the vehicles. Red light has the least effect on the lion's or prey animal's night vision, because night vision is based on having more rods and red light is viewed by the cones. Still care was taken when shining the lights on one of the animals. The red light was used for identification of the lions and the position they took. When prey were encountered, the light was pointed on a spot nearby the animals. This way the animals were not blinded by the light, so they had no disadvantage trying to escape from the lions. The light was only a few seconds pointed on lions when the prey were nearby. The red light made them more visible, especially when darkness was their main cover.

4.4 Classification of hunts

Sometimes lions saw an animal, but just ignored it, or had no intention to catch it. Also at times they only walked a few meters towards the prey, and did nothing to stay hidden. The prey ran away and the lions did not start to chase. Lions behaved different when seeing prey animals, therefore a definition of a hunt was needed to classify a hunt. Only when the lions hunted according to the definition, notes were taken. The following definition was used to define a hunt:

A group is considered to be hunting when at least one lion moves towards potential prey while exhibiting any of the following behavioral patterns: alert face (Schaller p93-94) (Orientated towards prey) combined with waiting in ambush, alert walk, stalking walk, crouching walk, crouch, trot, head-low trot or rush (Schaller p99-100). At least one lion has to stalk the prey for more than ten meters, only abandoning the hunt when the prey escape (Scheel & Packer, 1991; Stander, 1992b).

When the lions behaved according to the definition of a hunt, there are three classes the hunt was placed regarding the cooperation in that hunt. Stander (1992b) suggested three different classes regarding to cooperation:

- 1) Class A: there is no cooperation at all, one or more lions try to capture the prey. The lions try to capture the prey without taking the other one's position into account. All the lions take the direct approach to get to the prey animal, and no lion moves to the left or right to approach from a different direction. When lions refuse to cooperate and start hunting solitary, the hunt is also put in this class.
- 2) Class B: there is cooperation, but less precisely as in class C. In class B more than one lion stalks the prey. In this class type the lions do not surround the prey, but still attack from the same direction. The lions do take more distance from each other, which results some lions can have a shorter route to cut off the escaping prey.
- 3) Class C: cooperation, more precise than class B. There is a clear division of labor, and positions are taken carefully and the lions do surround the prey. One or some lions will chase the prey, while others ambush the prey when it tries to escape. The chasers lead the prey into the direction of another lion.

In the field, the lions showed very wide behavior in class B, which is why class B was separated into two different classes: B1 and B2 (Fig. 3). This extra class was also added to make the gap between class B and C smaller, so it was easier to give an indication of the level of cooperation. In class A all the lions took the direct approach, and none of the lions bent its path to try attack from one of the flanks. In both classes B1 and B2, at least one of the lions took the left or right approach, which made the lion use a longer route to the prey. The difference was that in B1 the lion was still at the same side in comparison to the prey, where in B2 the lion managed to reach one of the flanks, attacking

from a different direction. Hunts were only classified as class C, when the lions succeeded to let the prey run in the direction of another lion, and the prey got within 10 meters of that lion.

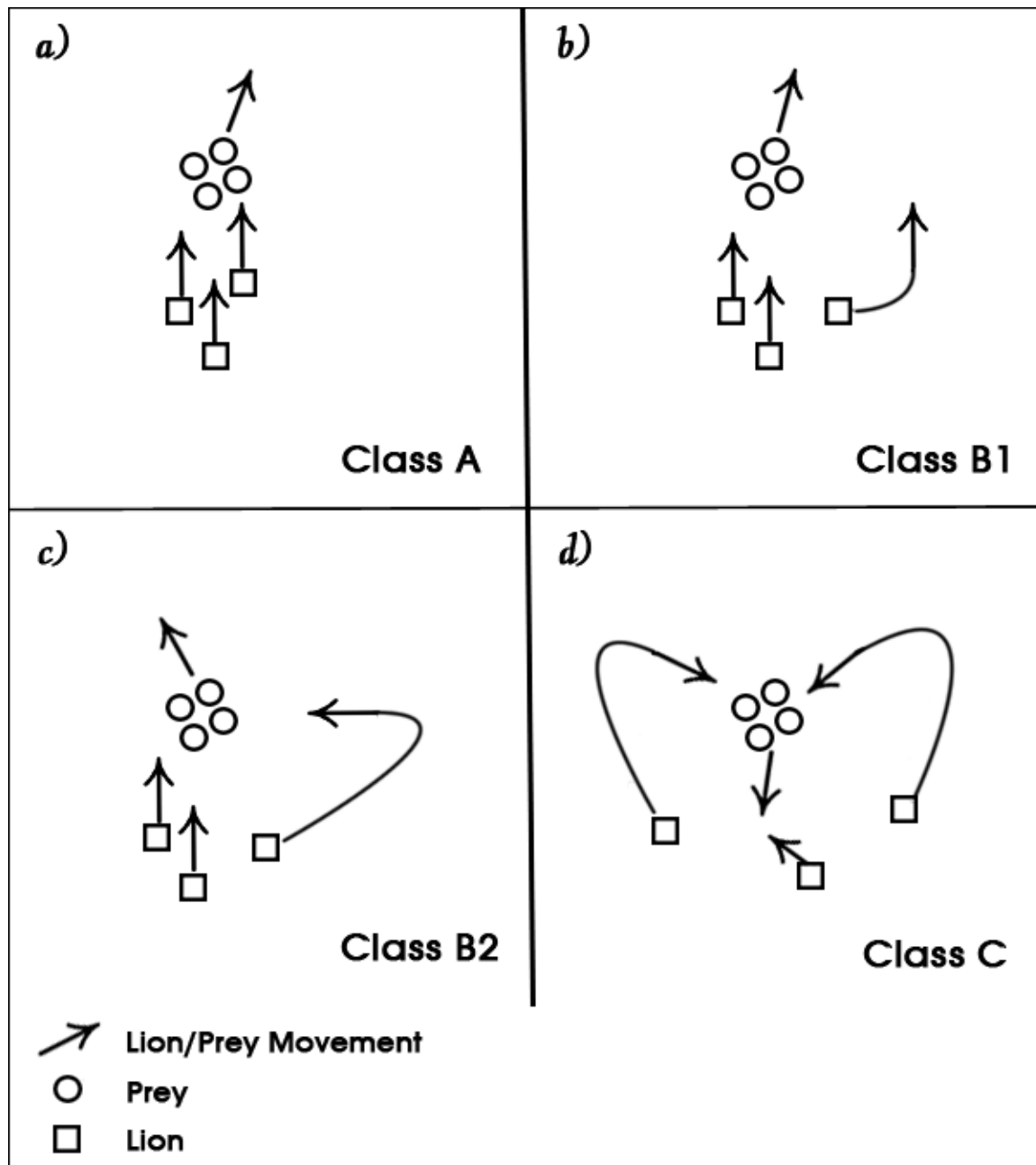


Figure 3. The four hunting classes used in this study. Class A: no cooperation, all direct approach; Class B1: little cooperation, attack from one direction; Class B2: little cooperation, attack from two directions; Class C: cooperation, short chase.

4.5 Other variables during the hunt

As not only cooperation affects the hunting success, also group-, prey- and environmental variables were taken into account. For each observation several aspects had to be looked at, and to be written down on a form, first starting with day of observation and the time of the day. The day was separated into four periods, namely:

- 1) AM, Night Encounter (12 midnight-6 AM)
- 2) AM, Day Encounter (6 AM-12 noon)
- 3) PM, Day Encounter (12 noon-6 PM)
- 4) PM, Night Encounter (6 PM-12 midnight)

Times of sunrise was between 6AM and 7AM, and the sunset was between 6PM and 7PM, having 12 hours daylight every day. Most observation during the night started around dusk. There was only one Night Encounter in the early morning, starting around 4 AM.

Before an observation started, first the details of a hunting group were noted. For each hunting group two variables were written down:

- 1) Group size
- 2) Group composition

Group size is one of the most important variables for prey choice and hunting success, especially hunting large prey is group size specific (Scheel, 1993). Group composition is the main question of the study and was analyzed. Hayward and Kerley (2005) reported that group composition is important when looking at the role of the individuals. When being in their preferred role, the hunting success seems to be higher. Additional to the lions in the group, also the original group (2KLs, LZTs, 2Rs, 2Ts), in which they were before the Night Encounter Program was mentioned.

Group size and compositions were the variables for the lion, but also the variables for the prey species hunted were written down. During the observations, the following was taken into account:

- 1) Prey species
- 2) Herd size
- 3) Prey Behavior
- 4) Distance to prey, when first spotted by one of the lions

Not only prey species and group size were important to measure cooperation, also environmental variables had to be taken into account. The environmental variables which affect lion hunting behavior and significantly influence hunting success, according to the literature, were measured during the observations. These variables are:

- 1) Presence/absence moonlight:
 - 0 = Not visible or heavily obscured
 - 1 = visible or lightly obscured.
- 2) Scrub cover:
 - O = Open habitat
 - M = Moderate cover
 - D = Dense cover.
- 3) Grass length:
 - S = Short (< 20 cm)
 - M = Medium (20-60 cm)
 - L = Long (>60 cm)
- 4) Wind direction:
 - U = Upwind
 - D = Downwind
 - C = Crosswind
 - N = No wind

The presence of the moon influenced the visibility of the lions. During moonless nights they were less visible than when the moon was present.

Scrub cover was divided into three categories. In open area there were no trees present, or only a few. Also only a few bushes were present. In moderate cover more trees were visible, and also more bushes. There was still enough space between the trees you could see through the cover. Dense cover had many trees and bushes, made it impossible looking through a group of trees or bushes.

The grass length was also put into three categories. Short grass was too small for decent cover, when laying down the lions were still visible. Medium grass was up to the lion's eye level. The lions could

still look above the grass, while long grass was too long to leave them with vision. Several prey stayed unnoticed because of the tall grass.

Next to these variables of course the hunting statistics were mentioned:

- 1) Stalking yes/no
- 2) Direct approach yes/no
- 3) Kill success of hunts yes/no
- 4) Level of cooperation
- 5) Lion which makes the kill

4.6 Experimental setup

An experimental study was done, to answer the main questions and test the hypotheses. It was a manipulative study, where there was control of the lions giving them the opportunity to hunt. It was up to the lions, whether they did hunt and cooperate. Different group compositions were compared to see whether the hypotheses were confirmed or rejected.

Before the start of an encounter, first a few things had to be decided (Fig. 4). The day and time of the encounter was up to the management of the reintroduction project. Handlers and the vehicle had to be available for an encounter. There was no apparent pattern in the time of the encounters, days in between and time of the day varied throughout the study. Also the composition of the lion group for the encounter was decided beforehand, sometimes by the management and sometimes by the researchers. The only consistent part was that every lion group had to be released three times during the observation period, at least once in a Day Encounter, and once in a Night Encounter.

When day, time and lion group was decided, an encounter could start. The lions for the encounter, were separated from the others. After opening the main gate to the release site, the encounter could start. At the start of the encounter, the vehicle was often in front of the lions. After being about 500 meters away from the enclosures, the lions took the lead. The vehicle followed the lions from a small distance.

During the encounter, prey were spotted by the lions. Most of the times the lions started a hunt, with a few exceptions. During a hunt three types of variables were taken, namely:

- 1) Prey related variables
- 2) Environmental variables
- 3) Hunt variables

These variables were written down during the encounter on a form (Appendix I). When the hunt failed, the lions could continue the encounter. The encounter took at least three hours, till the lions were brought back to their enclosure. After three hours the lions were tired, or not interested in hunting anymore. They went back to the enclosure by following the vehicle. When back in the enclosure, the main gate was closed again, and the lions were united with the other lions.

After the encounter, the collected data was discussed with at least two other persons, to make sure the right data was written down.

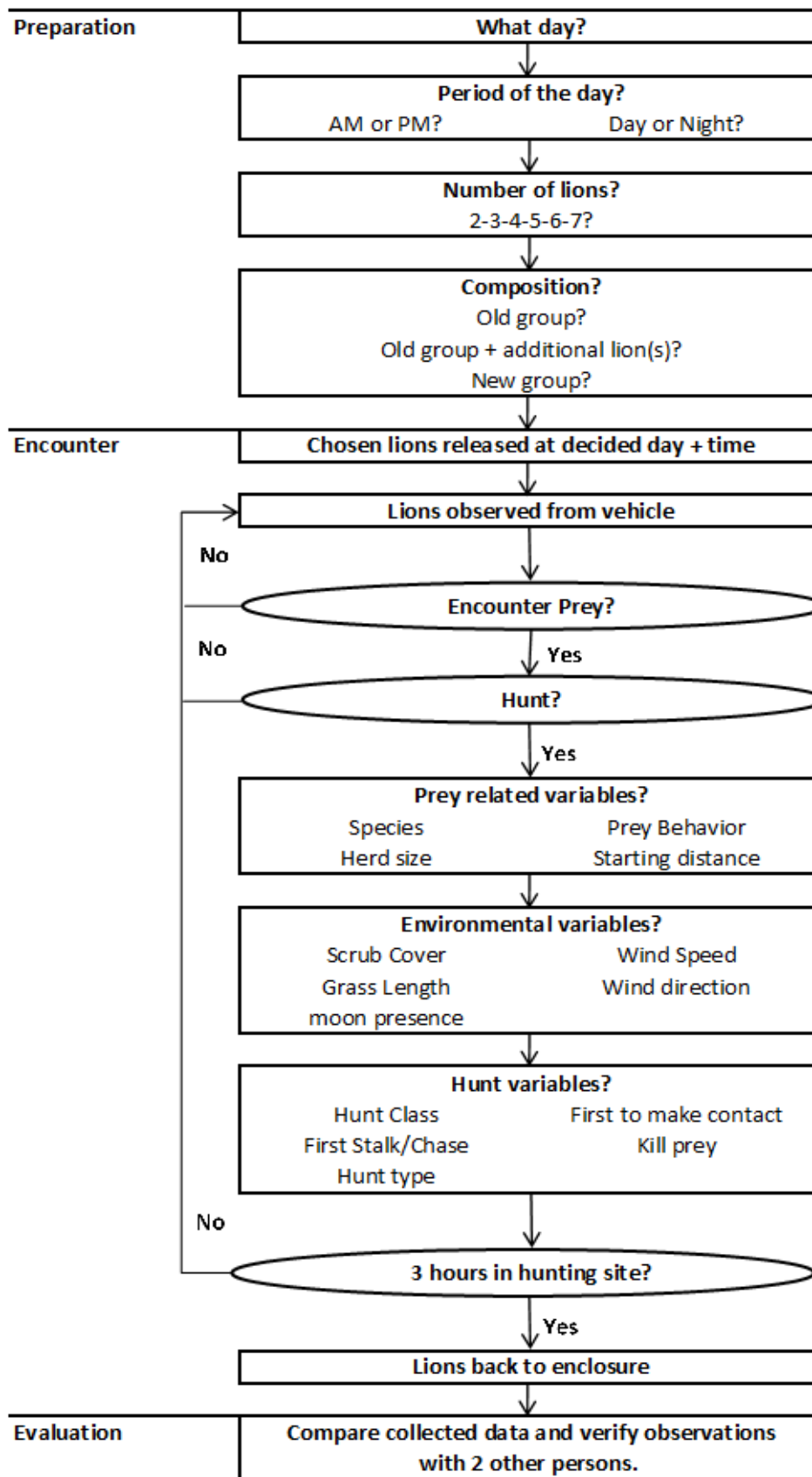


Figure 4. Schematic overview of experimental setup

5. Data Analysis

5.1 Differences between groups

To answer the question whether there are differences in cooperation among the different group compositions, the groups were categorized. The groups were divided into three categories (Table 2), namely:

- 1) "Old Groups" (OG)
- 2) "New complete groups" (NC)
- 3) "New incomplete groups" (NI)

Table 2. Characteristics of the three hunting group categories

3 Categories	Characteristics	Examples
Old groups (OG)	Old group composition Walked and hunted in first stage of the program No changes made.	1. 2KLs 2. 2Rs
New complete (NC)	New group composition At least one complete "old group" in the group composition. One or more lions from other groups added to the "old group"	1. 2KLs + Leya 2. 2Rs + 2Ts
New incomplete (NI)	New group composition. No complete "old groups" in the group composition. Maximum of two lions from the same group (2KLs or LZTs), maximal one member from 2Rs or 2Ts	1. Toka, Kela, Rundi, Temi 2. Leya + Kwandi

For each category the different levels of cooperation were counted (Table 3). Class C hunting had only two measurements, which is why class C hunting was left out of some of the analyses. After counting, a X^2 analysis was done to investigate differences. In total three different analyses were done, one comparing the three separate and two times combining two categories (Table 4).

Table 3. Count for each group category the different levels of cooperation

Hunt class		Group Category		
		Old groups	New (complete)	New (incomplete)
A	0
B1	1
B2	1
(C)	1	(..)	(..)	(..)

The second analysis was done to compare all new groups to the old groups. Thus no difference was made whether a complete old group was part of the new group.

The third analysis was done to see whether there was a difference in cooperation when an old group was present or not. Thus all groups with an original old group were compared to all new groups without a complete old group in there.

After these three analyses another three were done, by combining hunting classes. The level of cooperation was now put into two classes (Table 4):

- 1) 0 = no cooperation (class A)
- 2) 1= cooperation (class B1 + B2 + C)

In the last three analyses class C hunting was included. Also here a X^2 analysis was done to look for any differences.

Table 4. Different analyses to compare cooperation among hunting groups

Analysis	Hunt Class	Group categories
1	A,B1, B2	OG, NC, NI
2	A,B1, B2	OG, NC-NI
3	A,B1, B2	OG-NC, NI
4	0,1	OG, NC, NI
5	0,1	OG, NC-NI
6	0,1	OG-NC, NI

A, B1, B2 = different hunting classes compared

0,1 = no cooperation compared to cooperation

OG = Old groups, NC = New complete groups, NI = New incomplete groups

5.2 Size related

At the end of the study several measurements were taken regarding the size of the lions. The length of the paws, the size from head to tail, and chest girth were measured. The front leg size (FL) says shoulder height and tells which lion is the tallest. The chest girth (CG) was measured, because it was not possible to measure weight. The heaviest lion is assumed to have the largest chest girth, because Bertram (1975) showed there is a correlation between chest girth and weight of the lion.

For each hunt was written down whether the smallest lion was starting the stalk or starting the chase (Table 5). The smaller lions were assumed to start the stalk and chase more often, because they were lighter and possibly faster. The heavier lions were waiting, trying to ambush the prey. For each measurement the totals were counted, the observed values. The expected values were calculated with the group sizes of each hunt. The expected value was calculated with the probability for each hunt, that the smallest lion would start the stalk or chase.

A X^2 analysis was done to investigate whether the smallest lion started stalking or chasing more often than the other lions. The X^2 analysis was done for both the CG and FL.

5.3 Regression

To investigate whether the lions showed a learning progress during the observation period, also two temporal analyses was done. Two factors were analyzed, namely level of cooperation and wind direction. A logistic regression was done in both cases, having the independent variable on the x-axis, which in this case were the different hunts. On the y-axis the dependent variable was placed, which were wind direction or hunting class.

First wind direction was analyzed, not taking the "no wind" measurements into account. The three remaining wind directions were put into two classes: class 1 for upwind, class 0 for downwind and crosswind. For the level of cooperation, class A cooperation was put as a "0" and the classes B1, B2 and C were put as a "1". Class A is the only no cooperation class, and the other three classes all show at least a little cooperation. Significant results mean the lions hunted more upwind or cooperative, in case of a positive slope. When the slope is negative, the lions hunted less upwind or cooperative.

Table 5. Size related analysis

Which lion starts the stalk?				
	Chest Girth (CG) - weight		Front Leg (FL) - height	
Hunt	Smallest?		Smallest?	
	yes	no	yes	no
1
2
3
etc.

Which lion starts the chase?				
	Chest Girth (CG) - weight		Front Leg (FL) - height	
Hunt	Smallest?		Smallest?	
	yes	no	yes	no
1
2
3
etc.

6. Results

6.1 General

This research was done in three months, starting halfway June. It was during the dry season, having no rain at all. The result was that everything was quite dry, and the environment was yellow/brown colored, which seemed a good cover for the lions. The temperatures were around 25 degrees Celsius during the day, and dropped to 10 degrees Celsius after sunset. During the observation period 54 hunts were observed, which means 54 times the lions started a hunt according to the given definition in the material and methods section. These were measured on 34 encounters (Fig. 5), of which eight had no hunts. Thus on 26 encounters at least one hunt occurred. The maximum number of hunts during one encounter was five.



Figure 5. Frequency distribution of the number of hunts on the different encounters

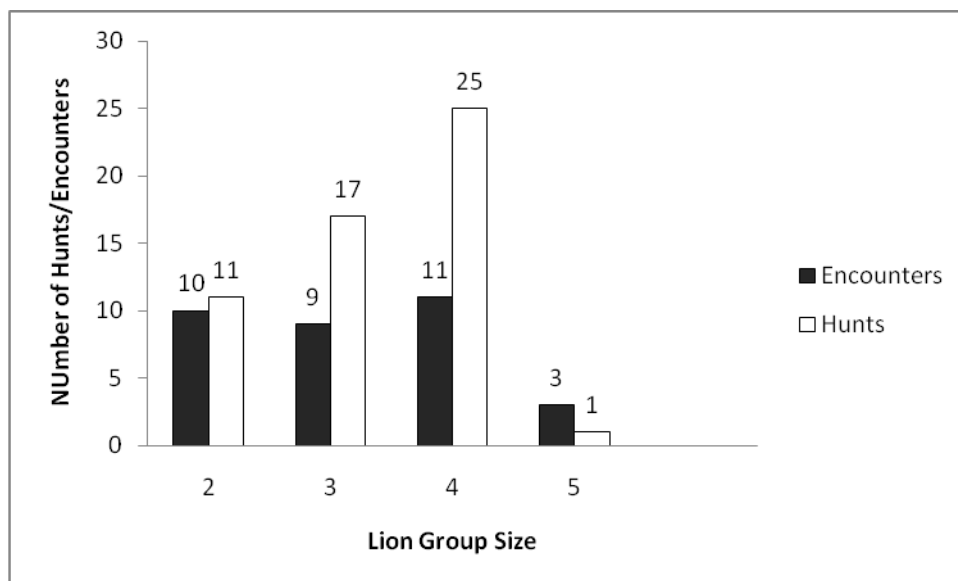


Figure 6. The number of encounters and hunts for the different lion group sizes.

The group compositions were from a size of two lions, up to seven lions (Fig. 6). Most of the times there were 2-4 lions out, and only four times 5 and 7. The encounters with three and four lions resulted in more hunting. To look whether this is significant, a X^2 analysis was done. The result was that there is a more significant difference ($p = 0.094$, $\alpha = 0.10$) from the expected number of hunts based on the number of encounters. Group size of 7 lions was not included in the analysis, because no hunting was observed for this group size. In this analysis an α of 0.10 was used, and this α was used for all analyses. The dataset is small, and that is why a larger α is used.

In total thirteen different group compositions were on an encounter (Table 6). Most went on three encounters, but there are four exceptions. The group of 2R2Ts had one extra encounter. The 2Rs refused to walk by themselves, moving only a few hundred meters away from the enclosures. The group composition with seven lions was a try out, but those lions were too playful to hunt. No hunts happened on this encounter, because the lions were not paying much attention to their environment.

The last one with only one encounter were the LZTs with Kela and Loma, where Leya walked back to the enclosures. The remaining four lions did go on the encounter and also hunted. This has been written down as a separate group, and not included with the other three encounters of the five lion group, because Leya was absent almost the entire time.

Table 6. Group compositions and their number of encounters

Group Composition	Total Encounters	Day Encounters	Night Encounters
2Ks	3	2	1
LZTs	3	2	1
2Rs	1	1	0
2Ts	3	2	1
2Ks + Leya	3	1	2
Leya, Loma, Kela	3	1	2
Toka + Zulu	3	3	0
2Rs + 2Ts	4	3	1
LZTs + Kela + Loma	3	1	2
2Ks + Leya + Zulu + Rundi + Tswana	1	1	0
Toka, Zulu, Kela, Loma	1	0	1
Toka, Kela, Rundi, Temi	3	1	2
Kwandi + Leya	3	2	1

The group compositions were divided into three different categories (Table 2, M&M), to investigate whether there are differences in the cooperation between the compositions. In all three categories were similar number of responses, namely 17 for the old groups, 20 for the new complete groups (NC), and 17 responses for new incomplete groups (NI).

Like mentioned before, the original plan was to do only night encounters, but because that would result in a very small dataset, also day encounters were included. There were only 14 Night encounters during the observation period. There were 20 Day encounters, which more than doubled the dataset. For every group composition was tried to have at least one day and one night encounter. Only the group of two males had Day encounters only.

6.2 Species hunted

In total nine different species were hunted (Table 7), of which the impala and wildebeest were the most commonly hunted species. Those were also the species which were most abundant in the hunting site, both above 40, while there were 15 puku and 5 zebra. The wildebeest were always, when spotted, together as one group, while impala also divided into smaller groups. Four species were only spotted solitary, the rabbit, scrub hare, Common duiker and Kori Bustard.

Most of the time the prey were standing (61%), when spotted. In the other cases they were walking (19%), running (9%) or feeding (11%).

Table 7. Species hunted, herd sizes, and total times hunted

Species	Herd Size					Total
	1	2	3	4	5	
Baboon					2	2
Common Duiker	1					1
Impala	2	5	7	8	1	23
Kori Bustard	1					1
Puku	2	2				4
Rabbit	3					3
Scrub hare	1					1
Wildebeest					12	12
Wildebeest/ Zebra					2	2
Wildebeest/ Zebra/Impala					2	2
Zebra	1	2				3

Herd sizes: 1 = 1 animal, 2 = 2-5 animals, 3 = 6-10 animals, 4 = 11-25 animals, 5 = 25+ animals

6.3 Environmental variables

To compare hunting behavior also a look was taken at the environmental variables. First of all they hunted in different scrub cover and grass lengths (Table 8). They hunted the most in medium grass length (44%), and medium scrub cover (44%). Open landscapes (26%) and long grass (15%) have both less hunts, than the other categories.

Table 8. Scrub cover and Grass length when hunting

Scrub Cover	Grass Length			Total
	S	M	L	
O	7	5	2	14
M	8	12	4	24
D	7	7	2	16
Total	22	24	8	54

Grass length: S = Small (<20 cm), M = Medium (20-60 cm), L = Long (>60 cm)

Scrub Cover: O = Open, M = Medium, D = Dense

Besides grass and bushes also the moon presence and wind direction were analyzed. Of the 20 hunts during the Night Encounters, the moon was visible on 12 encounters (60%), and 8 times there was no moon visible (40%). Related to wind direction, of the 54 hunts there was 35 times no wind (65%). Of the remaining 19 hunts, the lions hunted 6 times upwind, 4 times downwind, and 9 times crosswind.

Investigating if the lions hunted more often in one of the scrub covers or grass lengths, a χ^2 test was done. First for the scrub cover, where no significant difference was found between the frequency of the different scrub covers ($\chi^2 = 3.111$, $N = 54$, $p = 0.211$).

The same was done for the grass lengths, and here a significant difference was found ($\chi^2 = 8.444$, $N = 54$, $p = 0.015$). There seems to be less hunting in long grass than the other grass types.

6.4 Cooperation between different groups

All the different groups showed different levels of cooperation. Still most hunts (Fig. 7) were solitary hunts (63%), and only a few belonged to class C (4%). Around one third had a small level of cooperation (20% B1 and 13% B2). Of the 34 A-classed hunts, 14 hunts seemed to be an example of opportunistic hunting behavior, because the lions started chasing immediately without a stalk.

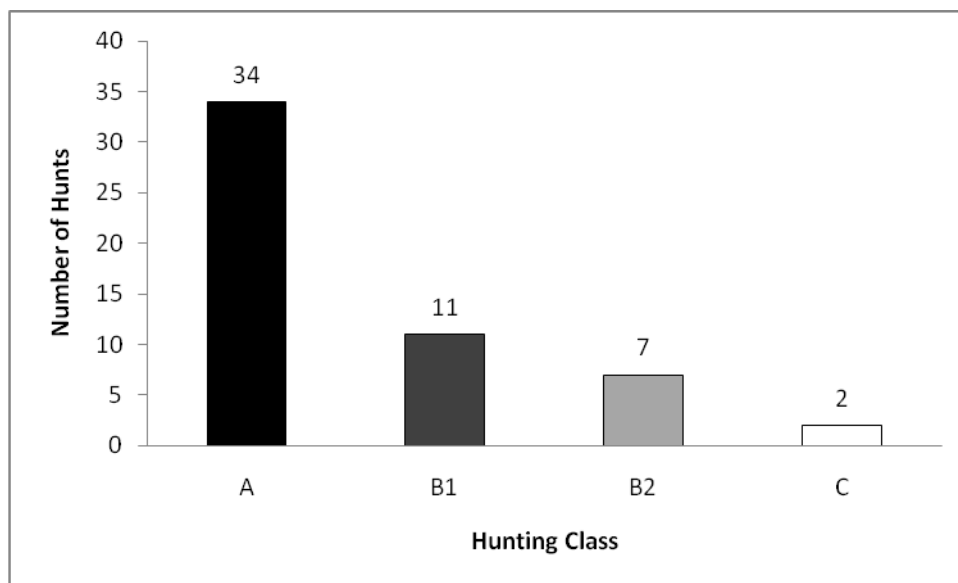


Figure 7. Number of hunts for each level of cooperation. Class A is no cooperation, and cooperation increases from class B1 to C.

There are no differences found between the groups when comparing the old groups with the new groups (Fig. 8). There were three combinations to compare the cooperation (Table 4, M&M): first is the old groups with every new group, which had no significant result ($p > 0.3$), also when only comparing no cooperation to cooperation. Secondly putting together the old groups and new groups with a complete old group in one category resulted in no significant difference either ($p > 0.15$). The last method was to look at the three different categories, the old groups, new groups with a complete old group, and the new groups without a complete old group. Also here no significant difference was found ($p > 0.35$).

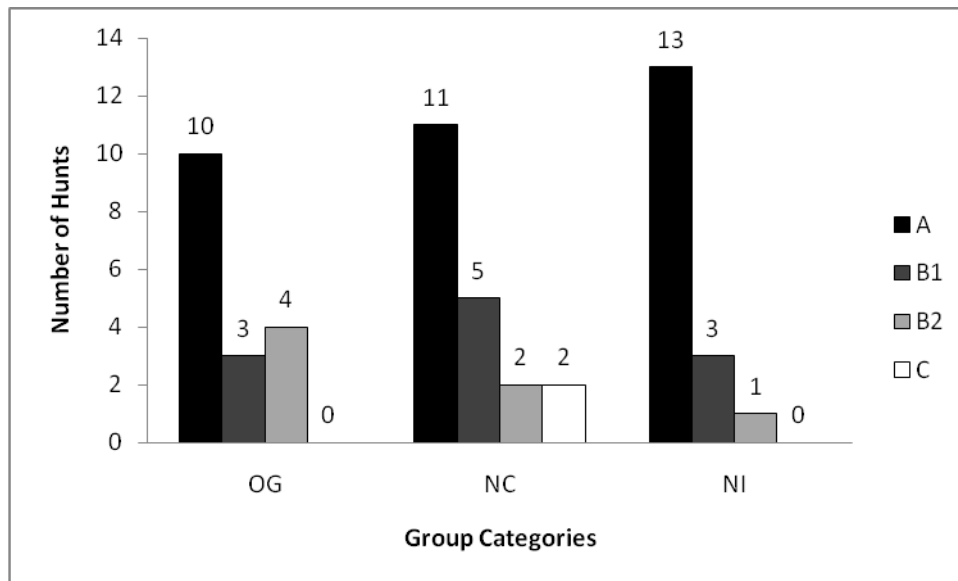


Figure 8. The number of hunts for each cooperation level for each lion group category.

Only three kills were observed. Interesting fact is only two times a class C hunt occurred, and both resulted in a kill. One kill was made on a female Puku, the other kill on a baboon. The Puku was killed by Zulu, when Leya and Loma chased it towards him. The baboon was killed, because Rusha climbed the tree and Rundi waited on the ground till the baboon jumped. The third kill was a class A hunt on a subadult baboon, Temi ran faster than the baboon.

6.5 Sizes and tasks within the group

After the observation period the lions were measured, to get an indication which lions were the larger and which the smaller ones. The measurements used are the chest girth and the front leg. The average chest girth of the lions was 102.4 centimeters, and the average front leg was 101.5 centimeters. The males had a higher chest girth and front leg, namely 120 cm and 112 cm, while the females had 98 cm and 99 cm.

In the three cases a kill was made, the heaviest lion (Largest CG) made the kill. In all three cases it was a different lion making the kill. This is significant ($p = 0.05$) more often than expected, looking at the probability the heaviest lion makes the kill.

There were 39 hunts (72%), which started with one of the lions stalking. During one hunt, one of the lions was out of sight, which resulted in the first stalker could not be identified from the observations. In the other 14 hunts the lions started the hunt with chasing.

Of the 39 hunts the lion with the smallest CG started stalking 21 times (54%). The other 18 times one of the other lions in the group started. The lion with the smallest CG stalked first more often than the others, and this was near significant ($X^2 = 2.885$, $N = 39$, $p = 0.092$). The lion with the smallest FL started stalking 16 out of the 39 times (41%). This does not result in a significant difference ($X^2 = 1.038$, $N = 39$, $p = 0.302$).

Out of 54 hunts there was 45 times chasing involved (83%). 14 times they chased immediately, and the other 31 times there was a stalk first. For both the smallest CG and the smallest FL there was no significant difference. For the smallest CG it was 17 out of 45 times (38%), which is not significant ($X^2 = 0.807$, $N = 45$, $p = 0.369$). For the smallest FL it was 18 out of 45 (40%), which is also not significant ($X^2 = 1.486$, $N = 45$, $p = 0.223$).

6.6 Logistic regression

To see if the lions had a learning curve, a temporal analysis was done. This was to investigate whether cooperation increased in time. Also for wind direction, to see if they started to take wind direction into account when they hunted. For both was a logistic regression done.

When looking at wind direction (Fig. 9), it seems there was more wind at the end of the observation period. However the lions never hunted upwind, the best wind direction when hunting, at the start of the observation period. They hunted six times upwind at the second half of the observation period. When doing the logistic regression, there is a near significant result regarding the learning for wind direction ($B = 0.106$, $N = 54$, $p = 0.064$).

When looking at the cooperation, it seemed the lions cooperated less and less during the observation period. Also figure 10 shows that there are less cooperated hunts during the end of the observation period. Also a logistic regression was done on these data, and cooperation became significant less in time ($B = -0.045$, $N = 54$, $p = 0.024$). Thus instead of improving their hunts by more cooperation, the lions hunted less together at the end. They preferred to hunt solitary instead of working together with the others in the group.

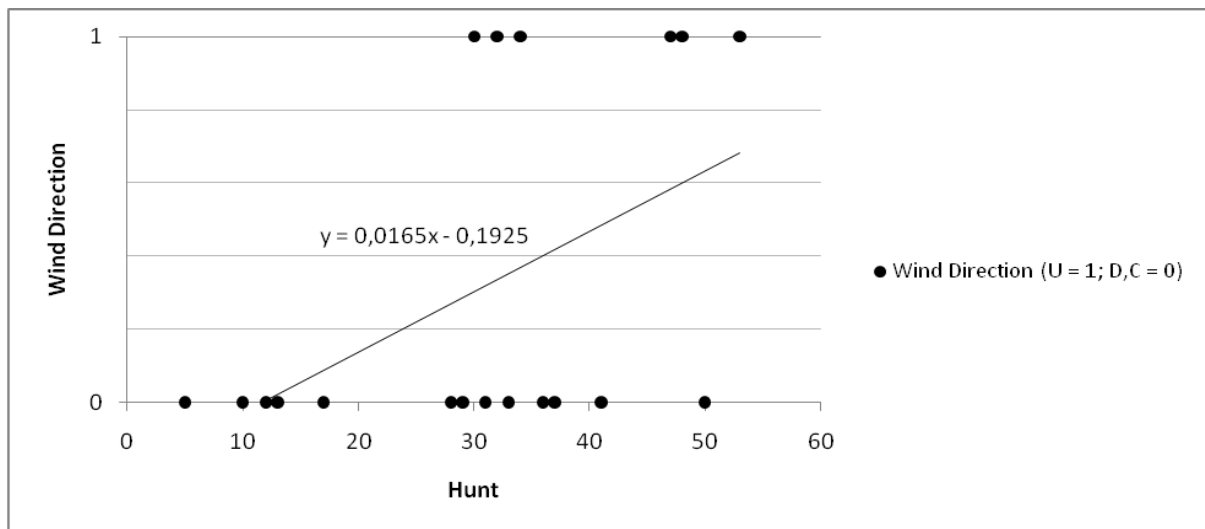


Figure 9. Wind direction in time, showing upwind compared to downwind and crosswind hunts. The wind direction is given for every response, when there was wind ("No wind" excluded in the figure).

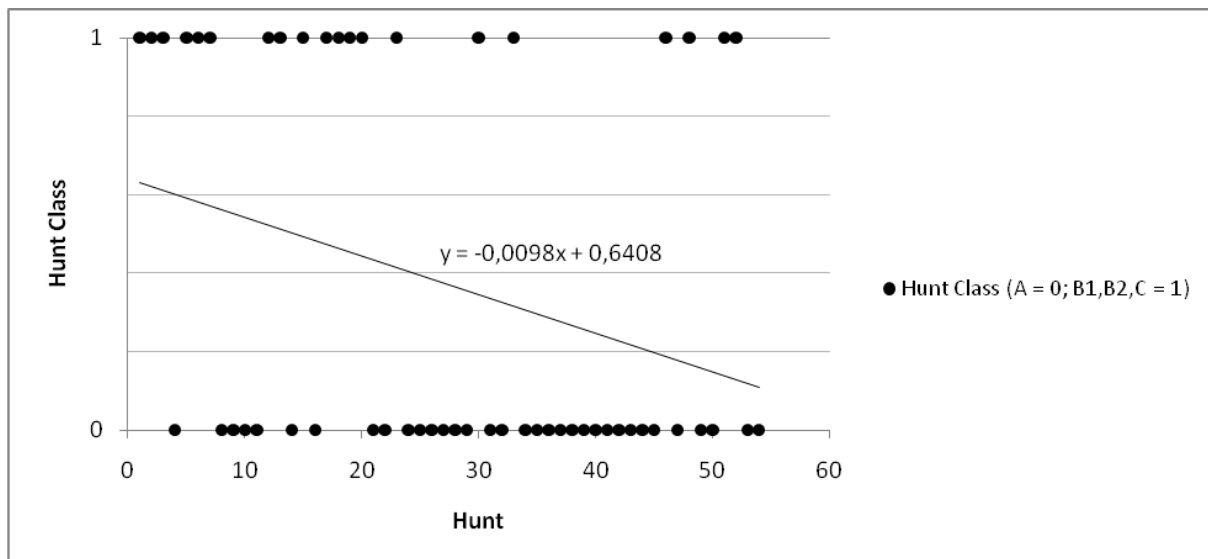


Figure 10. Cooperation in time, showing cooperation (class B1, B2, C) compared to no cooperation (class A). For every response the level of cooperation is shown.

7. Discussion

In this section the results will be discussed, starting with hunting variables. Second the cooperation in the different groups will be discussed, followed by the size related results. The last part consist of placing the results in this reintroduction program and also compare to other reintroduction programs.

7.1 Prey, lion and environmental variables

In total nine different species were hunted, with Impala and Wildebeest the most hunted. Those two species are also the most abundant species. Also Funston et al. (1998) stated lions hunt the most abundant species, which seem to reflect their opportunistic behavior. But it is hard to draw hard conclusions, because the prey species were limited, and there was not a possibility to choose from multiple species from the same size. Large prey species were not present in the hunting site, so nothing can be said about hunting large prey.

The results show lions hunt less in long grass, and hunt more in short and medium sized grass. There are no measurements of the availability of the three grass lengths in the hunting site, thus no conclusions can be drawn for preferences. However you would expect taller grass will be avoided by the lions, because it is above eye height. The lions could not see through the grass, and also did not spot several prey animals, which were hiding in the tall grass. A few animals were only 20 meters away, and the lions showed no behavior they noticed those prey.

The lions show more hunting behavior in groups of three or four, than larger groups or in pairs. In the wild lions also prefer to hunt with 3-4 lions to maximize efficiency (Funston et al., 2001). It seems the lions in the project are acting the same as lions in the wild. Pairs seem not the best way to hunt, and mostly hunting success is lower than in groups of 3 or 4. Groups from five and up, prefer larger prey like buffalo (Funston et al., 2001). Large prey were not included in the hunting site, which might explain why less hunting was observed in the larger groups.

7.2 Cooperation in hunting groups

The lions showed only 37% of the hunts a level of cooperation. The other 63% was opportunistic behavior, running after an animal that suddenly appeared, or solitary hunting. Stander (1992b) observed the opposite in wild prides, 71% of the hunts were cooperative attacks. A reason might be the age of the lions in the reintroduction project and their limited hunting experience. All lions in this study were younger than three years old, while Stander observed lions from two up to fourteen. Also several researchers state lions learn by observing their pride members (Funston et al., 2001; Stander, 1992a), and the lions in this project had no adults to observe.

The best coordinated attacks (Class C cooperation) resulted both times in a kill. No failed class C hunts were observed. This suggests that cooperation influences the hunt positively, and success rates can increase by working together in a group. In the wild as well, success rates are the highest with cooperative attacks (Stander & Albon, 1993). One C-classed hunt was by a group of two lions, and one by a group of five, thus cooperation is not only for larger group sizes. Also no significant influence of group size on cooperation was found.

Besides class C, there was also a successful class A hunt. No success was observed during a class B cooperative hunt. Also Stander (1992b) observed a low success rate (4%) in class B hunts, compared to class C (17%) and class A (14%) hunts. The high success rate in class A was explained by hunting smaller, easier prey. This study shows a similar pattern, because rabbits and springhare were only hunted because of a lion's opportunistic attempt. Also class B hunting seems to fail a lot, because one of the lions starts the chase too soon. The other lions are not in a good position to catch the prey by using a shortcut. Most prey animals can outrun lions (Schaller, 1972), thus when they get the chance to reach high speeds, they are able to escape.

In this study no difference in hunting composition was found. There was more cooperation in old groups, and old groups with additional lions, but this was not significant. One reason could be the small dataset for the data analysis, because only 54 responses were measured. Most studies have a couple of hundred hunts to do a data analysis. The other reason might be that it is better to hunt

with a new member in the group, than hunting solitary. Also in the wild it has been observed that solitary lions joined other groups to increase hunting success for their selves and the group (Packer et al., 1990).

7.3 Size related hunting behavior

In the wild, lions show a division of labor in cooperated attacks, in which the smaller lions stalk and chase, and lead the prey to the heavier lions (Stander, 1992a). The heavier lions can catch and kill the prey from an ambush position. In this study the lighter lions started the stalk near significant more often than the heavier lions. This supports Stander's theory (1992a) about the division of labor.

Different in this study is that the lighter lions do not start the chase more often. A reason might be that the lions do not show many class C cooperative hunts. One of the characteristics of class B cooperation is that any lion can start the chase, too soon for others to get in the right position. In this study there is more class B hunting than class C hunting, so this might be the reason, that stalking starts with the smallest lion, but not the chasing. The small sample size might be another explanation for the difference with Stander's theory.

Stander observed that the larger lions make the kill more often than the smaller lions. In this study only three kills have been observed, however all kills were made by the largest lion of the group. This supports Stander's theory, especially because two kills were made using a class C cooperation. The third kill was made on a subadult baboon, which was not fast enough to outrun the two lions chasing him. It seems heavier lions can use their weight as an advantage to capture the prey. Especially when a prey animal runs in the lion's direction, a heavier build could help for the impact.

Some of the lions were taller than others, but still lighter in weight. It seems the division of labor is weight dependent, and not height dependent. No significant differences were found when investigating front leg size and the stalking and chasing behaviors. Being lighter has as an advantage, being able to run faster. The slower heavier lions can wait from an ambush position to have a short chase. However more research needs to be done, because height and weight are correlated in this study.

7.4 Learning progress during the study

Wind direction has an important influence on the outcome of a hunt (Stander, 1992b). Downwind results in that the prey animals will notice the lions by smell. When there is upwind, the wind goes from the animals towards the lions. The prey animals will not smell the lions in this case from a large distance. During the study the lions used the wind more in their advantage at the end of the study. All six hunts upwind were in the last half of the observation period. There was more wind during the last month, but the lions did not hunt upwind at the start. Schaller (1972) did not find any difference in wind direction used by lions, and concluded lions do not take wind direction into account. This study seems to show different, because the lions hunted more often upwind with increasing experience.

There was no difference found in cooperation among the different groups. However a difference is found in time, the lions hunted less cooperatively at the end of the observation period. More new groups were on an encounter at the end of the observation period. Because no significant difference was found between old and new groups, this seems not the cause of the decreasing cooperation. It could be that the mixing itself is the reason for the decreasing cooperation. The lions were put in groups at random, and it changed almost every time, and only a few times the same lions were taken out two times in a row. The result seems to be the lions decide to hunt on their own, instead of working together with the other lions. To prove whether this is true, more research is needed by less frequently mixing the lion groups. The method used in this research seems to be incorrect and has a negative effect on lion hunting behavior regarding cooperation.

7.5 This reintroduction project

The reintroduction project of ALERT is unique in the world, and a setup like this has not been done before. That's why it is important to do research about the methods used, and analyze those to find

possible improvements. In this project the captive lions seem to behave like wild lions. Not in every aspect yet, but they are still in the stage to improve their skills. They hunt most often in groups of 3-4 during a single encounter. The lions do cooperate by a division of labor, letting the lighter lions stalk first. However the chasing, is still not like it should be for higher classed cooperative hunts. Also a learning progress has been observed regarding the wind direction. The lions started to use wind direction in their advantage by increasing hunting experience. There was a negative response regarding cooperation caused possible by the changing groups. Mixing the different lion groups do not have to be a problem within this reintroduction project, but the timescale should increase. During this study the mixing of groups has been too close to each other, and the lions cooperated less. The goal of this stage is to develop their hunting skills more, and cooperation is an important part in hunting. Mixing groups frequently seems to have a negative influence, and might result that the lions are not able to hunt efficiently in a later stage.

7.6 Broader view on reintroductions

Like lions, also African wild dogs live in groups, called packs (Creel & Creel, 1996). In South Africa a reintroduction project was done with wild dogs. In pre-release holding facilities in Hluhluwe-iMfolozi Park, they tested the importance of social binding in groups. Gusset et al. (2006) showed that social binding is important in wild dogs and this results in a more successful reintroduction of wild dogs. The social binding starts in ALERT's program from stage one, and continues to stage three.

Also Hunter (1998) stated that soft releases are important when releasing carnivores. Reintroduced cheetahs and lions, did not show homing behavior. Import is that social carnivores need social stability within a group, so getting used to each other is important in their survival (Gusset et al., 2006; Hunter, 1998).

In another carnivore, the European otter, captive-bred animals were compared to wild-caught animals by Sjöåsen (1996), and he suggested that wild-caught have a higher changes of successful reintroductions. Also Jule et al. (2008) showed with a literature study so far wild-caught animals have higher success rates than captive bred carnivores. Frantzen et al. (2001) compared wild-caught and captive-bred wild dogs. Here captive-bred dogs became dependent on humans, what made them poor hunters. They also have higher susceptibility to diseases and predation by other large carnivores, resulting in bad surviving chances.

8. Conclusions & Recommendations

8.1 Conclusions

During this study no differences were found in the level of cooperation among the different group compositions. Though no difference was found between different groups, there was a decrease in cooperation over time. The lions in the project showed a division of labor, more often the smallest lion started the stalk and the heaviest made the kill.

8.2 Recommendations

This study resulted in a small dataset, therefore continuing the measurements would help to increase the dataset and draw more conclusions regarding lions hunting behavior. Using the level of cooperation as a measurement could help to understand the hunting success of the lions. It would contribute to a better understanding on cooperative hunting behavior of the lions in the project, and could be an indication to change the used methods.

Also investigating the effect of the mixing frequency would help to understand its effect on cooperative hunting behavior. The lions showed less cooperation during hunts towards the end of the study, so lowering mixing frequency might prevent this decrease.

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Appendix I: Night Encounter data sheet and key

Date:		Success:	<i>Y/N (+ which lion)</i>
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Lions	<i>Name</i>						
Gender	<i>M/F</i>						
Age	<i>Months</i>						
Hunt Type	<i>D/I/S/C</i>						
Hunt class	<i>A/B/C</i>						
Wind Direction	<i>U/D/C/N</i>						

Prey	<i>Species</i>			Distance (metres)	
Herd Size	<i>1/2/3/4/5</i>			Prey behaviour	<i>S/W/R/F</i>

Wind	<i>0/1/2</i>			Shrub cover	<i>O/M/D</i>
Moon	<i>0/1</i>			Grass length	<i>S/M/L</i>

Date:		Success:	<i>Y/N (+ which lion)</i>
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Lions	<i>Name</i>						
Gender	<i>M/F</i>						
Age	<i>Months</i>						
Hunt Type	<i>D/I/S/C</i>						
Hunt class	<i>A/B/C</i>						
Wind Direction	<i>U/D/C/N</i>						

Prey	<i>Species</i>			Distance (metres)	
Herd Size	<i>1/2/3/4/5</i>			Prey behaviour	<i>S/W/R/F</i>

Wind	<i>0/1/2</i>			Shrub cover	<i>O/M/D</i>
Moon	<i>0/1</i>			Grass length	<i>S/M/L</i>

Date:		Success:	<i>Y/N (+ which lion)</i>
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Lions	<i>Name</i>						
Gender	<i>M/F</i>						
Age	<i>Months</i>						
Hunt Type	<i>D/I/S/C</i>						
Hunt class	<i>A/B/C</i>						
Wind Direction	<i>U/D/C/N</i>						

Prey	<i>Species</i>			Distance (metres)	
Herd Size	<i>1/2/3/4/5</i>			Prey behaviour	<i>S/W/R/F</i>

Wind	<i>0/1/2</i>			Shrub cover	<i>O/M/D</i>
Moon	<i>0/1</i>			Grass length	<i>S/M/L</i>

Notes:

Hunt type	D = Did not see	I = Ignore	S = Stalk	C = Chase	
Wind direction	U = Upwind	D = Downwind	C = Crosswind	N = No wind	
Prey behaviors	S = standing	W = Walking	R = Running	F = Feeding	
Herd size	1 = 1 animal	2 = 2-5 animals	3 = 3-6 animals	4 = 11-25 animals	5 = over 25 animals
Wind	0 = No wind	1 = Light wind	3 = Strong wind		
Moon	0 = Not visible or heavily obscured	1 = Visible or lightly obscured			
Shrub cover	O = open	M = moderate	D = Dense		
Grass length	S = Short (<20cm)	M = Medium (20-60cm)	L = Long (>60cm)		
Hunting class	A = Class A cooperation	B = Class B cooperation	C = Class C cooperation		

Appendix II: Raw Data of Encounters

There is one large table for the collected data, which is not possible to place in this Appendix. That's the reason it's only included on the CD-ROM and not on this page.

Appendix III: Lion Measurements

<u>LION</u>	CHEST GIRTH	HEAD TO TAIL	TAIL	FRONT LEG	BACK LEG
Toka	115cm	146cm	91cm	110cm	104cm
Zulu	125cm	167cm	104cm	114cm	114cm
Kela	98cm	134cm	87cm	101cm	100cm
Kwandi	94cm	137cm	91cm	97cm	94cm
Loma	97cm	146cm	83cm	99cm	100cm
Leya	104cm	147cm	83cm	101cm	94cm
Temi	96cm	143cm	79cm	94cm	96cm
Tswana	94cm	135cm	83cm	96cm	92cm
Rundi	96cm	143cm	85cm	99cm	104cm
Rusha	105cm	145cm	87cm	104cm	102cm

<u>LION</u>	FRONT PAW			BACK PAW		
	TOTAL LENGTH	TOTAL WIDTH	MAIN PAD HEIGHT	TOTAL LENGTH	TOTAL WIDTH	MAIN PAD HEIGHT
Toka	12cm	9cm	6.8cm	13cm	8cm	6.7cm
Zulu	12.4cm	9cm	6.2cm	11.7cm	7.8cm	6.2cm
Kela	11cm	8cm	5.6cm	10.2cm	6.7cm	5cm
Kwandi	10cm	7.8cm	6cm	11.3cm	6.5cm	5.3cm
Loma	11cm	8.2cm	7cm	12cm	7.8cm	6.5cm
Leya	11cm	8cm	6.3cm	11.8cm	7.9cm	6cm
Temi	11.8cm	7.6cm	6.8cm	11cm	7cm	5.2cm
Tswana	11cm	8cm	5.8cm	11cm	7.5cm	6.5cm
Rundi	11.7cm	8cm	6cm	11cm	7.5cm	6cm
Rusha	12cm	8.3cm	6.2cm	12cm	8cm	7cm