SHORT COMMUNICATION

Does captivity influence territorial and hunting behaviour? Assessment for an ex-situ reintroduction program of African lions *Panthera leo*

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ABSTRACT

Maintaining a territory and being able to hunt are imperative for the success of African lion *Panthera leo* prides. We aimed to determine whether captive-origin prides display similar territorial and hunting behaviour to wild lions. Behaviours and locations of two captive-origin prides and one wild pride were collected through direct observation. All prides established territories, and core areas corresponded with resource requirements. There was no evidence that pride origin affected territorial or hunting behaviour. Captive-origin prides exhibited behaviours that lead us to be optimistic about each pride's ability to establish and defend a territory successfully, and to hunt, following reintroduction.

Keywords: African lion, territorial behaviour, hunting behaviour, home range

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INTRODUCTION

Territory maintenance is a key aspect of pride success for African lions *Panthera leo*. Territory sizes differ between habitats, ranging between 11.5 and 1002 km² throughout

southern Africa (Loveridge et al. 2009, Andreassen et al. 2014). The size of a pride's territory and the way it is used is influenced by factors such as lion population density, pride size, social dynamics, prey availability and distribution, season, and locations of water sources and den sites (Loveridge et al. 2009, Valeix et al. 2010). Territories of lionesses are influenced by resource availability; those of males are additionally influenced by access to females (Loveridge et al. 2009), resulting in their territories often extending beyond those of females, covering numerous prides (Hunter 1998). Males protect their territory from invading conspecifics via two methods: directly, through their presence with the pride and by confronting competing males, and indirectly, by patrolling and maintaining territory boundaries (Lehmann et al. 2008). Prides and coalitions use roaring and scent marking for within-group and between-group communication (Hanby et al. 1995) and for territory maintenance (Schaller 1972, Benhamou et al. 2014).

Lions are known to hunt alone and in groups, but also scavenge, obtaining carcasses from conspecifics and competitive species via kleptoparasitism (Davies et al. 2016). Lionesses are the predominant hunters, although when pursuing large prey species, such as buffalo *Syncerus caffer*, giraffe *Giraffa camelopardalis* and elephants *Loxodonta*, the assistance of males is often required.

The conservation of wild lion populations has been a challenge for some time, and one approach to supplement and re-establish populations is to reintroduce captive-origin lion prides (Abell et al. 2013). It is imperative that captive-origin lions undergoing a reintroduction program are assessed to determine whether they show behavioural patterns that will allow them to thrive upon release. Knowing whether captive-origin prides possess the behaviours necessary to establish and maintain a territory, to utilise resource-rich areas, and to hunt effectively is crucial for determining whether lions will be successful post-release. To assess the likelihood of their success after release, we compared the territorial and hunting behaviour of prides comprised of captive-origin lions and their wild-born offspring with the behaviour of a wild lion pride.

METHODS

Two captive-origin prides (Ngamo and Dambwa) and one wild pride (in two study periods: Makhutswi 1 and Makhutswi 2) of lions were observed (pride details are shown in Table 1); the location of each pride was recorded at the beginning and end of each 1-3 hour observation session (Global Positioning System, Garmin eTrex 10). Territorial and hunting behaviours

were noted at all occurrences, and individual lions that initiated and participated in these behaviours were observed. For territorial behaviour, the type of behaviour (vocalisation or urine marking) was also recorded; a bout was considered to cease once vocalisations had stopped for >1 minute, or when the lion sat down or lay down (scent marking). For hunting behaviour, the target species, the approach type (flank or direct) of each lion, whether there was a chase, and whether a kill was made was recorded. If a kill was witnessed or found, the pride members who presented visible signs of having eaten were documented. A bout of hunting behaviour was deemed to have ceased when all pride members terminated associated behaviours towards prey for more than 1 minute.

A total of 1805 locations were recorded for the Ngamo pride, 1793 for the Dambwa, 406 for Makhutswi 1 and 169 for Makhutswi 2. Mapping software (ArcGIS version 10.3.1, Anonymous 2015) was used to quantify territory size by calculating a minimum convex polygon (Laffan & Taylor 2013) and a kernel density for each pride (Home Range Tool for ArcGIS 10 Version 2.0.20; Rodgers et al. 2015). Probability contours were calculated at 5% intervals from 5 – 95% probability estimates per pride. Territorial behaviours of the adults were divided into spraying, scraping and vocalisations; adults were compiled into ‘captive-origin’, ‘wild’, ‘male’ and female’ categories for analysis via Mann-Whitney U tests (GenStat 17th Edition; Anonymous 2014). Hunting behaviour was compiled into species hunted and killed by adults, sub-adults or by unknown lions, and the total number of hunts by adults and sub-adult lions was calculated.

RESULTS

The captive origin prides had territories that extended over the majority of the reserves (76 – 88%): the Ngamo pride occupied a 1.5 km² territory within a 1.7 km² reserve (Figure 1a); the Dambwa pride had a 2.2 km² territory within a 2.9 km² reserve (Figure 1b). The wild pride established territories of 28.5 km² (Makhutswi 1, Figure 1c) and 56 km² (Makhutswi 2, Figure 1d), within a 234.8 km² reserve. Kernel densities indicated the areas most used by each pride. The Ngamo pride used two areas (Figure 2a), the Dambwa pride three areas (Figure 2d), both had one area situated around a waterhole. The areas most used by the Makhutswi pride extended along the river that dissects the reserve (Figure 2g, j). In 2014, the Makhutswi 1 pride also used an area situated around a dam south of the river (Figure 2g). Movements of adult males and females within each reserve showed similar patterns except

for the Makhutswi 2 pride males' territory, which extended beyond that of the lionesses (Figure 2).

Lions in the captive-origin and Makhutswi 1 prides were observed to conduct all territorial behaviours. Frequencies of all territorial behaviours did not differ significantly between captive-origin and wild prides (Table 2). Males initiated more vocalisations ($U = 72.0$, $p = 0.032$) than females. Males were more likely to urinate spray than females ($U = 70.5$, $p = 0.052$).

Lions in the Ngamo, Dambwa and Makhutswi 1 prides successfully hunted and killed prey. In 2015, the Makhutswi 2 pride successfully killed a kudu *Tragelaphus strepsiceros* and a zebra *Equus quagga* during the study, however, the chase and kill were not witnessed. Impala *Aepyceros melampus* were hunted and killed by the Ngamo and Dambwa prides, while sub-adult females were observed to hunt guinea fowl *Numididae*. Adult and sub-adult lionesses of the Makhutswi 1 pride were observed to stalk and chase kudu, nyala *Tragelaphus angasii* and white rhinoceros *Ceratotherium simum*, while the adults killed nyala, impala, giraffe *Giraffa camelopardalis*, wildebeest *Connochaetes* and zebra. Only the Makhutswi 1 pride made a kill during an observation session; however the chase and kill of the impala occurred in closed woodland and out of view. All other recorded kills for prides were from locating the pride on or near a carcass, or from lions showing signs of having eaten.

DISCUSSION

All prides established territories within their fenced reserves. Although direct comparisons in spacing behaviour between the captive-origin and wild prides were not possible due to differences in reserve size, some observations indicate the possibility of similar spacing behaviour. Captive-origin territories were close to the size of their reserves (1.7 and 2.9 km²) and so were smaller than those reported for wild prides; a minimum territory size of 11.5 km² was recorded by Andreassen et al. (2014). Captive-origin prides were often located near reserve boundaries, which may indicate their willingness to expand their territory. A captive history does not appear to have led to a preference for occupying small areas. Stimuli beyond the reserve boundaries may have attracted the attention of captive-origin prides. A non-predator game reserve borders the north-western boundary of the Ngmao release site, and large game species may have provided a visual stimulus, as the release site contained low prey density during the study. The Ngamo and Dambwa prides were also often observed at a

specific corner of their reserve. Within audible distance were captive lions that vocalised daily and were fed regularly, providing another form of stimulus.

The formation of a territory by the wild pride was not directly influenced by a small reserve, but rather by environmental factors. We recorded territories of 28.5 km² and 56 km² for the wild pride in 2014 and 2015, which reflects those previously observed for prides within the Greater Makalali Private Game Reserve (24.9–106.8 km², Lehmann et al. 2008). The presence of other prides and coalitions on the reserve influenced our pride, as evidenced by a change in territory size of the adult males between Makhutswi 1 and Makhutswi 2. Male coalitions located to the west and north-east of the Makhutswi 1 territory vacated these areas between the two study periods, subsequently resulting in the expansion of the Makhutswi 2 pride's territory, and facilitating movement of the adult males to the western reserve boundary. Our captive-origin prides were not directly influenced in this way, as their reserves contained no other lions, therefore it is currently unknown whether they would show similar responses as the wild prides.

The territory of the Makhutswi pride was located along the river during both study periods, indicating that the river is central to the territory of this pride while reflecting resource use. Resource distribution, such as the distance between water sources and prey density, has been found to influence the size and movement of lion prides (Loveridge et al. 2009, Valeix et al. 2012). As all prides were studied during the dry season, water availability influenced the location of core areas of all of our prides, and both captive-origin prides had one core area located at a water source, indicating that they too respond to resource distribution.

Frequencies of urination scent marking and vocalisations did not differ significantly between captive-origin and wild prides. While captive-origin prides were not faced with direct competition with other lions within their reserves, the fact that these territorial behaviours were observed suggests that these prides have competitive competency. It also suggests that captivity has had no lasting impacts upon territorial behaviours, and upon release, captive-origin prides can be expected to exhibit the natural behaviours that will facilitate the maintenance of their territory. In all prides, adult males were observed to roar and were more likely to spray than females, as is the case in other wild prides (Schaller 1972, Hanby et al. 1995). This indicates that, in all prides, both sexes were displaying appropriate territorial behaviours, hence being located within a fenced reserve did not inhibit these behaviours.

Observed hunting behaviour indicated that there is no evidence of any important biological differences between captive-origin and wild prides, suggesting that captive-origin prides are capable of becoming self-sustainable. Prey density within the Ngamo and Dambwa release sites was insufficient to maintain each pride during the study, therefore to maintain healthy body weights, the diets of captive-origin lions were supplemented with scavenge. This encouraged lions to scavenge, which is a natural behaviour that is important for survival (Schaller 1972, Hanby et al. 1995, Grant et al. 2005); captive-origin prides consumed all provided scavenge, indicating their ability to utilise this food source. The wild pride killed and hunted during daylight hours, facilitated by a higher prey base and dense vegetation. Observed hunting behaviour by the captive-origin prides indicated their ability to hunt successfully individually, however, whether they are capable of co-operative hunting remains to be established. Hunting behaviour, particularly during daylight, occurs infrequently, requiring large prey bases, longitudinal studies and or the inclusion of night observations to allow for meaningful statistical comparison.

CONCLUSION

Our study provided the first assessment of territories, territorial behaviour and hunting behaviour of captive-origin lion prides. Lack of resources and space inhibited hunting behaviour and influenced pride movements within the reserves in which they had been released. However, all indications suggest that, upon relocation to a larger reserve with a stable prey base, these captive-origin prides are capable of establishing and defending a territory, and of becoming self-sufficient. Studies like this one are crucial for the pre-release assessment of prides within ex-situ reintroduction programs.

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Figure legends

Figure 1. Recorded locations of each lion pride, and the territory size of each pride (calculated as a minimum convex polygon) within its fenced reserve (size also indicated). Darker shaded areas indicate the reserve size and boundaries, lighter shaded area indicates pride territory. Territories of captive-origin prides are shown in a) and b), the wild pride in c) and d).

Figure 2. Territory utilisation distribution for each lion pride, presented by fixed kernel contours set at 5% intervals from 5-95%, using smoothing factor 'href' (a, b, c, and d). Kernel isopleth values refer to the probability of all pride locations occurring within the area enclosed by the contours. The movement patterns, via spider diagrams, recorded for adult male(s) (e, f, g and h) and adult females (i, j, k and l) throughout the period in which they were studied, per pride. Calculated kernel isopleth values are shown below the spider diagrams, to show lion movements between core areas within pride territories.

Table 1. Lion pride and reserve descriptions

		Ngamo Pride	Dambwa Pride	Makhutswi 1 pride	Makhutswi 2 pride
Origin		Captive-origin	Captive-origin	Wild	Wild
Study Period		14 May – 21 June 2014	21 September 2014 – 19 June 2015	1 July – 12 September 2014	17 August – 20 October 2015
Location		19°30'S, 29°44'E Zimbabwe	17°50'31.3S 25°45'14".2'E	29°09'S 30°42'E	29°09'S 30°42'E
Reserve size		1.7 km ²	2.9 km ²	234.8 km ²	234.8 km
Pride Composition	Adult ♀	5	5	3	2
	Adult ♂	1	1	2	2
	Sub-adult ♀	4	0	1	1
	Sub-adult ♂	1	0	4	0
	Cub ♀	0	3	1	3
	Cub ♂	0	3	1	2
	Cub unknown sex	0	0	0	2
	Total	11	12	12	12
Reserve lion population		12	12	39	39
Prey availability		Small game species (common duiker, steenbok, impala)	Small game species (common duiker, puku)	Big 5 game reserve containing small and large prey	Big 5 game reserve containing small and large prey
Vegetation type		Open grassland and	Woodland	Mixed lowveld	Mixed lowveld

		dry miombo woodland		bushveld and mopane bushveld	bushveld and mopane bushveld
Climate	°C range	-0.6 - 35°C	-2.8 – 40.6°C	3 - 36°C	3 - 36°C
	Annual precipitation	673 mm	780 mm	450 mm	450 mm

Table 2. Mean frequencies ($\pm$ standard error) of adult lion territorial behaviours observed over the duration of the entire study, for each sex and pride

Pride		Scrape	Spray	Vocalisation	Total
Ngamo	♀	0.006 $\pm$ 0.006	0.000 $\pm$ 0.000	0.015 $\pm$ 0.015	0.020 $\pm$ 0.015
	♂	0.473 $\pm$ 0.000	0.455 $\pm$ 0.000	0.273 $\pm$ 0.000	1.200 $\pm$ 0.000
	Total	0.083 $\pm$ 0.078	0.076 $\pm$ 0.076	0.058 $\pm$ 0.045	0.217 $\pm$ 0.200
Dambwa	♀	0.029 $\pm$ 0.016	0.027 $\pm$ 0.027	0.012 $\pm$ 0.012	0.068 $\pm$ 0.039
	♂	0.072 $\pm$ 0.000	0.414 $\pm$ 0.000	0.072 $\pm$ 0.000	0.559 $\pm$ 0.000
	Total	0.036 $\pm$ 0.015	0.091 $\pm$ 0.068	0.022 $\pm$ 0.014	0.149 $\pm$ 0.088
Makhutswi 1	♀	0.033 $\pm$ 0.033	0.143 $\pm$ 0.011	0.000 $\pm$ 0.000	0.175 $\pm$ 0.022
	♂	0.358 $\pm$ 0.122	0.446 $\pm$ 0.086	0.210 $\pm$ 0.151	1.014 $\pm$ 0.187
	Total	0.196 $\pm$ 0.107	0.294 $\pm$ 0.094	0.105 $\pm$ 0.086	0.595 $\pm$ 0.254
Makhutswi 2	♀	0.000 $\pm$ 0.000	0.000 $\pm$ 0.000	0.000 $\pm$ 0.000	0.000 $\pm$ 0.000
	♂	0.000 $\pm$ 0.000	0.038 $\pm$ 0.038	0.031 $\pm$ 0.031	0.069 $\pm$ 0.006

A. Ngamo **C. Makhutswi 1** **B. Dambwa** **D. Makhutswi 1** **Figure 1.**

A. Ngamo **D. Makhutswi 2** **B. Dambwa** **E. Ngamo adult male** **C. Makhutswi 1** **F. Dambwa adult male**

G. Makhutswi 1 adult male

J. Dambwa adult female

H. Makhutswi 1 adult male

K. Makhutswi 1 adult female

I. Ngamo adult female

L. Makhutswi 2 adult female

Figure 2.

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