

*The Ecology and Conservation of Lions:  
Human-Wildlife Conflict in semi-arid  
Botswana.*

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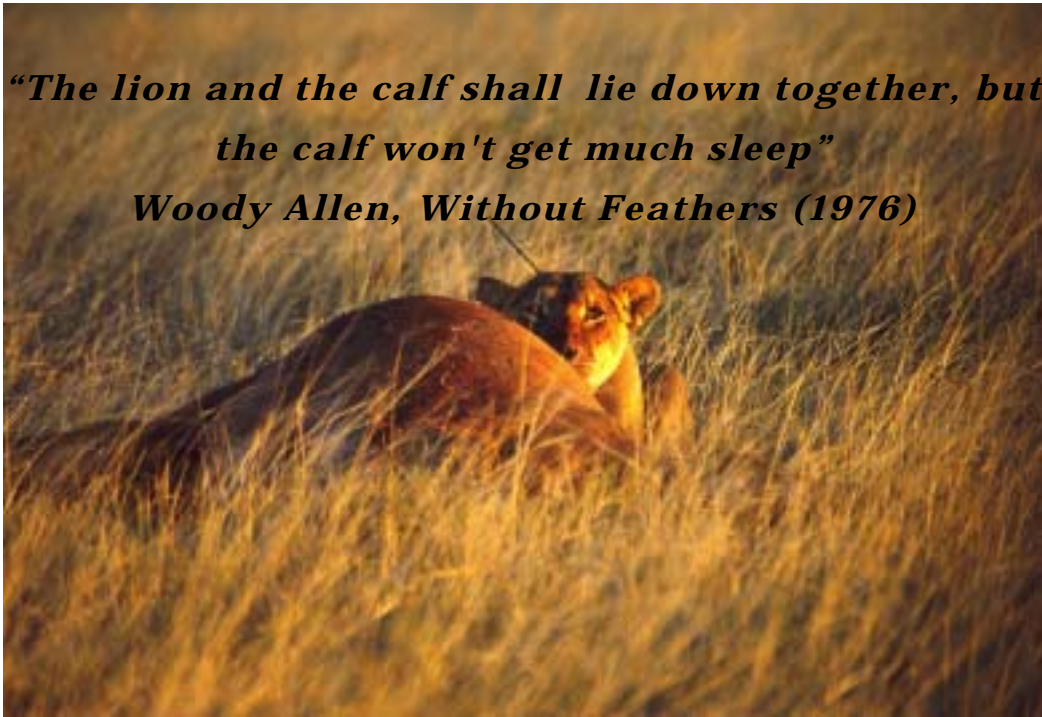
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***“The lion and the calf shall lie down together, but  
the calf won't get much sleep”  
Woody Allen, Without Feathers (1976)***



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# **The Ecology and Conservation of Lions:**

## **Human-Wildlife Conflict in semi-arid Botswana.**

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### **Abstract**

Many large carnivore populations are under threat from persecution for killing livestock. Our ability to deal with this threat is limited by our understanding of the aspects of the ecology of large carnivores and the socio-economics of humans relevant to livestock predation. This study adds new evidence to debates surrounding lion ecology, home-range analysis and human-large carnivore conflict mitigation. I use novel methods and try to span the divide between human sciences and ecology to create a holistic view of a conflict and make recommendations based on both ecology and socio-economics.

I used variation in the availability of migratory wild prey as a natural experiment to investigate the feeding and spatial ecology of lions. I demonstrate a link between rises in wild prey abundance and declines in the frequency of livestock predation per unit abundance that supports claims that wild prey can buffer people against livestock losses. Changes in livestock predation frequency were not passive responses to changes in prey abundance and stock-raiding lions changed their movements to increase livestock encounter rates although rarely seemed to attack livestock at cattleposts. Instead they spent most time in areas where livestock grazed untended and in which they strayed at night suggesting that, at least in the Makgadikgadi that herding vigilance may be at least as important as static defences (such as reinforced livestock enclosures) at reducing livestock losses. Livestock predation appeared to allow stock-raiders to use smaller home-ranges than other lions which became smaller yet when wild prey was least abundant.

People attitudes towards lions and wildlife seemed to reflect a mismatch between revenue and livestock predation distributions in the community. Most benefits accrued to employees while losses accrued to livestock owners and I argue that treating wages as a community benefit is perhaps unwise. Investments in prevention were minimal among livestock owners who blamed the government for the conflict thereby negating their responsibility. However, there were promising signs that joint government/community investment in preventions would be welcomed.

In developing the spatial analyses I tested the performance kernel home-range estimation using data from GPS-collars. The results suggest that the preferred implementation of this method is subject to considerable limitations of accuracy and stability and that computer simulated data lacks important similarities with animal movement data.

The changes in home-range sizes of stock raiding lions prompted me to re-address previous analysis relating lion social and spatial ecology to prey abundance by trying to incorporate several new studies and the concept of resource dispersion. My analysis, while not conclusive does hint that resource dispersion may play a role in regulating lion social ecology that merits further study.

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# Introduction

## ***Carnivore/Human Conflict***

In Botswana, and several other developing countries, populations of large carnivores are sources of conflict with livestock-owning people. Some of these large carnivores prey upon livestock causing economic damage and bad-will frequently leading to their destruction (Mills, 1998; Mills, 1991; Nowell & Jackson, 1996b; Weber & Rabinowitz, 1996). It is reasonable to assume that this type of conflict has existed at least since *Homo sapiens* first domesticated ungulates and that competition between man and predators is perhaps older still (Kruuk, 2002). However, as human populations have grown and countries developed, competition for natural resources has stiffened. Technological advances have exacerbated this effect by giving man a considerable competitive advantage over large carnivores. Consequently the status and viability of an increasing number of wildlife populations and species which conflict with humans and their crops and livestock has become questionable (IUCN, 2003). Populations of lions (*Panthera leo*), jaguars (*Panthera onca*), tigers (*Panthera tigris*), Eurasian lynx (*Lynx lynx*), Iberian lynx (*Lynx pardinus*), snow leopards (*Uncia uncia*) and cheetah (*Acinonyx jubatus*) and several other species continue to decline at least in part, if not largely due to conflict with people (IUCN, 2003; Nowell & Jackson, 1996).

These trends and the damage that conflict can cause to conservation and rural development initiatives has prompted a considerable amount of research into conflict between carnivores and people (reviews include Macdonald & Sillero-Zubiri, 2002; Sillero-Zubiri & Laurenson, 2001; Weber & Rabinowitz, 1996). Furthermore governments and non governmental organisations (NGO's) now spend large sums of money on trying to mitigate and control conflict often with inadequate data. Despite what appear to be similar targets (decreasing losses and increasing tolerance for losses) (Macdonald & Sillero-Zubiri, In press) widely applicable solutions to conflict between large carnivores and humans remain elusive. Even within the relatively narrow field of lion-human conflict, mitigations that may work for large ranches in Kenya (Frank, 1998; Ogada *et al.*, 2003) may not be the same as those acceptable to the Fulbé and Arab Choa people around Waza national park in Cameroon (Bauer &

Kari, 2001) the Ju/Hoan communities in Namibia (Stander, 1997) or stock owners in the Southern Kalahari (Funston, 2001). Each area has its own economic, ecological, political and sociological profile that may ultimately determine the potential for mitigations to succeed.

Livestock production in Africa ranges from large-scale ranching operations e.g. (Frank, 1998; Mizutani, 1999) to small-scale and often subsistence livestock ownership typical of the majority of rural Africa e.g. (Kruuk, 1980; Stander, 1997). However, while larger scale operators may have different motivations and attitudes they may still employ traditional livestock husbandry techniques (Ogada *et al.*, 2003). Small-scale farming is the prevalent form of agriculture in Botswana and the principle economic activity for the majority rural Batswana (people of Botswana) (Twyman, 2001; Wint, 1997). Nationally the central statistics office identified 180 commercial cattle operations and 64,707 traditional cattle farms in 1997; between them they hosted 2.2 million head of cattle, more than the 1.6 million human population of Botswana (Botswana Central Statistics Office, 2002).

In the face of this variation and despite some generalities it seems that rather than magic bullets and global solutions, it may be more reasonable to begin by seeking solutions applicable to a narrower range of situations using ecological and socio-economic research. The lion is a good example of a species whose distribution and conservation status is affected by conflict (IUCN, 2003; Nowell & Jackson, 1996b). They are widespread, ecologically and spatially needy, large enough to tackle all species of livestock and people, and relatively easily poisoned and trapped (Funston, 2001; Stander, 1990).

### ***Why conserve large carnivores?***

The conservation of large carnivores presents the conservation community with unique challenges, they are a paradox. There are few animals that share the potential of large carnivores to foster hatred and wonder simultaneously (Kruuk, 2002) becoming both icons of strength and nobility for some and symbols of evil and danger for others e.g.(Fritts *et al.*, 2003). Few animals, except maybe elephants (O'Connell-Rodwell *et al.*, 2000), have the capacity to cause so much damage to human

livelihoods. However many would argue that equally few have the potential to act as umbrella species (Caro, 2003), flagship species (Seidensticker *et al.*, 1999; Simberloff, 1997) and generate revenue through their capacity to attract consumptive and non-consumptive tourists. In a time when single species conservation efforts are sometimes maligned (Simberloff, 1997), large carnivores add a familiar charismatic face to conservation efforts. While they may occupy an important role in ecosystems (Mills & Shenk, 1992; Terborgh *et al.*, 2001) (but see also (Sinclair *et al.*, 2003)), their worth is as much in their ability to add value to conservation as it is about maintaining ecosystem function.

### ***The African lion (Panthera leo)***

#### **Ecology**

The African lion is Africa's largest terrestrial carnivore and between 18,000 and 27,000 are estimated to persist in the wild (Bauer & Merwe, 2002). The species is polygynous and highly dimorphic (Clutton-Brock, 1989), the mean weight of females is 126kg and males 190kg (Smithers & Skinner, 1990). Unusually for felids, the African lion is social and lives in fission-fusion groups called prides (Bygott *et al.*, 1979; Packer *et al.*, 1990; Schaller, 1972). The foundation of the pride is a group of closely related adult females and their offspring (Hanby & Bygott, 1987; Pusey & Packer, 1987; Schaller, 1972; Smuts *et al.*, 1978). The relatively stable composition of these groups makes using the number of adult females the most reliable way of assessing pride size (Van Orsdol *et al.*, 1985). Mean pride sizes vary between study sites: 7.1 in the Serengeti (Schaller, 1972), Masai Mara 9.2 (Ogutu & Dublin, 2002), 4.2 in Etosha woodland (Stander, 1990), 4.2 in Kruger (Smuts, 1976), 3.5 in Luangwa Valley (Yamazaki, 1996) and 4.2 in Kalahari Transfrontier Park (KTP) (Funston & Hermann, 2002; Mills *et al.*, 1978) and appear to be positively correlated with abundance of prey during the period of least abundance (lean season) (Hanby & Bygott, 1979; Van Orsdol *et al.*, 1985). Entire prides are rarely found together and lionesses typically forage in smaller sub-groups often associated through reproductive status (Packer & Rutten, 1988; Packer *et al.*, 1990; Schaller, 1972).

Male lions are transient in the life of the pride and generally form stable single sex groups during sub-adulthood and adulthood (Schaller, 1972) these groups or

coalitions are typically 2-3 males (range 1-7) and while they may be siblings or close relatives they are not exclusively so (Bygott *et al.*, 1979; Packer & Pusey, 1982). In plains habitats it has been suggested that these coalitions disperse considerable distances and become nomadic for their sub-adult life however, recent data from Kruger national park in South Africa, a wooded environment, suggests that males may settle closer to their natal range (Funston *et al.*, 2003; Hanby & Bygott, 1987; Pusey & Packer, 1987). At approximately 4-6 years old, a male coalition may begin challenging for pride tenure. Their reproductive success largely depends on the outcome of these challenges and serious combat and fatalities are observed (Schaller, 1972; Grinnell *et al.* 1995). Relatively little is known about sub-adult male dispersal distances and mortality, as most research has concentrated on the behavioural ecology of the females, but dispersal may be local or as far as 120km (Funston *et al.*, 2003; Pusey & Packer, 1987)

Prides defend exclusive territories (Schaller, 1972) although individual responses to interlopers are varied (Heinsohn & Packer, 1995). They are able to identify both numbers and identities of other lions by their roars and this may facilitate both spacing and avoidance of potentially infanticidal males (McComb *et al.*, 1994; McComb *et al.*, 1993).

Lions are capable of producing quite large litters of cubs (mean 2.6 cubs, range 1-6 (Smithers & Skinner, 1990)) every 24 months (Pusey & Packer, 1987) but mortality is often high, particularly in the first year and inter birth intervals may be as high as 40 months in some areas (Funston *et al.*, 2003; Packer *et al.*, 1988; Schaller, 1972). Pride size appears to be density dependent and is maintained by emigration of females in the Serengeti (Bertram, 1973; Hanby & Bygott, 1987).

In culling and modelling exercises in South Africa, large lion populations demonstrated remarkable resilience to high cropping intensities with depopulated areas being re-colonised by nearby prides and sub-adults, and prides occasionally forming from possibly unrelated females (Smuts, 1978; Starfield *et al.*, 1981). Such unrelated groups have not been recorded in 30 years of continuous observation in the Serengeti (Whitman & Packer, 1997). In contrast smaller or wider ranging populations may be more susceptible to the undesirable affects of culling (Whitman &

Packer, 1997; Woodroffe & Ginsberg, 1998a) and culling of territorial males may have a significant impact on reproduction as male turnover is associated with infanticide, delayed impregnation and male biased cub sex ratios (Pusey & Packer, 1987; Schaller, 1972; Whitman & Packer, 1997). It has been surmised that the removal of sub-adult and/or nomadic males may have a minimal negative influence on the population and may increase male tenure length and cub survival (Starfield *et al.*, 1981; Whitman & Packer, 1997). However recent modelling has implied that population stability may be maximised when older males are removed after being allowed to raise at least one cohort of cubs to an age when they are no longer susceptible to infanticide (Whitman *et al.*, 2004).

Lions are found in a considerable diversity of habitats including monsoon forest, desert and swamp but are most often associated with plains, scrub, deciduous woodland and savannah (Boitani, 1998; Nowell & Jackson, 1996a). One estimate of the availability of suitable habitat suggests there may be 6,740,000 km<sup>2</sup> within the lion's extent of occurrence (Boitani, 1998). In plains habitat females do most of the hunting and males scavenge meals from these hunts (Schaller, 1972; Stander, 1992b) in contrast males hunted frequently and successfully in the thicker habitats in Kruger (Funston *et al.*, 2001; Funston *et al.*, 1998). Cooperative hunting has been recorded in some detail in Etosha National Park and individual lions demonstrated preferences for position in hunting formations (Standar, 1992a). Although cooperative hunting was initially proposed as a reason for sociality in lions (Schaller, 1972) subsequent work has suggested that it may be the dispersion of prey (Macdonald, 1983) or the combination of large carcasses, open habitat and high density (Packer *et al.*, 1990) that creates conditions favourable for sociality. Having argued the general case for resource dispersion to create circumstances favourable to group formation in carnivores (Macdonald, 1983), Macdonald suggests that it might also have played a role in the evolution of lion sociality. In his hypothesis both large prey and herds of large prey are examples of rich patches and he develops arguments for how such patches might facilitate social group formation without any reference to cooperative hunting (Kruuk & Macdonald, 1985; Macdonald, 1992).

Locally the diet of the African lion is likely to consist predominately of 2-5 species of the most locally abundant medium/large ungulates such as greater kudu (*Tragelaphus*

*strepciceros*), plains zebra (*Equus burchelli*), buffalo (*Syncerus caffra*) and wildebeest (*Connochaetes taurinus*) (Mills & Shenk, 1992; Schaller, 1972; Scheel, 1993; Stander, 1992b) and lions may show preference for smaller herds of these species (Scheel, 1993). Prey preferences track seasonal or longer term changes in prey availability (Dunham, 1992; Schaller, 1972; Scheel & Packer, 1993; Viljoen, 1993) and lion density is positively and home range size negatively correlated with prey density at the time of least abundance (Van Orsdol *et al.*, 1985). Recorded home range sizes (calculated with minimum convex polygons) vary from between 22km<sup>2</sup> to over 2,000km<sup>2</sup> (Stander, 2001; Stander & Hanssen, 2003; Van Orsdol *et al.*, 1985).

### **Lions and conflict**

Lions have been identified as major livestock predators in several studies, often killing both more and larger, more valuable livestock than other large carnivores (Butler, 2000; Frank, 1998; Funston, 2001; Karani *et al.*, 1995; Kruuk, 1980; Mills, 1991; Saberwal *et al.*, 1994). Only two studies of aspects of lion ecology in conflict with livestock owners have been published (Bauer, 2003; Stander, 1997). Flip Stander demonstrated that the population of lions within the Kaudom protected area in Namibia had different population characteristics than that of the population outside the park. Inside Kaudom the population was similar to other studied populations whereas outside most lions were young males and there were few groups of females. Over four years, the population outside the park was all but eradicated by the local communities despite Stander's findings that stock predation by these lions was relatively rare (Stander, 1997). Hans Bauer studied lions in Northern Cameroon where they killed more livestock during the rainy seasons and appeared to live in smaller groups than elsewhere, perhaps as a result of their predilection for livestock predation. These lions spent a considerable time outside the protected area killing quite large numbers of livestock each year (valued at \$130,000 from a population of approximately 50 lions). These losses were viewed as unacceptable to herders who killed lions in retaliation (Bauer, 2003). Similar situations to this have resulted in the increasing restriction of lions to protected areas (PA) which make up only 10% of area in which lions are known to occur (Boitani, 1998; Nowell & Jackson, 1996). Although this area may be over 100,000 km<sup>2</sup> many of these PA's may be too small for lions (Nowell & Jackson, 1996; Olivieri *et al.*, 2003) and there are concerns that the



killing of lions on the edges of larger PA's may compromise notionally protected populations therein (Brashares, 2003; Woodroffe & Ginsberg, 1998b, 2000).

### **Benefits from lions**

While lions can cost people large sums of money they can also generate benefits from several sources. Many large carnivores are highly sought after by tourists wishing to view, photograph and/or kill these animals (Lewis & Alpert, 1996; Wint, 1997). Governments may be paid hunting licence fees, resource rentals and taxes on expenditures within the country and communities may receive wages, community levies and resource rentals or be part of joint venture agreements with hunting or photographic safari operators (Arntzen, 2002; Lewis & Alpert, 1996; ULG, 2001). In Botswana a 14-day lion hunt could gross US\$23,200 (ULG, 2001). Large carnivores also have substantial value to the media and revenues may accrue to both communities and governments from television crews, journalists, photographers and writers wishing to record the behaviour of these animals for the wider public. Underpinning this economic value is the symbolic value of lions (Kruuk, 2002).

### ***Controlling Human-Wildlife Conflict in Botswana***

In Botswana the potential economic value of lions and their impact on and persecution by livestock owning communities has prompted research by the Botswana Department of Wildlife and National Parks (DWNP). Their study used questionnaire and interview data gathered from communities between the Makgadikgadi Pans National Park and the Central Kalahari Game Reserve to assess perceived trends in livestock predation and local predator populations. The report highlights a local decline in lion numbers and the need for a study to investigate the causes for this decline (Nagafela & Kalikawe, 1993). More recently Botswana has started mapping out a strategic management plan for all of its large carnivore population and as such is looking towards improving its approach to problem animal species.

### **Compensation**

Botswana is the only member of the Southern African Development Community (SADC) to employ a state funded compensation system. Compensation systems are

based upon paying reparations to property owners for losses incurred to wildlife. The underlying tenet of all compensation schemes is that payments encourage tolerance for losses by minimising the economic impact of these losses (Nyhus *et al.*, 2003). In essence compensation is a method for increasing tolerance for a problem and not a method of preventing the problem from occurring (Macdonald & Sillero-Zubiri, In press).

People suffering losses from leopard, lion, elephant, rhinoceros, buffalo, crocodile, spotted hyaenas and wild dogs are able to claim for compensation for damages to livestock, crops or other property. Payments are not for the replacement value of the losses but are generally made for no more than 80% of the value (DWNP, 1998). Once a claim has been filed the DWNP are required to validate it by investigating the evidence that the damage was indeed caused by one of the animals on the list. In practice DWNP officials may not be able to verify many claims, as they may only attend the scene after as much as 14 days from the occurrence (DWNP, 1998).

### **State Managed Problem Animal Control**

The phrase ‘problem animal control’ (PAC) is used here to describe any action taken with the intention to reduce the damage caused by animals to people and their livelihoods, not only the killing of problem animals by the state or by other parties. In Botswana, PAC is predominately the responsibility of designated DWNP PAC teams who receive specific training to these ends. In some areas or circumstances other DWNP staff may also become involved as the need arises. Botswana’s DWNP PAC protocol is loosely sequential whereby interventions escalate in their impact on the problem animal after preceding failures to limit damage caused by that animal.

After an initial report to the police, local officials, the kgotla or other DWNP staff, PAC officials may follow up on compensation validation to advise the complainants of methods available to them to reduce the problem. Livestock owners are typically advised to herd stock during the day and ensure that it is enclosed in a sturdy kraal at night. PAC officials may also address entire communities through the forum of the kgotla (traditional council meeting). For example in areas where problems occur frequently or affect many members of the community addressing a kgotla may enable

officials to communicate with members of the community who may disseminate this information more widely.

The second stage in PAC is non-lethal control. These interventions consist of attempts to scare or otherwise encourage problem animals away from conflict areas and translocation of problem animals. The former approach typically requires a vehicle to patrol in conflict hotspot areas, often at night, searching for the potential problem animals. If located, PAC teams may chase the animals in the vehicle, shoot over the animal's head and use non lethal explosives such as thunder flashes to move the animal away, normally towards a protected area. The DWNP has herded elephants and buffalo using helicopters and vehicles and regularly patrols conflict hotspots for large carnivores. Translocations require animals to be captured and transported into an area where they pose no threat. Capture techniques are limited by veterinary legislation which prevents anyone but licensed veterinarians from immobilizing wild animals in Botswana.

The final stage of PAC is lethal control and requires PAC officials to shoot the problem animal. This is targeted only towards persistent problem animals that have not been deterred by preceding stages of PAC or animals that represent a clear and present danger to human life (Sechele & Nzehengwa, 2002).

### **Community Problem Animal Control**

Community PAC are methods employed by the members of a community in attempts to reduce livestock loss. Within Botswana these can be divided into methods aimed at keeping problem animals separated from property and those that reduce the numbers of problem animals in the area.

Livestock herders/owners try to limit livestock loss primarily by using static defences at the cattlepost and enclosing livestock at night in an enclosure (kraal). The structures of kraals are variable and within the study area can be piled thorn bush walls, gum poles and wire or mopane stockades depending upon the local availability of materials. People may also employ herders, light fires next to their kraals, use dogs to alert them to a predator's presence or to intimidate them. They may also attempt to

chase predators away with torches, pots and pans or firearms in attempts to limit stock loss. Conversations with herders also suggest that less orthodox techniques are employed. One farmer insisted that lions would not step over a length of black PVC piping as they thought it was a snake and thus surrounded his kraals with the material and several we spoke to buried, or hung in trees, mixtures of animal parts and plants which they had concocted themselves or purchased from local traditional healers to deter predators.

Reduction of predator numbers by local communities generally means the killing of the predators. Legally, people have been prohibited from killing lions since 2001 (Hermann, 2002). Previous to this, lions could be killed in defence of property. People were not allowed to use dogs, poison or snares to help kill predators and there was widespread confusion as to whether traps other than wire snares were allowed. In reality lions are generally trapped and shot therein, less often lions are tracked and shot or poisoned or snared. Pre 2001 most lethal removal of lions was undertaken by members of the public rather than DWNP (Hermann, 2002).

## **Fencing**

Fences have been used to separate wildlife from people and their property. Botswana has a chequered history with fencing due in part to its widespread use of fences to control disease transmission between wildlife and livestock. The impacts of a series of these fences on Botswana's ungulate populations have been subject to considerable interest and are now assumed to have been considerably negative (EIA, 2003; Thouless, 1998; Williamson *et al.*, 1988). Experience of fences designed to control movements of problem animals in Botswana are limited to a single example. The Kalahari Trans Frontier Park has a fence designed to prevent predators from leaving the park and killing livestock. Unfortunately the maintenance budget for this fence is quite low (US\$5 /km/year as compared to US\$40 km/year for the South African maintained section). As such the fence is porous and boundary transgressions by lions are regular occurrences, as are livestock losses and the killing of lions (Funston, 2001; Hermann, 2002). In areas where elephants or warthogs are abundant the costs of maintaining fences may be higher and without sufficient investment the value of the barrier is quickly lost (Stander, 1990). There are also potential ecological and

sociological costs to fences which may be difficult to quantify especially if understanding of local ecology is limited.

### **Study Site**

The Makgadikgadi Pans lie between 20 and 21 degrees South and 20 and 26 degrees East in the Eastern Central Kalahari region of Botswana (Thomas & Shaw, 1991). The MPNP is 4900 km<sup>2</sup>, bounded on the West by the Boteti river bed, in the south by an east-west cut line 20.84 degrees South, in the north by the tarred Nata/Maun road (between 20.25 and 20.19 degrees South) and a north-south cut line 25.11 degrees East in the East.

The entire Kalahari region has one wet and one dry season per annum with over 80% of rainfall occurring in the wet, between November and April (Thomas & Shaw, 1991) with occasional late rains in June/July associated with westward tracking depressions after the Inter Tropical Convergence Zone has retreated north (Thomas & Shaw, 1991). Rainfall within the greater Kalahari area increases in amount and decreases in seasonality with proximity to the equator (Thomas & Shaw, 1991) and in the Makgadikgadi annual average precipitation is 450mm (Meynell & Parry, 2002). However, variability is high with 35% inter annual variation and rainfall between 50mm in drought years to over 1200mm in wetter years (Thomas & Shaw, 1991). An 18 year cycle from wet to drought years has been identified from long term records in the region and we are currently heading into a drought phase (Thomas & Shaw, 1991). The last drought phase was associated with a significant ungulate die off which is thought to have been exacerbated by fences and human encroachments around surface water (Thouless, 1998; Williamson *et al.*, 1988). Potential evapo-transpiration exceeds rainfall in all months at 3058mm annually. The annual mean temperature in Maun is 22°C, mean maximum temperature is 35.5°C and mean minimum is 8.5°C with extremes between -6°C and 42°C (Thomas & Shaw, 1991).

To the South and East of the MPNP lie the Makgadikgadi Salt Pans, Botswana's largest wetland area. The pans are the result of prehistoric lacustrine deposition by the Zambezi, Okavango, Kafue, Lualaba and Nata rivers in the Pleistocene (Ringrose *et al.*, 1999). The subsequent diversion and drying of these permanent rivers was followed

by a period of evaporation and associated salination of the lowest points resulting in the formation of the saltpans. They are seasonally inundated by rainfall and rivers flowing from the north and east. These inundations are erratic in longevity and size and cause algal proliferation, mass hatching of small crustaceans and support large-scale breeding of many species of water bird (McCulloch *et al.*, 2003; Seaman *et al.*, 1991; Simmons, 1996). The Makgadikgadi is currently being considered as Botswana's second RAMSAR site (McCulloch *et al.*, 2003; Meynell & Parry, 2002)

Historically the Boteti River (the western boundary of the MPNP) contained significant amounts of water augmented by late floods from the Okavango system as recently as 1991. In recent years the flood waters have not made it within 80km of MPNP as outflow from the Okavango into the Boteti has declined over the past 15 years (Meynell & Parry, 2002).

In 1970 the MPNP was gazetted as a Game Reserve and inhabitants resettled; in 1992 it was upgraded to National Park status and extended to the Boteti in the south western corner and to link with Nxai Pan in the north to open a corridor for game movement between the two protected areas. Vegetation approximately follows a cline outwards from the main pan sumps (Parry, 1995).

- Saline Pan Sump
- Grassland with Scattered Pans: - generally poorly drained soils of varying salinity dominated by halophytic *Sporobolus* species and *Odysea paucinervis*.
- Grassland on saline sands: - better drained sandier soils decreasing in salinity with distance from the main pan sumps dominated by *Schmidtia pappohporoides*, *Digitaria eriantha*, *Odysea paucinervis* and *Schmidtia uniplumis* with scattered islands of *Hyphaena petersiana*, *Grewia flava*, *G. flavescens*, *Acacia tortillis*, *A. arenarea*, *A. eriolobas*, *A. mellifera* and *Dichrostatys cinerea*.
- Savannah:- dominated by *A. eriolobas*, *A. mellifera*, *A. ataxacantha*, *D. cinerea*, *G. flava*, *G. flavescens*, *D. cinerea*, *Salvia lanceolata*, *Grewia flava* and *G. flavescens*.

- Scrub savannah: dominated by *A. eriolobas*, *A. mellifera*, *A. ataxacantha*, *D. cinerea*, *Longocarpus capassa*, *L. nelsii*, *G. flava*, *G. flavescens*, *B. petersiana*, *Terminalia prunoides* and *T. sericea*.
- River Bank:- Very thick tangle of *T. prunoides*, *D. cinerea*, *A. eriolobas* and *A. ataxacantha*.
- Boteti riverbed:- predominately grassy with occasional stands of young *A. eriolobas*.

This cline follows soil changes from alkaline clay soils near the pans to deeper sandy aeolian sands along the Boteti. There is considerable variation in species composition within these areas reflecting local soil types, elevation and drainage variation and the effects of recent fires. Not all the small pans in the southern and eastern parts of the MPNP are saline, and many hold fresh water during and shortly after the rains. The only permanent sources of water available to wildlife are pools in the Boteti river bed concentrated just north of Kumaga and a pumped water source in the central northern section of the park adjacent to the Makolwane Game Scout Camp.

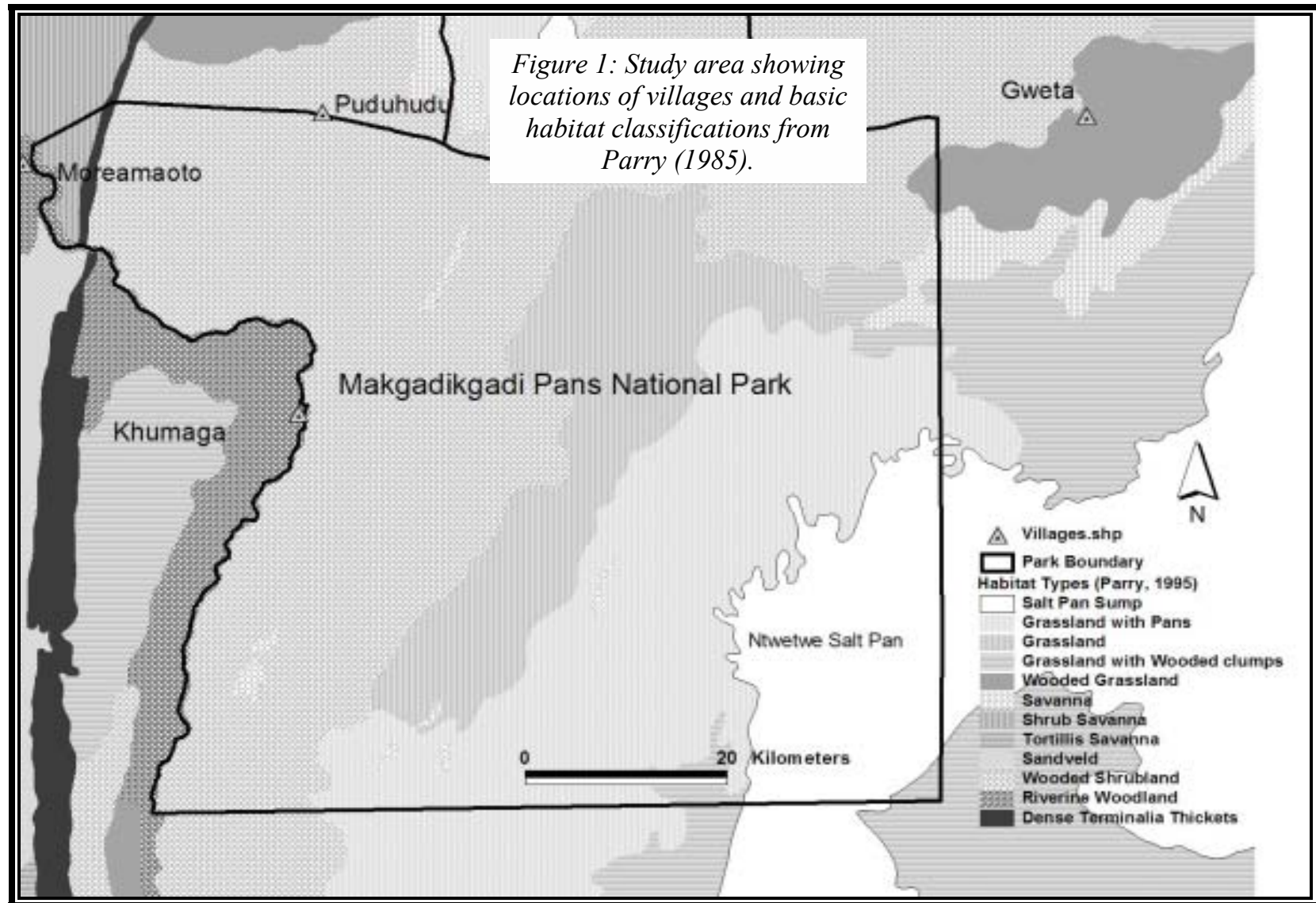
At the beginning of the last century, the San (bushman) people were the dominant ethnic group in the Makgadikgadi area. After the 1930's increasing numbers of Bakalanga, Bakurutshe, Bangwato, Bananja, Barotsi, Bakwe, BaYei, Bateti and Nyadzwbye people and their livestock settled the area as technology for accessing ground water improved. The Bakalanga are now the largest ethnic group in the area accounting for 36% of the population (Ferrar, 1995) and the San now limited to Remote Area Dweller settlements in and around Pudukudu. Overall, the area supports less than 1 person per km<sup>2</sup>, well below the national average of 3 per km<sup>2</sup> a product in part of surface aridity and saline ground water restricting suitability for agricultural diversity. The predominate source of income in the area is from livestock (Meynell & Parry, 2002).

Four major settlements are significant to this study, Kumaga (397 inhabitants), Gweta (2,715), Pudukudu (314) and Moreomaoto (245) (Meynell & Parry, 2002). These communities are currently without mains electricity but are served by tar roads and telephone connections. The bulk of the people affected directly by livestock predation

live in cattle posts. Cattle posts are typically 2-10 huts and associated livestock pens or kraals and access to a well or borehole. Cattle post dwellers are either owner-herders or herders employed at often sub-minimum wages by absentee owners. Meynell and Parry (2002) suggest that there is net migration away from the cattleposts to the villages and from the villages to larger urbanisations outside the region as younger able bodied individuals move out in search of employment. They also suggest that conflict with wildlife may have exacerbated this effect as cattle posts have become decreasingly profitable as losses to wildlife (predominately lions) have increased. Nationally urbanisation is an accepted phenomenon with 16% of the population living in urban settlements in 1981 and 50% in 1999 (Central Statistics Office, 2002).

The wildlife of the area is more diverse than typical for the Kalahari, probably as a result of the ecological variation between the salt pans and the Boteti riverine area. Mesic species such as elephant and hippopotamus (*Hippopotamus amphibius*) occur along the Boteti as well as xeric ungulates like gemsbok (*Oryx gazella*) and springbok (*Antidorcas marsupialis*) nearer the salt pans. Perhaps most significantly the area supports southern Africa's largest migratory population of Burchell's zebra (*Equus burchelli*) and remnant population of migratory blue wildebeest (*Connochaetes taurinus*) (Kgathi & Kalikawe, 1993; Meynell & Parry, 2002). Other common ungulate species include greater kudu, red hartebeest, steenbok, common duiker, impala and giraffe. Unknown populations of lion, spotted hyaena, brown hyaena (*Hyaena brunnea*), cheetah, leopard (*Panthera pardus*), caracal (*Felis caracal*), African wildcat (*Felis lybicus*), black footed cat (*Felis nigripes*) and wild dog (*Lycaon pictus*) also inhabit the area. No scientific population estimate for any carnivore species exists for this area and no scientific investigation of any carnivore species had been undertaken.





## ***Key Questions***

### **What impact does wild prey abundance relative to livestock abundance have on the frequency of livestock predation?**

The role of alternative wild prey species in reducing livestock predation is speculative and anecdotal. It is thought that the presence of wild prey may reduce the frequency of livestock predation. While the logic behind this concept is appealing and creeps into conflict mitigation recommendations e.g. (Hoogestein, 2000) there is a need to investigate this relationship in more detail. Stander (1997) suggests that lions living in areas with livestock appeared to prey mainly upon wild prey species and that livestock predation was infrequent. Of 52 lion kills he recorded between 1991 and 1995 none were livestock although 17 reports of lions killing livestock were received over the same period. Frank (1998) noted that livestock predation appears to be less frequent on some ranches where the ratio of wildlife to livestock is highest. While suggestive Frank notes that these weak trends need to be examined in more detail (Frank, 1998).

Seasonal changes in local wild prey abundance, caused by movements of migratory ungulates across the Makgadikgadi create an unusual natural laboratory in which to try and quantify the relationship between wild prey and livestock abundances, and the frequency of livestock predation. I draw on data from DWNP aerial surveys of ungulate abundance and lion predation data to investigate the influence of wild prey on livestock predation rates. Optimal foraging theory provides a framework with which to formalise these data which has yet to be applied to the problem of livestock predation.

### **Where and when do lions encounter and kill livestock?**

There is no data available on the detailed movements of stock-raiding lions and the anthropogenic and ecological factors that may influence them. Furthermore there is no empirical data on how the presence of livestock may influence the spatial ecology of lions and what significance this may have for conflict mitigation and conservation. Studies in east Africa suggest that livestock predation occurs predominately at

livestock enclosures (Frank, 1998; Kruuk, 1980) while Stander's work in Namibia (1997) suggests most predation occurs away from the enclosures. Much emphasis has now been placed on the role that static defences (enclosure construction, dogs and night watchmen) should have on reducing livestock predation. However the studies in east Africa and Namibia suggest quite different levels of success might be expected.

I use data from radio-collared and GPS-collared lions and GPS-collared cattle, remote sensed habitat data and the movements of migratory ungulates to investigate the influence of livestock movements, habitat and wild prey availability on the movements of stock-raiding and non stock-raiding lions. I wanted to quantify where and when livestock and lions were most likely to meet and where livestock was killed.

### **How do benefits from tourism, static defences at cattleposts and the attitudes of local people influence the magnitude of the conflict and human tolerance for it?**

A key component of conflicts between people and wildlife is the community that perceive themselves as disadvantaged by the conflict. The attitudes of these people towards the animals they are in conflict with, the organisations that are involved in trying to mitigate this conflict and other people that depend upon these species for a living is crucial (Hulme & Murphee, 2001; Kiss, 1990; Stander, 1997). It has been proposed that tourism (consumptive and non-consumptive) could provide economic incentives to tolerate large carnivores and losses to them, and motivation to manage conflicts without extirpating populations of conflict species (Giannecchini, 1993; Hackel, 1999; Kiss, 1990; Shogren *et al.*, 1999). Ranchers in Laikipia, many of whom benefit from tourism are quite tolerant of problem animals whereas herders who generally do not benefit from tourism on nearby communal lands, are markedly less so (Frank, 1998; Frank & Woodroffe, 2002). Despite concerns over the widespread applicability of tourism as a tool to mitigate conflict (Hulme & Murphee, 2001; Walpole & Thouless, in press) successes of this approach e.g (Lewis & Alpert, 1996; Western, 1989), have had a considerable influence on the conservation community at a time when preservationist or 'fortress conservation' approaches have become less acceptable to many conservation organisations.

Chapter 2 questions the potential for tourism to create incentives for people to live with large carnivores. Using data gathered from interviewing people living in cattleposts, larger villages and working in tourism I explore their attitudes towards and understanding of, the conflict between humans and lions and current efforts to mitigate it. At the same time by using locations of cattleposts and measurements of the static defences each used to prevent livestock loss I quantify their roles in reducing livestock loss and evaluate them in the light of the results of Chapters 1.

### **How is lion spatial and social ecology related to the abundance and dispersion of resources?**

The literature on the ecological correlates of lion social and spatial ecology has been reviewed before in 1985 (Van Orsdol *et al.*, 1985) and aspects incorporated into a more recent inter-specific meta analysis of carnivore population density (Carbone & Gittleman, 2002). While these studies have provided valuable insights into the influence of prey abundance on lion ecology they have been hampered by the incorporation of poor quality data (Carbone & Gittleman, 2002) or limited by the scarcity of good quality data (Van Orsdol *et al.*, 1985). However recent advances in the reliability and sophistication of radio- and GPS-telemetry, standardisation of ecological techniques and the popularity of the lion as a study animal have resulted in considerable volume of good quality data with which these correlations can be revisited.

Chapter 3 presents an analysis of these data and explores their implications for the understanding of the relationships between prey abundance and dispersion, and lion spatial and social ecology. I explore both the potential for these data to contribute to establishing predictions of lion density and ecology from more readily available ungulate abundance, rainfall or primary productivity data and the implications of the findings for the understanding of the role of resource dispersion in lion social ecology.

## **Do kernel home-range estimates accurately represent the distributions from which they are drawn?**

Before attempting to analyse the spatial aspects of lion ecology and lion/livestock conflict in the Makgadikgadi (Chapter 1), I wanted to use the detailed spatial data gathered from GPS-collars on lions to test the performance of my chosen home range estimation technique; kernel density estimation using least squares cross-validation (Worton, 1989). While this method has performed well using computer simulated data and short term radio-tracking data (Kenward, 2001; Powell, 2000; Seaman *et al.*, 1999; Seaman & Powell, 1996), and has become an accepted method of home range analysis it has not yet been satisfactorily tested using detailed spatial data such as that produced by GPS-collars. These large data sets create the potential to sub-sample longer term animal movement data to mimic the quality of data from radio tracking studies in the volume possible using computer simulations. I use novel techniques to evaluate the performance of the method and expand on previous estimates of the minimum sample sizes needed to establish a reasonably accurate home range estimate. Chapter 2 presents this investigation, the results of which may be important in interpreting analyses in which kernels are used to estimate home-ranges.

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# Chapter 1. Stock raiding lions, movements, risks and prey.

## Summary

1. There is speculation that the abundance of wild prey may influence the frequency of livestock predation by large carnivores e.g. (Hoogestein, 2000; Mizutani, 1999; Rasmussen, 1999). However there are few data to quantify this effect and establish a relationship between wild prey abundance, livestock abundance and livestock predation frequencies.
2. Information on the movements of problem carnivores relative to livestock, human habitation and wild prey is likely to be important in minimising the spatio-temporal overlap between livestock and large carnivores thereby reducing livestock predation. There are no data describing lion movements near human habitation in detail.
3. We investigated the frequencies of predation on livestock and wild prey by lions in a natural laboratory, the Makgadikgadi Pans National Park, Botswana. Seasonal immigrations and emigrations of wild prey allowed us to quantify the influence of changes in the relative abundances of wild prey and livestock on livestock predation. We used simple optimal foraging concepts to interpret these data and formalise a relationship between the relative abundances of prey types and their consumption.
4. GPS-collars on lions (*Panthera leo*) and cattle allowed us to study the nocturnal movements of lions and their domestic prey in areas where wild prey migrations created periods of local wild prey abundance (good periods) and scarcity (lean periods). Lions were classified as stock-raiders (65% of adult females (n =17) and 100% of adult males (n=9)), or non-stock-raiders using predation data.
5. Local increases of wild prey abundance resulted in increased intensity of predation (frequency of killing relative to abundance) of the most abundant class of wild prey (zebra and wildebeest) and a lower intensity of livestock predation.

6. During periods of wild prey scarcity, when wildebeest and zebra had moved away, resident lions preyed upon resident wild prey more than expected from measures of abundance and increased their predation on livestock to near proportional use. Wild prey classes were at all times more intensely utilised than were livestock, despite being the least abundant prey class during lean periods, and resident wild prey may be an important buffer against livestock predation.
7. We suggest that lions are sensitive to the anthropogenic risks of livestock predation, the risk of starvation and the relative availabilities of prey classes per unit abundance. Further use of simple foraging models may help clarify how stock-raiding predators forage and aid in evaluating the contributions that different interventions aimed at reducing livestock losses may have.
8. Our study provides empirical support for simultaneously increasing local wild prey availability and decreasing livestock availability as a strategy for reducing predator/human conflict.
9. Stock-raiders home-ranges remained in similar localities between periods of different prey abundance but were smaller (Wilcoxon Signed Rank Test,  $p = 0.018$  estimated median = +100.8%,  $n=6$ , good 206km<sup>2</sup> & lean 112km<sup>2</sup>) and closer to cattleposts when wild prey was locally scarce. Non-stock-raiders moved their home-ranges between seasons and thus maintained proximity to migratory ungulates.
10. Stock-raiders responded to the movements of livestock and the risk associated with hunting it (8 of 10 recorded mortalities of adult lions were stock-raiders killed by herders). Generally they did not kill livestock by raiding stock enclosures (kraals) at night, but searched for strays and wild prey away from human habitation.
11. All males were stock-raiders with larger home-ranges (mean 713km<sup>2</sup> during good periods and 546km<sup>2</sup> in lean periods) than stock-raiding females. Males' ranges were also significantly larger than females' home-ranges during good (mean 299km<sup>2</sup>) but not during lean periods (mean 295km<sup>2</sup>).
12. The influence of herding practices on livestock availability and distribution is important in reducing livestock losses and should be examined before implementing changes recommended in other areas. Larger home-ranges increase the probability of being killed by herders as they increase the



probability of the lion encountering livestock and becoming a stock-raider. As such males may be more vulnerable than females to anthropogenic mortality.

## ***Introduction***

Stock-raiding by large carnivores, including lions (*Panthera leo*), causes conflict between predators and local people (Bauer & Kari, 2001; Frank, 1998; Funston, 2001; Kruuk, 1980; Mills, 1991). This conflict impacts upon carnivore populations through retaliatory and pre-emptive killings by livestock owner and herders, and sometimes wildlife managers (Macdonald & Sillero-Zubiri, 2002; Nowell & Jackson, 1996; Weber & Rabinowitz, 1996). Consequently many small, isolated populations of large carnivores are under threat despite being notionally protected in protected areas (Nowell & Jackson, 1996; Woodroffe & Ginsberg, 1999; Woodroffe & Ginsberg, 2000). Conflict may also have negative effects on attitudes to other local conservation initiatives, protected areas and wildlife (Hemson *et al.*, submitted-a), and can restrict community cooperation and support (Newmark *et al.*, 1993; O'Connell-Rodwell *et al.*, 2000) at a time when conservation in Africa is becoming more inclusive and decentralized (Hulme & Murphee, 2001; Western, 1989). If viable predator populations are to be conserved alongside or among livestock farming areas, and local communities convinced of the merits of sustainable conservation practices, then conflict over livestock predation may need to be mitigated (Sillero-Zubiri & Laurenson, 2001; Weber & Rabinowitz, 1996; Wint, 1997).

In the Makgadikgadi Pans area of Botswana livestock predation by lions is perceived as the major negative impact of wildlife by local people (Hemson *et al.*, submitted-a) and the killing of lions by local people is viewed as a source of conservation/wildlife management concern by the Department of Wildlife and National Parks (Nagafela & Kalikawe, 1993). There has been national concern that lion populations are falling resulting in the enforcement of a moratorium on the killing of lions by both farmers and trophy hunters. Despite a small population in the Makgadikgadi (39 adult and sub-adult lions) 8 adult lions were killed by livestock owners in 12 months and the density of lions in the area was only 0.74 lions/100 km<sup>2</sup>, comparable to more arid areas in Namibia and the Kalahari (Funston, 2001; Stander & Hanssen, 2003).

It is often implied that the abundance of wild prey affects livestock predation rates and several studies have described the impact of large predators upon human communities and methods employed to reduce stock losses e.g. (Frank, 1998a; Frank, 1998b; Karani *et al.*, 1995; Kruuk, 1980; Marker *et al.*, Submitted; Meriggi & Lovari, 1996; Mishra, 1997; Mizutani, 1999; Newmark *et al.*, 1993; O'Connell-Rodwell *et al.*, 2000; Ogutu & Dublin, 2002; Rabinowitz, 1986; Stander, 1990; Treves *et al.*, 2002). However, there are few empirical data on the effect that relative abundances of livestock and wildlife may have on the frequency of livestock predation by large carnivores (Meriggi & Lovari, 1996; Mizutani, 1999; Sidorovich *et al.*, 2003) and on the movements of carnivores at the human wildlife interface (Polisar *et al.*, 2003; Rabinowitz, 1986; Rasmussen, 1999; Stander, 1997; Vos, 2000). Despite this lack, there is a growing confidence that large carnivore livestock depredations can be most effectively limited by improving static defences (reinforced stock enclosures, guard dogs, guards etc) (Fritts *et al.*, 1992; Jackson, 1996; Kruuk, 1972; Ogada *et al.*, 2003; Stahl *et al.*, 2002).

## Foraging Lions and Livestock

Lions have been described as risk sensitive (energy gain) rate maximizing predators, selecting the most profitable prey classes when most abundant (often buffalo (*Syncerus caffer*), zebra (*Equus burchelli*) and blue wildebeest (*Connochaetes taurinus*)) and consuming more 'less profitable' prey such as Thomson's gazelle's (*Gazella thomsoni*) when the availability of the most profitable prey declines (Scheel, 1993; Scheel & Packer, 1993; Stephens & Krebs, 1986). Here profitability is defined in terms of net energy gain.

A simple energy gain rate maximising optimal diet model predicts that predators will rank prey according to the ratio of  $E_i/h_i$  ( $E_i$  = energy gained by consuming prey type  $i$ ,  $h_i$  = total handling time as an index of the energy expended in finding, killing and consuming prey item  $i$ ), or profitability. Here the inclusion of prey type  $i$  depends not upon the availability of prey type  $i$ , but on the availability of prey that ranks above it (Lacher *et al.*, 1982; Pyke *et al.*, 1977) as well as the energy content of each prey

item. The most available profitable prey, that for which expected handling time ( $h_i$ ) is minimal, will be predated upon to the exclusion of all other prey types (most intensely) when it is maximally more available than the next most available prey.

Abundance and the energy expended in locating, capturing and handling the prey, will all contribute to availability in this interpretation and the amount of each captured prey item that can be consumed and the risk of injury or mortality associated with each prey type may also affect the potential profitability. If livestock is as energetically valuable, as easy, or easier, to find and catch than wild prey, less dangerous to overpower, and the most abundant prey in an area, a qualitative rate maximizing model predicts that it will also be the most intensively utilized. Indeed if livestock was much easier to find and catch than wild prey, and thus had a considerably higher availability per unit abundance than wild prey species (a plausible scenario), then even if it was less abundant it might yet be the most intensively utilised.

### **Spatial Aspects of Lion/Human Conflict**

While livestock availability may be one factor regulating stock-raiding, minimising livestock losses is also likely to depend upon minimising the spatio-temporal overlap between livestock and carnivores. Knowledge of the movements of livestock and predators will help achieve this and contribute to the understanding of the exposure of large carnivores to the effects of persecution (Brashares, 2003; Woodroffe & Ginsberg, 1998, 2000). Furthermore, identifying culprit classes from the population, and understanding their vulnerability, will help focus protective measures and advise lethal control procedures.

Studies of territory and home-range sizes demonstrate that they are negatively correlated with resource abundance as well as competitor density and strength (Adams, 2001). Prey abundance at times of scarcity appears to be the most significant factor regulating lion social ecology with evidence of correlations between lean season prey biomass and home-range size, pride size, cub survival and through these, lion population density (Van Orsdol *et al.*, 1985). In Savuti, Botswana, lion home-ranges were larger during seasons when prey was less abundant (Viljoen, 1993) and

during periods of prey scarcity some Serengeti lionesses used areas so large, they were mistakenly categorised as nomads (Packer, 1986; Schaller, 1972).

## **Hypotheses**

Do changes in the relative abundances of wild prey and livestock (as indices of availability) affect the predation of livestock beyond changes proportional to changes to prey abundance alone? We hypothesised that local declines in wild prey abundance would be associated with increases in local livestock predation per lion and a broadening of lion diet as less profitable prey items are included.

After describing the diet of the lions relative to prey availabilities in the Makgadikgadi Pans area, we asked:

- Whether changes in livestock killing frequency were ‘passive’ responses to increases in the abundance of livestock relative to alternative wild prey or an active change in the behaviour of stock-raiding lions to increase encounter rates with livestock when wild prey became locally scarcer.
- If males have similar ranging patterns to females and if they do not, how this affects their relative vulnerability to persecution by herders.
- Are home-range sizes of lions larger during periods of lower resource availability with their occupants covering greater distances in search of these resources than during periods of relative abundance.

A question of methodological interest was whether locations recorded at night gave different home-range estimates to those sampled by day and if so, whether daytime home-range estimates for stock-raiding lions may underestimate spatial overlap with human activity. This would be an important consideration when interpreting diurnal data, such as that commonly gathered by radio tracking from an aeroplane.

## **Natural laboratory**

Monitoring lions, their diet and their prey is expensive and time consuming and it was not financially or logistically feasible to set-up duplicate studies across a range of

sites controlling for the effects of habitat and different prey assemblages as we did so. Rather we identified an area with a surveyed prey population and lions that killed livestock. The majority of wild ungulate biomass in the study area was seasonally migratory zebra (*Equus burchelli*) and blue wildebeest (*Connochaetes taurinus*). In contrast distribution of livestock (cattle, horses, donkeys and goats) did not appear to vary between seasons. Seasonal movements of zebra and wildebeest created distinct local periods of wild prey abundance and scarcity. These large changes in local prey abundance provided a “natural laboratory” in which to investigate the influence of different resource abundances on lion range use and movements and livestock predation.

## **Methods**

### **Study Area**

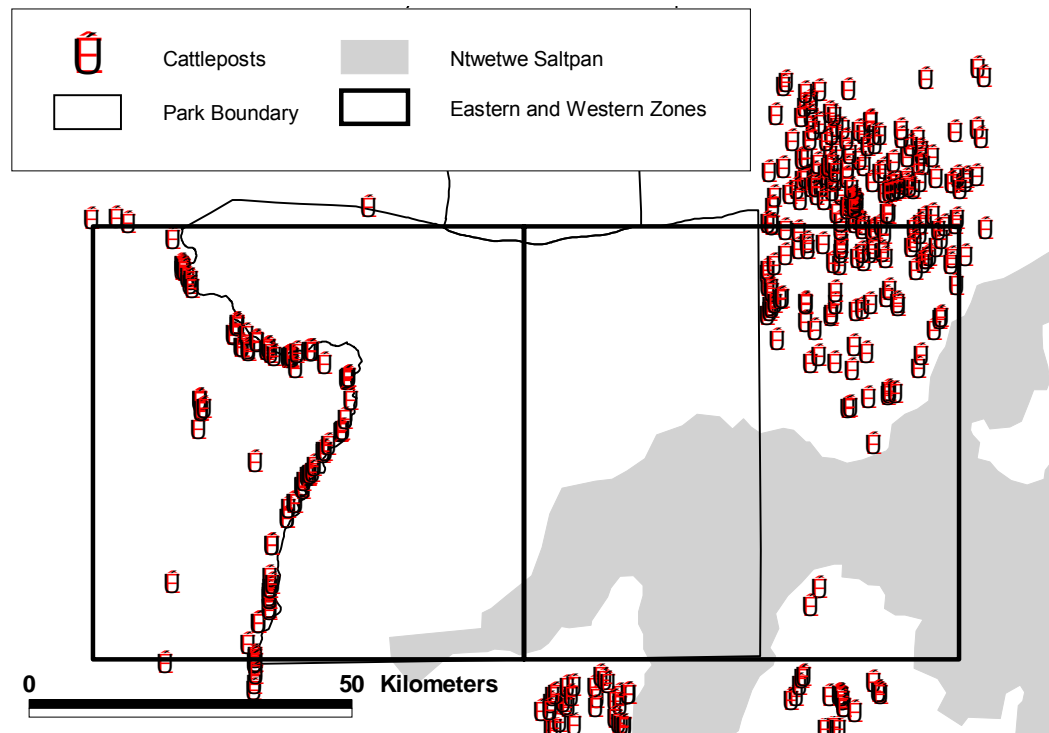
The study area encompassed the 4,900 km<sup>2</sup> Makgadikgadi Pans National Park (MPNP) and 3,500km<sup>2</sup> of the adjacent land used for livestock grazing and low density human habitation (Figure 1). The area is a mix of semi-arid grassland, salt pans, scrub, savannah and pockets of woodland centred on 20° 28' 00.0"S; 24° 45' 00.0"E. The MPNP is bounded to the west by the dry Boteti riverbed along which a few perennial waterholes remain and to the south-east by Ntwetwe salt pan. The area falls between the 250 mm and 450mm isohyets and rainfall is seasonal with a single wet (October to April) and dry season annually. Over 80% of rainfall is between October and April, but inter-annual spatial and temporal variation is considerable (Thomas & Shaw, 1991). A calling station survey in 1999, using methods outlined in (Ogutu & Dublin, 1998), indicated that 39 (95% confidence limits between 28-59) adult and sub adult lions lived in the area and subsequent data from individual identification, spoor, radio and GPS-collar tracking and problem animal control reports enabled us to narrow our estimate to between 32-41 adults and sub-adults resident at a density of 1 per 140-180 km<sup>2</sup> (Hemson, 2002).

In all directions except to the south-east and the central northern boundary, the MPNP is surrounded by scattered human settlements (over 150 cattle posts (family farms) and 3 villages) with which livestock are associated (Hemson *et al.*, submitted-a). The

park and surrounding area support a population of zebra and wildebeest that move *en masse* from west to east in the wet season returning to the west in the dry season as the availability of potable surface water changes (Kgathi & Kalikawe, 1993; Thomas & Shaw, 1991), Brooks, *unpublished data*) as well as populations of resident game species. The local fluctuations in prey abundance caused by movements of zebra and wildebeest create periods of local wild prey abundance and scarcity in different parts of the study area on a seasonal basis.

## Prey Data

*Figure 1: The study area showing distribution of cattleposts the two study zones the Makgadikgadi National Park and Ntwetwe Salt Pan. Kill data and prey abundances were compiled within each zone and stratified into lean and good periods based on detection of zebra as an indicator of the presence of large herds of migratory prey.*



The study area was split in half along a north/south axis into eastern and western zones (Figure 1), each 4,200 km<sup>2</sup> encompassing the dry and wet season ranges of the migratory zebra and wildebeest in the west and east respectively. Prey was

categorised as wild (resident and migratory) and livestock (table 1) and population estimates made using data from the Botswana Department of Wildlife and National Parks (DWNP) aerial survey data and Botswana Aerial Surveys Information System (BASIS) analysis package (Wint, 2000). The surveys are flown over much of western, central and northern Botswana, twice annually (September to October and February to March) to capture seasonal variation in wildlife distribution and population estimates e.g. (Verlinden, 1998). Only survey data collected by the DWNP within the study period (January 1999 and March 2003) were used in this analysis. Biomass estimates for prey species were calculated using the mean mass of adult females of the species from (Smithers, 1983) and (Mason, 1988).

*Table 1. Masses and classes used to calculate prey abundance in numbers of animals and biomass.*

Species	Mean mass of adult females in kg	Class
Cattle ( <i>Bos domesticus</i> )	338	Livestock
Zebra ( <i>Equus burchelli</i> )	302	Wild/Migratory
Wildebeest ( <i>Connochaetes taurinus</i> )	180	Wild/Migratory
Gemsbok ( <i>Oryx gazella</i> )	210	Wild/Resident
Ostrich ( <i>Struthio camelus</i> )	100	Wild/Resident
Kudu ( <i>Tragelaphus strepciceros</i> )	155	Wild/Resident
Horse ( <i>Equus caballus</i> )	200	Livestock
Sheep/Goat ( <i>Ovis aries</i> & <i>Capra hircus</i> )	35	Livestock
Donkey ( <i>Equus asinus</i> )	200	Livestock
Hartebeest ( <i>Alcelaphus buselaphus</i> )	120	Wild/Resident
Springbok ( <i>Antidorcas marsupialis</i> )	37	Wild/Resident
Impala ( <i>Aepyceros melampus</i> )	40	Wild/Resident

Population estimates of livestock species, zebra and wildebeest were calculated from the most recent aerial census of the entire area (dry season 2001). Prey abundance of other species were calculated using either the 2001 dry or extrapolated 2002 wet surveys as appropriate (see below). As abundance estimates fell within 95% confidence intervals from preceding years their abundances within seasons were assumed to be constant throughout the study period. In 2002 only the national park and a proportion of the study area outside the park (totalling 66.64% of study area) were surveyed and overall population estimates were extrapolated from these

samples. The resulting estimates closely approximated the measures made directly over the entire area during the previous year.

Despite approximate conformity of zebra and wildebeest movements to wet and dry seasons, we noted several occasions when they returned to the permanent pools in the Boteti during wet seasons for periods of a few days to a few weeks. These events coincided with the drying of pans in the east, that otherwise held the only surface-water available in this zone during wet seasons. To account for these ‘un-seasonal’ movements and to limit biases introduced by assuming that movements conformed to seasons, we defined periods of prey abundance on the presence or absence of zebra in a zone as reported by a network of observers; DWNP officials, safari guides, researchers, local cattle owners and ourselves.

We defined the period during which zebra were detectable in a zone as good periods (roughly equivalent to the dry season in the west and the wet season in the east) and the periods during which zebra were not detected in a zone as lean periods. Population estimates were made for each zone in each period type and the measures used for each subsequent period of that type (Figure 2). Zebra were good indicators of the presence of the migratory herds as they were the most abundant, conspicuous, vocal and widespread of the two species (wildebeest and zebra) and as such, least likely to be overlooked. Although it was not possible to standardise sampling effort of so many people from so many different backgrounds, access rights to the large study area and levels of motivation, we do not think any inaccuracy in defining these mass movements will significantly bias our data and are confident that mass movements were noted to an accuracy of within 3-5 days. In a drought prone country with erratic rainfall such as Botswana, we contend that this method was preferable to using wet and dry seasons defined on average long-term rainfall patterns as these ignore within season and inter-annual variation in rainfall. In all further calculations it is assumed that no zebra or wildebeest were present in a zone during lean periods.



Table 2: Population estimates for the two zones during lean and good periods.

<b>Area</b>	<b>Season</b>	<b>Species</b>	<b>Numbers</b>	<b>Total Weight (kg)</b>
<b>West</b>	<b>Dry (Good)</b>	<b>Wildebeest</b>	3366	605880
		<b>Zebra</b>	15522	4687644
		<b>Gemsbok</b>	777	163170
		<b>Hartebeest</b>	29	3480
		<b>Impala</b>	269	10760
		<b>Kudu</b>	1215	188325
		<b>Ostrich</b>	1158	115800
		<b>Springbok</b>	0	0
		<b>Cattle</b>	10420	3521960
		<b>Donkey</b>	268	34840
		<b>Horses</b>	54	10800
		<b>Sheep/Goat</b>	717	25095
	<b>Wet (Lean)</b>	<b>Zebra</b>	0	0
		<b>Wildebeest</b>	0	0
		<b>Kudu</b>	1479	229245
		<b>Gemsbok</b>	1055	221550
		<b>Springbok</b>	44	1628
		<b>Ostrich</b>	1777	177700
		<b>Impala</b>	251	10040
		<b>Hartebeest</b>	209	25080
		<b>Cattle</b>	10420	3521960
		<b>Sheep/Goat</b>	717	25095
		<b>Donkey</b>	268	34840
		<b>Horses</b>	54	10800
		<b>Zebra</b>	0	0
<b>East</b>	<b>Dry (Lean)</b>	<b>Wildebeest</b>	0	0
		<b>Kudu</b>	46	7130
		<b>Gemsbok</b>	152	31920
		<b>Ostrich</b>	1135	113500
		<b>Springbok</b>	58	2146
		<b>Impala</b>	0	0
		<b>Hartebeest</b>	0	0
		<b>Cattle</b>	13070	4417660
		<b>Horses</b>	957	191400
		<b>Donkey</b>	696	90480

<b>Wet (Good)</b>	<b>Sheep/Goat</b>	3076	107660
	<b>Zebra</b>	15522	4687644
	<b>Wildebeest</b>	3366	605880
	<b>Ostrich</b>	688	68800
	<b>Hartebeest</b>	175	21000
	<b>Springbok</b>	875	32375
	<b>Kudu</b>	125	19375
	<b>Impala</b>	0	0
	<b>Gemsbok</b>	600	126000
	<b>Cattle</b>	13070	4417660
	<b>Sheep/Goat</b>	3076	107660
	<b>Horses</b>	957	191400
	<b>Donkey</b>	696	90480

Prey species not detected by the aerial surveys e.g. porcupines, were excluded from the analyses of prey abundance and lion predation. Although prey species <20kg are occasionally captured and eaten by lions the contribution to their energy requirements is relatively minor compared with larger prey. During 370 h of continuous observations of lions at night only one korhaan-sized bird was killed and from a sample of 277 kills; one porcupine (*Hystrix africaustralis*), two aardvarks (*Oryzomys afer*) and one secretary bird (*Sagittarius serpentarius*) were found, representing 0.2% of the biomass observed killed. Other lion studies confirm that small prey make up a minimal proportion of lion diet (Biswas & Sankar, 2002; Cooper *et al.*, 1999; Funston *et al.*, 1998; Mills & Shenk, 1992; Schaller, 1972; Scheel, 1993; Scheel & Packer, 1993).

## Prey Movements

The areas used by the migratory zebra and wildebeest during good and lean periods were calculated using radio-tracking data from an ongoing study of zebra (n=22) and wildebeest (n=7) ecology in the Makgadikgadi (Brookes *unpublished data*). Data was stratified into lean and good periods and areas used by migratory ungulates approximated using 95% minimum convex polygons around all location data, using the harmonic mean as a point from which to exclude outliers. Overlaps between these polygons and individual lion home-ranges were calculated as the percentage of the latter that overlapped with the former as an index of the availability of these key

species to lions during different periods. All ranges were calculated using Ranges 6 (Kenward *et al.*, 2002).

The area utilised by cattle was estimated by creating a buffer around all mapped cattleposts using data from 9 cows, from different cattleposts, fitted with GPS-collars (Televilt, GPS-Simplex). The collars took 1 fix per hour for a total of 177 cow days (mean 20 days) and data were gathered during both periods (72 days lean and 105 good) and during wet and dry seasons. There was no evidence to suggest that there was a seasonal difference between distances moved from cattleposts. Throughout this paper we assume that the movements of these collared cattle are representative of cattle movements to and from cattleposts and an approximation of these same patterns for livestock in general. While published data from Botswana suggests that goats/sheep and donkeys do not move quite as far from water (generally made available at cattleposts) as do cattle (Verlinden *et al.*, 1998) our use of cattle data as representative of livestock is conservative in this context. In terms of both biomass and numbers, cattle considerably outnumber other livestock species in the area (Table 2).

For each of the 3847 GPS locations the distance to the closest cattlepost that that cow had over'nighted at (cows occasionally over'nighted in cattleposts other than their own) was calculated using ArcView 3.2 GIS (ESRI 1992) and the Animal Movement Extension (Hooge *et al.*, 1999). These distances were analysed by hour to describe the daily movements of the cattle. The distance within which 95% of all points were encompassed was used as the outer limit of the intensive cattle area and used to create the 'cattle buffer' by merging radii from each cattlepost using ArcView 3.2 (ESRI 1992). The density of stock within different radii from cattleposts was calculated by dividing the percentage of locations for a given hour that were within each 1km wide radius from the cattlepost minus the next inner radius to give densities with a series of rings at 0-1km, 1-2km, 2-3km, 3-4km etc. Locations within 250m of a cattlepost were conservatively assumed to be inside the kraal (livestock enclosure).

### **Lion Kill Data**

Lion predation data were collected between January 1999 and March 2003. Data were collected using:-

1. Continuous observation of foraging lions fitted with VHF radio-collars with activity sensors (Sirtrack New Zealand) using binoculars (Zeiss 8 x 58B) and a red filtered spot light from a vehicle (370 hours over 39 nights).
2. Radio-collared lions located for a study of movement and range use were sometimes found feeding and less often hunting.
3. Opportunistic location of feeding lions and carcasses discovered whilst traversing the study area or tracking lions on foot.

For each carcass we attempted to verify predation by lions by looking for or investigating;

- Signs typical of lion kills (e.g. pharyngeal and/or nasal punctures and scratches and/or bites on shoulder and rump, deep lion tracks with splayed toes and extended claws (a charge towards prey) and evidence of a struggle (drag marks, blood trails etc)).
- Feeding signs commensurate with observations of carcasses that lions were witnessed feeding from (eating from inner thighs around anus and through the brisket).
- Fresh lion tracks.
- Location data from GPS-collared lions demonstrating lion presence at the carcass at the estimated time of death.
- Distance to nearest known lions (located by radio telemetry of tracking) and signs that these lions had fed recently (bloated stomachs and bloody faces).

Carcasses that we could not confirm as lion prey beyond reasonable doubt (including those that may have been scavenged) were excluded from this analysis. Scavenging was only noted once during continuous observations and we ascribe this low incidence to the low frequency of encounters we had with spotted hyaenas (*Crocuta crocuta*), cheetah (*Acinonyx jubatus*), wild dogs (*Lycaon pictus*) and leopard (*Panthera pardus*) during the study. Only one cheetah and one leopard kill were found during the study despite taking considerable time to locate and investigate kills. All kills were categorised by species and, when possible, details of amount eaten at lion departure, were collected. Amount eaten was based on the percentage of mass of the animal eaten (excluding the inedible components such as the larger bones, horns etc) using a four step scale (0-25%, 26-50%, 51-75% and 76-100%) and was assessed immediately after the lions had left and before scavengers arrived, when an inspection

on foot was possible. Kill incidences were separated into eastern and western zones by location and further into lean and good periods using dates as estimated above. We measured the distance of each kill, for which the proportion consumed could be estimated, to the nearest cattlepost using ArcView 3.2 (ESRI 1992).

For the purpose of our analysis we used kill incidences rather than numbers of animals or biomass killed. A kill incident was defined as an event during which one or more of a prey species was killed and partly or completely consumed. Kill incidences were used in preference to numbers or biomass killed in order to remove the effect of occasional surplus killing of livestock by lions from the analysis, such as 43 goats being killed by two lions in one night. Unlike other studies e.g. (Frank, 1998; Mizutani, 1999) our method does not attempt to account for the magnitude of the impact on local people of predation events. Rather we attempt to quantify the shift in the frequency of predation of livestock during two periods of different prey availability to better understand the behaviour of the predator, a major component of the cause of the conflict.

Different frequencies of predation relative to estimated prey abundance (predation intensity), were estimated using a variant of the forage ratio (equation 1) (Pienaar, 1969) perhaps the simplest of the various selection/electivity indices (Chesson, 1978; Ivlev, 1961; Jacobs, 1974; Krebs, 1999).

*Equation 1: The forage ratio.*

$$f_i = \frac{r_i}{n_i}$$

$r_i$  = proportion of prey type  $i$  in the diet

$n_i$  = proportion of prey type  $i$  in the environment

$f_i$  = forage ratio for prey type  $i$

A limitation of the forage ratio is the underweighting of values less than 1, indicative of resource use below that predicted by abundance (being constrained between 1 and 0 whilst values above 1 are unconstrained). This can lead to a perception that most intensively utilised prey are more ‘over-utilised’ than prey that is ‘under-utilised’. To

control for this perceived effect we added a logic statement to our calculations such that, values of  $f_i$  less than 1 were replaced with;  $-((1/f_i)-1)$  and values larger than 1 were replaced with  $f_i - 1$ . This gave values whose magnitude and direction of deviation from 0, were an index of the intensity of utilisation of that prey class; negative values indicating utilisation below that expected from the abundance of the prey category and vice versa. In this paper we shall hereafter refer to this value as the reciprocated forage ratio (RFR).

Niche breadth was estimated for each period (good and lean) using Levin's standardized niche breadth index (equation 2) (Krebs, 1999). Estimates were made for each period within each zone and then for each period pooling the data from each zone to look for any overall trend.

*Equation 2: Levin's standardized niche breadth index*

$$B = \frac{\left( \frac{1}{\sum p_i^2} \right) - 1}{n - 1}$$

$B$  = Levin's standardised niche breadth index

$P_i$  = proportion of items in the diet that are of category  $i$

$n$  = number of possible resource categories.

## **Lion Movements**

Lions were classified as stock-raiding or non-stock-raiding based upon whether the animals were known to have killed livestock at least three times during the study (Stander, 1990). Pride sizes in the Makgadikgadi were small (mean number of adult females = 1.9, SD 0.8  $n = 8$ ) and in our experience if one adult female in a pride was a stock-raider then all other adult pride members were likewise stock-raiders. As these prides frequently split up into smaller groups or individuals, it was possible to verify that each pride member was a stock-raider rather than inferring this from observations of all pride members at livestock kills. The largest number of livestock kills was 18 recorded by female 6 with further suggestive evidence of several more from GPS-collar data.

Over the course of the study 28 lions (7 adult males, 17 adult females, 3 sub-adult males and 1 sub-adult female) were immobilised and fitted with radio-collars. 18 were fitted with VHF radio-collars (Sirtrack) and 10 with GPS/VHF collars (Televilt Simplex 2-D). Radio-collared lions were located as often as possible throughout the study period but rarely more than once a day. GPS-collars were programmed to take 13 fixes per night, hourly from 18:00 through until 06:00 and then one fix at 09:00 and another at 16:00. These data were stored onboard, broadcast from the collar and downloaded by radio-link to a Televilt RX-900 receiver monthly or bi-monthly.

GPS data were split into day and night fixes. Night fixes were those taken at 01:00 or 02:00 (the times the GPS unit was most successful at recording positions) and daytime fixes were 9:00 or 16:00. Due to a considerable failure rate (70% of collars failed within 30-200 days) (Hemson, 2002) continuous data were available for three males and seven females (of which one produced insufficient samples for day versus night comparisons during good periods). Seven collared lions were killed by local herders and three collared males dispersed (one was sighted over 400 km south of the study area near the Khutse Game Reserve (Schiess-Meier and Ramsaur pers comm). Several VHF collars were also placed on individuals within prides that already contained a GPS-collared animal to ensure retrieval of the GPS-collar if it failed. In these cases it is not possible to view pride members as independent data sources and data from GPS-collared lions were used in preference to radio collared animals to indicate the movement of the females in that pride.

Radio-tracked lions were located throughout the day and their datasets are a mixture of night and day fixes (predominately day). However, small sample sizes prevents sub-sampling of these datasets into night and day and while addressing hypotheses related to nocturnal movements, data from only GPS-collared animals is used (six females and three males). In the analysis of changes in home-range size between good and lean periods and overlap with areas utilised by cattle, data from three radio-collared females are also included. Home-ranges for GPS-collared lions were calculated from night fixes preferentially whereas all radio-tracking fixes were used if at least 24 hours apart. If more than one location was recorded within any given 24 hour period night fixes were used in preference to day.

## Home Range Methods

Concave polygons containing 95% of locations were plotted in preference to kernels which we found produced unacceptable results (Hemson *et al.*, submitted-b). Concave polygons were created using the clustering technique (Concave Clusters), restricting minimum side length to 0.5 of the range span (Kenward *et al.*, 2001). Concave clusters (CC) create minimal estimates of range use by excluding unvisited or underutilised areas of the home-range, whilst allowing depiction of multiple centres of activity thus avoiding two limitations of minimum convex polygons (Kenward *et al.*, 2001). Estimates are also given for 100% minimum convex polygons to facilitate comparison with other studies (note home-ranges are seasonal and not year round) and all range sizes are given in square kilometres (km<sup>2</sup>). Overlaps of seasonal home-ranges within individuals were calculated to examine whether individuals remained in the same area or moved locality as wild prey migrated. Overlaps are presented as percentages of the lean period range overlapped by the good period range. Home-ranges were calculated using Ranges6 (Kenward *et al.*, 2002).

To investigate changes in ranging behaviour between day and night, day range sizes were expressed as a percentage of the night range. For analysis of range size changes between periods, good period range size was expressed as percentage of lean period range size. Seasonal changes in overlap of lion home-ranges with the cattle buffer were calculated as a percentage of home-range calculated during the good period overlapping with the cattle buffer expressed as a percentage of the percentage of the lean period range overlapping the buffer. This enabled us to accommodate the considerable variation in CC home-range sizes of different lions (18.1 km<sup>2</sup>-1274 km<sup>2</sup>) and provided a robust index of the proportion of time the lions spent in different areas, irrespective of the absolute overlap.

For each lion location, the distance to the nearest cattle post was calculated. The mean of these distances was calculated for each lion, and additional means were calculated for each season and for each hour for which data were available. Mean straight line distances moved per hour were also calculated between successive points in a time series for each lion using the Animal Movement Extension (Hooge *et al.*, 1999) for ArcView 3.2 GIS (ESRI 1992), stratifying for night and day and good and lean



periods. The mean proportion of GPS locations (lean period stock-raiding males and females) in successive 1km radii from cattleposts was calculated for three periods; late evening (19:00–23:00), morning (00:00–05:00) and daytime (06:00–18:00), to test whether stock-raiders foraging strategies varied through the 24 hour cycle.

Sample sizes were insufficient for normality testing, so analysis relies on non-parametric tests (one tailed and two tailed Wilcoxon signed rank tests). Lions were classified either as raiders or non-raiders.

## **Habitat**

Habitat types were classified as salt pan (open saline clay surface some of which is seasonally inundated with rain water), grassland (open grassland with very few bushes and trees), savannah (open wooded grassland), scrub (woody shrubs and bushes often very dense), wooded (dense stands of trees often interspersed with shrubs and bushes) and bare earth (bare soil, typically associated with cattleposts). Habitat data were gathered with GPS locations every time lions were located visually and were used to improve an unsupervised classification of a geo-referenced Landsat 5 image of the area. Georeferencing was verified using clearly visible landmarks including roads, dry saltpan edges and cut lines (straight graded dirt tracks used as fire breaks, fence lines or mineral prospecting roads). The image was divided automatically into 200 classes in an unsupervised classification of all bands of the image, using an Iterative Self-Organizing Data Analysis Technique Algorithm (ISODATA). 30 iterations were performed with a minimum convergence threshold of 99% and the convergence threshold was attained before the 30<sup>th</sup> iteration. 200 classes were required to separate wet algae covered salt pan from dense acacia woodland areas which appeared as identical classes when fewer classes or fewer bands were used. Once divided, we merged these classes into the six habitat types listed above using GPS locations with associated habitat data (ground-truthed locations). Each location was identified on the image and the pixel, and all others of its class, classified according to the observed data taken on the ground. This procedure was undertaken with Erdas Imagine v8.5 (Erdas 2001).

Cattle habitat use was described by assigning a habitat variable for each GPS location from the habitat classification image. Sample periods were insufficiently long to permit stratification by season and we did not test for habitat selectivity as our aim was to compare lion habitat selectivity with the proportions of cattle locations within each habitat. Locations of 66 livestock kill incidents were used to investigate whether livestock killing by lions occurred in different habitats or distances from cattleposts from those that cattle routinely used. Only those kill incidents where collared lions were found with a kill or when a recent kill's time and location could be reliably correlated with data downloaded from a lion's GPS-collar were used. By excluding livestock kills reported to us by herders we limited any bias attributable to a greater likelihood that the remains of kills abandoned closer to cattle posts might be more readily found by villagers, and thus removed prior to discovery by the research team.

## **Results**

### **Prey Data**

The migratory zebra and wildebeest moved *en masse* in response to local rainfall and the availability of surface water occupying distinct wet and dry season ranges (Figure 3). The first major rains of the year resulted in the migrants leaving the Boteti area (where there is permanent water) for the summer grazing areas further east from where they returned when surface water evaporated. 95% of all cattle locations were within 6 km of cattleposts in which they over'nighted (Figure 2) and this radius was used to create the cattle buffer (Figure 3).

Figure 2: The proportion of hourly GPS locations of cattle within different radii of their natal cattleposts.

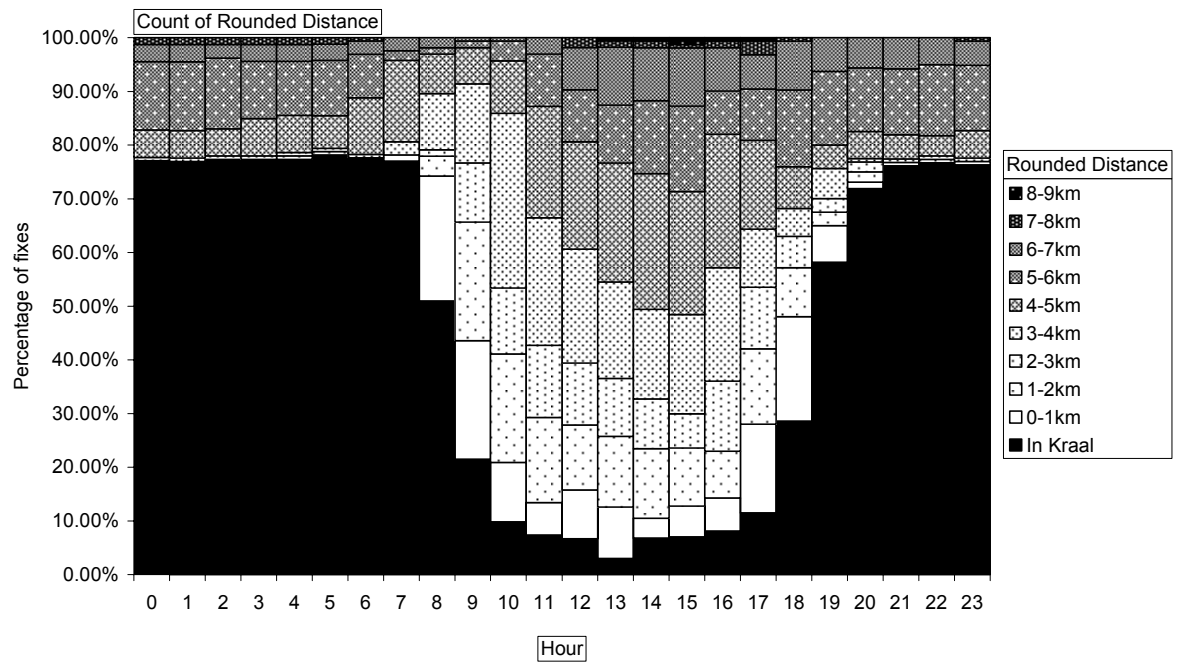
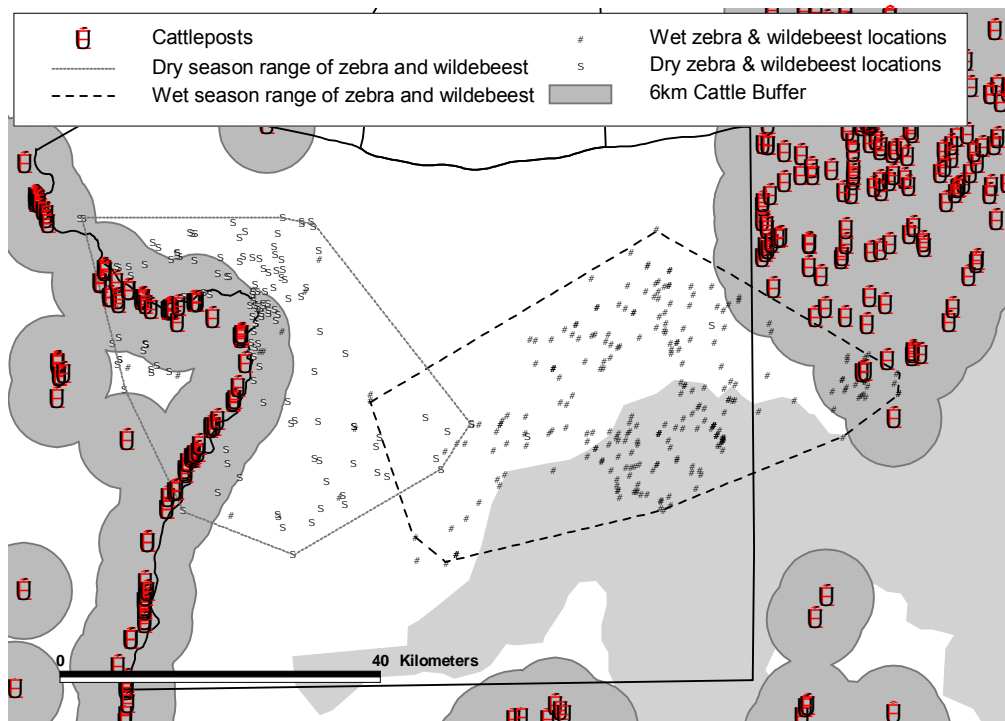


Figure 3. The study area including the cattleposts and 6 kilometres cattle buffer migrant prey home-ranges and Ntwetwe Salt Pan.



Migratory prey (zebra and wildebeest) was the most abundant class of prey available to lions during good periods. Livestock was the most abundant during lean periods and the next most abundant after migrants during good periods (Table 2). Resident prey was least abundant at all times and small variations in abundance suggested influxes of gemsbok (*Oryx gazella*), hartebeest (*Alcephalus buselaphus*), springbok (*Antidorcas marsupialis*) and ostrich (*Struthio camleus*) into the study area during the wet seasons. This bolstered wild prey abundance during the lean periods in the west and good periods in the east. Larger prey species made up a larger proportion of numbers and biomass of the wild migrant and livestock classes compared to the resident wild prey class.

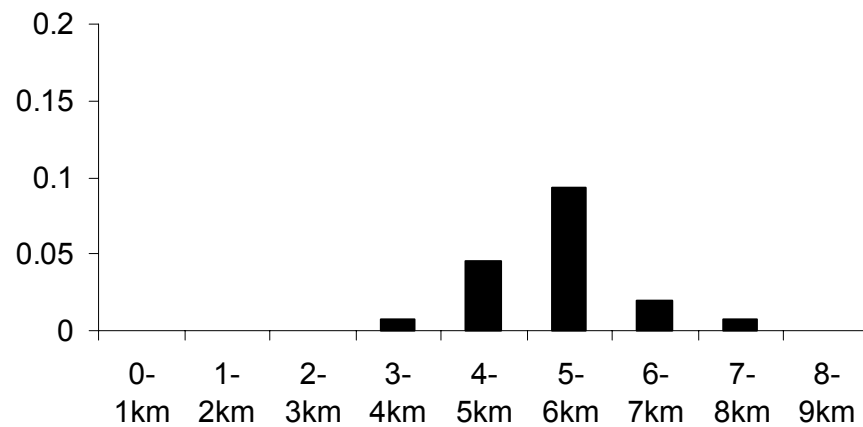
*Table 3: Estimated numbers of animals and biomass in different prey classes in Eastern and Western study zones during different periods of prey abundance, mean mass per individual and mean mass of species killed in kill incidences and proportions of biomass estimates by class within area and prey abundance periods.*

Zone	Period	Prey Class	Estimated number of animals	Estimated biomass in Tons (kg/1000)	Proportion of biomass	Mean Mass per animal (kg)	Proportion of Kill Incidences	Mean Mass of species per kill incident (kg)
<b>West</b>	<b>Good</b>	<b>Migratory</b>	18888	5293	0.56	280	0.86	278
		<b>Resident</b>	3448	482	0.05	140	0.05	137
		<b>Livestock</b>	11459	3593	0.38	314	0.09	292
	<b>Lean</b>	<b>Migratory</b>	0	0	0	-	0	-
		<b>Resident</b>	4815	665	0.16	138	0.14	169
		<b>Livestock</b>	11459	3593	0.84	314	0.86	349
<b>East</b>	<b>Good</b>	<b>Migratory</b>	18888	5293	0.51	280	0.70	279
		<b>Resident</b>	2463	267	0.03	109	0.03	110
		<b>Livestock</b>	17799	4807	0.36	270	0.26	299
	<b>Lean</b>	<b>Migratory</b>	0	0	0	-	0	-
		<b>Resident</b>	1391	154	0.03	111	0.16	167
		<b>Livestock</b>	17799	4807	0.97	270	0.84	344

Interview data indicates that livestock were rarely accompanied by herders during the day (Hemson *et al.*, submitted-a) while they are spread fairly homogenously throughout the cattle buffer, with locations being most widely dispersed between 13:00 and 15:00 (Figure 2). 20% of cattle locations were away from the cattleposts at night (compared with 13% as estimated by the herders themselves (Hemson *et al.*, submitted-a). These strays were concentrated between four and six km from the cattlepost (Figure 2) and the peak density of un-kraaled cattle locations occurred between five and six km from the cattleposts at night (Figure 4). One limitation of these data is that we cannot discern between cattle that are standing very close to the kraal to those inside. While we assumed that only cattle further than 250 metres from cattleposts were outside we did encounter unenclosed stock within 250 metres of cattleposts at night. Indeed this is perceived to occur so frequently that Wildlife Department officials have started patrolling around cattleposts at night and waking up herders when they find untended stock waiting outside the kraals. Our interpretation of these observations is that some animals return later than others and may not be let into the kraal if herders are asleep or elsewhere, and that the distribution of nocturnal cattle density (Figure 4) may be bimodal with a second peak of late returnees very close to the cattlepost.

Livestock were generally not let out of the enclosures (kraals) until between 08:00 and 10:00, after milking etc. Most stock returned to the cattleposts for water in the evenings under their own volition, but stragglers were sometimes gathered in by herders on foot (Hemson *et al.*, submitted-a).

*Figure 4. An index of livestock density within different radii of cattleposts at midnight % of total density per km<sup>2</sup>.*

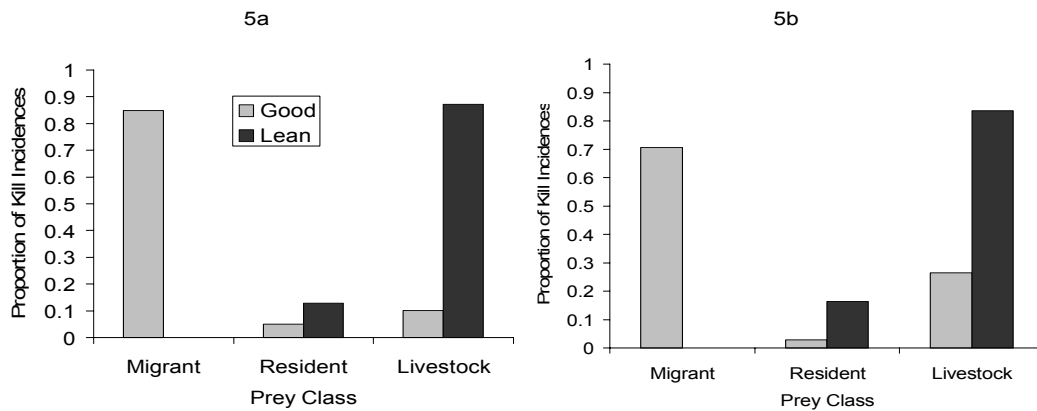


### **Lion Kill Data**

We recorded 276 kill incidences in which 344 animals were killed. Surplus/multiple killing events were most frequent for livestock species with 1.3 times as many animals killed per kill incident (predominately goats, of which 3.7 times as many were killed as kill incidents) compared to the same proportion for resident wild prey and 1.02 kills/kill incident for migratory prey.

During good periods, migratory prey were the main prey species, making up 71-85% of the kill incidences and during lean periods livestock were the predominate prey accounting for 79-87% of kill incidences (Figures 5a and 5b). Kill incidences involving resident prey increased from 3-5% of incidences in good periods to 14-16% during lean periods, despite being smaller, on average, than abundant livestock. Livestock made up 10-26% of kill incidences recorded in good periods. The mean mass of species targeted during kill incidences within a prey classes was similar to the mean mass of that available within the local environment. However, during lean periods lions tended to prey upon larger than average resident wild prey and livestock such as gemsbok and kudu, and cows and horses respectively, while during good periods they appeared to be less size selective within these classes.

Figures 5 a & b: Shifts in the pattern of lion predation in two study zones (5a west & 5b east) during different periods of wild prey abundance as measured by the proportion of total kill incidences for that period by prey class.



Makgadikgadi lions not only changed the absolute proportions of prey classes represented by kill incidences between periods but changed their intensity of utilisation (i.e. the proportion of kill incidences of a prey type relative to the proportion of abundance (biomass) of that prey type) of different prey classes under different regimes of prey abundance (Figure 5). Proportions of kill incidences per class were significantly different to that expected under the null hypothesis that kill incidences would be proportional to abundance for all zones and periods except the lean period in the west. Wild migratory prey was killed more frequently and livestock less frequently than expected from abundance during good periods in both zones (Table 4). During lean periods in the eastern zone the frequency of kill incidences was also significantly disproportional to abundance with many more resident prey killed than was expected from abundance. However, during lean periods in the western zone the pattern was not significantly different to that expected. The sample size was smaller for this subset of the data however; the relatively small value of  $\chi^2$  suggests that the frequency of kill incidences is indeed quite close to proportionality.

Table 4:  $\chi^2_{[2]}$  values and significances of tests for prey class utilisation disproportionate to estimated abundance (in brackets) by period and zone (number of kill incidences in italics).

Zone	Lean	Good
West	0.2 (ns) <i>31</i>	105.6 (<0.01) <i>115</i>
East	8.0 (<0.05) <i>55</i>	13.9 (<0.05) <i>68</i>

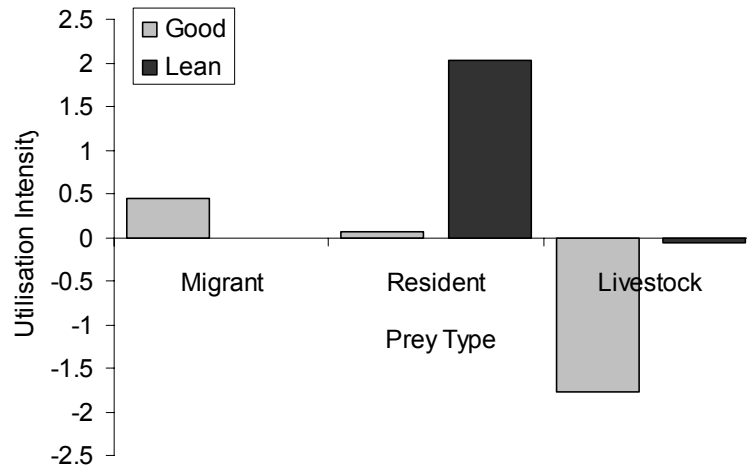
When data were merged to overall good and lean periods from both zones to calculate single measures of utilisation (Figure 6); utilisation during both good ( $\chi^2_{[2]} = 50.5$ ,  $p < 0.01$ ) and lean periods ( $\chi^2_{[2]} = 7.1$ ,  $p < 0.05$ ) differed from those expected if proportional to abundance. Lions took more migratory prey (71-85% of kill incidences,  $\chi^2_{[1]} = 21.2$ ,  $p < 0.01$ ) than expected on the basis of their abundance (51-57%) during good periods. During good periods they also killed less livestock than expected ( $\chi^2_{[1]} = 29.4$ ,  $p < 0.01$ ) if utilisation (10-26%) was proportional to abundance (38-46%). During lean periods livestock utilisation was not significantly different to proportional ( $\chi^2_{[1]} = 1.2$ ,  $p < \text{ns}$ ) whilst resident prey were utilised (13-16%) more intensely than expected ( $\chi^2_{[1]} = 5.1$ ,  $p < 0.05$ ) despite being relatively scarce (3-16%). Utilisation of livestock and wild resident prey increased during lean periods whilst migratory prey was most intensely utilised during the good periods.

Dietary niche breadth in the west decreased from 0.19 in the lean to 0.12 during good periods and increased from 0.17 in the lean to 0.20 during good periods in the east. Overall niche breadth did appear to broaden slightly during periods of wild prey scarcity rising from 0.13 during good periods to 0.16 during lean periods despite an overall decrease in the number of potential prey species in a zone.

For 37 kill incidences an assessment of how much of the prey item(s) had been eaten was made at the time the lions left and before scavengers arrived. 13 of these were livestock kills and 24 were wildlife. Mean consumption of kills at lion departure was lower at livestock kills (44%) than that of wildlife kills (65%) (Two sample t-test.  $P = 0.015$ ). Consumption was positively correlated with distance from cattlepost (Spearman's Rank Correlation  $r = 0.44$ ,  $P = 0.007$ ).



Figure 6: Intensity of utilisation (reciprocal forage ratio) of prey classes between periods averaged across zones (negative values reflect utilisation less than proportional to abundance and vice versa).

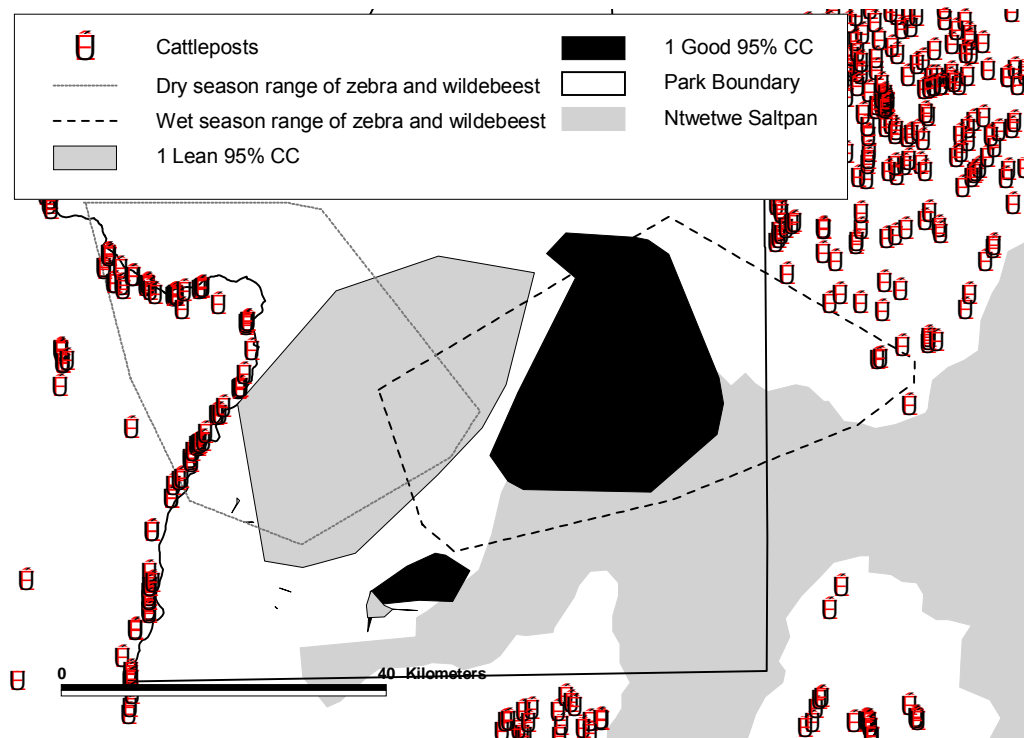


## Lion Movements

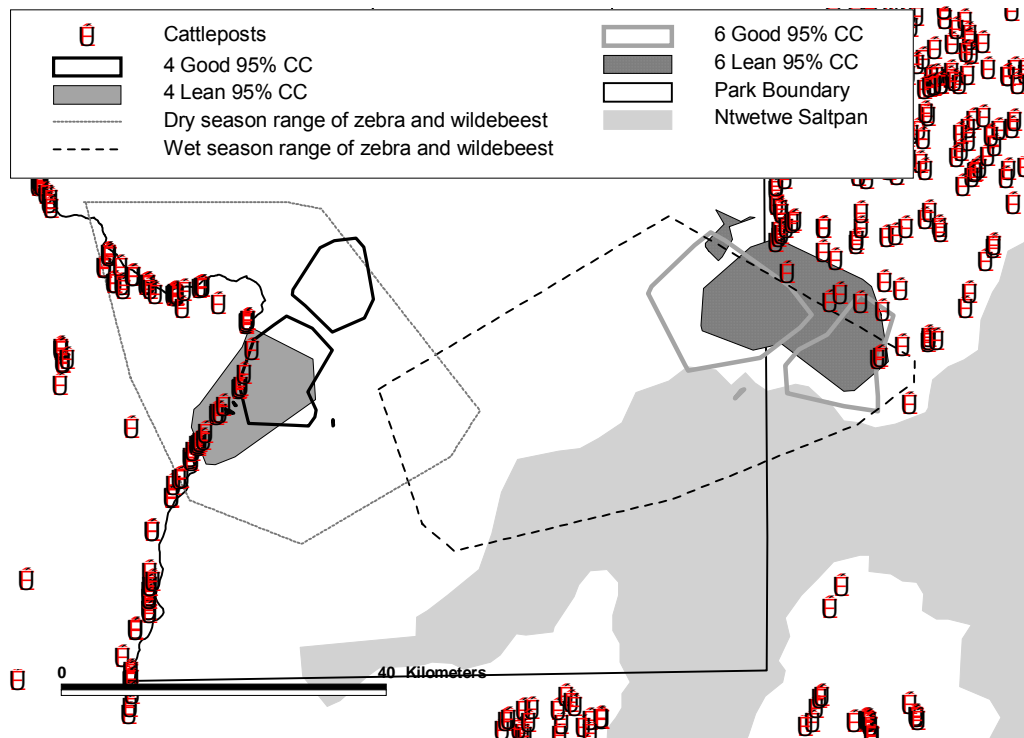
Six stock-raiding females (two radio collared and four GPS-collared), three non-stock-raiding females (GPS-collared) and three males (all stock-raiders and GPS-collared) were identified. Non-raiding lionesses retained an overlap (mean 80% of range, SD 13%) with the migratory zebra and wildebeest throughout the study (e.g. Figure 7a) and occupied home-ranges closest to the middle of the park. By following the migrating herds these lionesses shifted home-ranges between the home-ranges of the two resident coalitions of pride males, one in the east and one in the west. Stock-raiding lionesses (e.g. Figure 7b) and males did not overlap with the home-ranges of the zebra and wildebeest throughout the year and lived on the periphery of the park where access to livestock was best. During good periods, when they did share space with the herds, mean overlap with the home-range of the migration was high (98% SD 3%) but when the zebra and wildebeest moved on, stock-raiding lions did not follow and no longer overlapped with the migrant range and had no access to zebra or wildebeest as potential prey during lean periods.

Figure 7a-c. Three maps showing the seasonal shift in home-ranges of ((7a) non-stock-raiding lioness (ID=1), (7b) two stock-raiding lionesses (4 & 6) and (7c) two stock-raiding males 10 & 12, as estimated using 95% concave clustered polygons and the wet and dry season home-ranges of the migratory prey. Females 4 & 6 and males 10 & 12 shift range towards cattleposts during lean periods whereas 1 entirely relocates to the East to follow the migratory ungulates.

7a



7b



7c

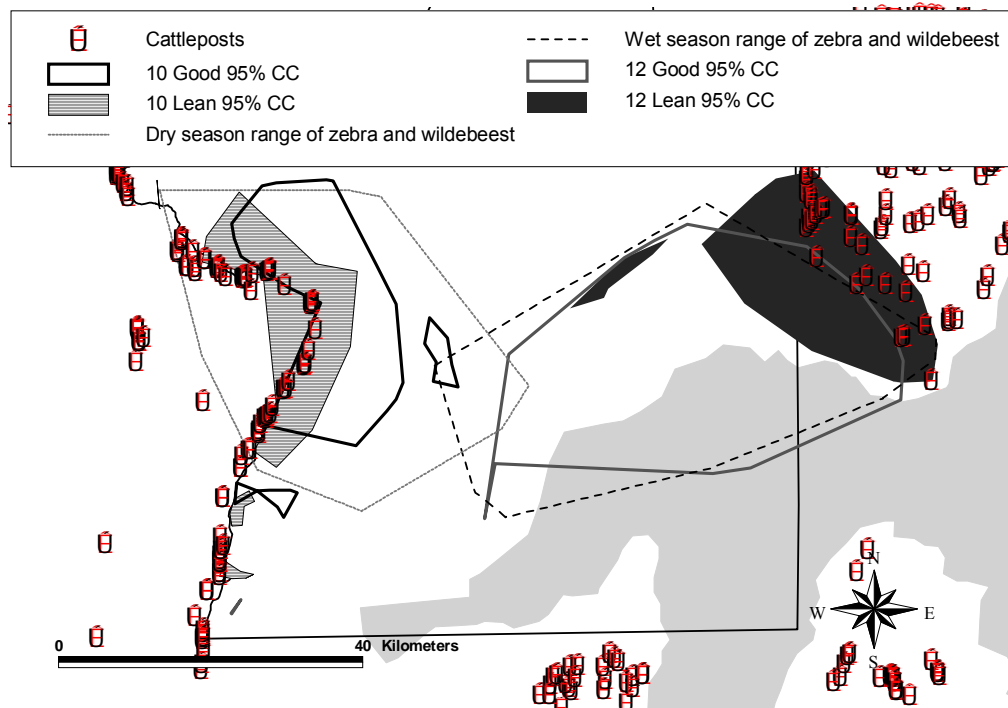


Table 5: The mean size of lion home-ranges used in this analysis and mean distance moved per hour at night by sex and stock-raiding category. 100% minimum convex polygon (MCP) and 95% concave cluster sizes are given for comparison with other studies.

Male=M/Female=F	Raiding =R/ Non-Raider = N	Good period = G/ Lean period = L	Mean 95% CC	St Dev	100% MCP	St Dev	Mean Distance Moved per hour at night (km/h)
F	N	G	450	218	1177	430	0.4
F	N	L	625	265	1725	662	0.5
F	N Total	L & G mean	538	238	1451	583	-
F	R	G	206	202	432	373	0.6
F	R	L	112	98	293	249	0.6
F	R Total	L & G mean	159	159	363	311	-
F Total	N & R	L & G mean	286	258	726	664	-
M	R	G	714	489	1719	494	1.1
M	R	L	346	153	1412	140	1.0
M Total	R Total	L & G mean	530	382	1566	366	-

Stock-raiding lionesses had smaller day ranges than night ranges during lean periods (Wilcoxon Signed Rank Test  $p = 0.050$ ,  $n = 4$ ) but not during good periods ( $p = 0.211$ ), although the trend in both periods was in the same direction. As such the sizes of stock-raider ranges were determined in part by a factor that changed between the lean and good periods. Non-raiding lionesses' home-ranges did not change in size significantly between the seasons ( $p = 0.181$  estimated median =  $-23.46\%$ ,  $n = 3$ ) nor between night and day. During both good and lean periods, the ranges of stock-raiding lionesses overlapped more than did those of non-raiding lionesses (Mann-Whitney  $p=0.0282$ ,  $n=3$  & 6) e.g. figures 7a-b) indicating they did not change the locality of their home-ranges as much as non-raiders who moved to keep track of the migration. They had smaller home-ranges than non-raiding lionesses during lean periods (Mann-Whitney Test  $n=6$  and 3,  $p=0.0282$ ) but not during good periods (Mann-Whitney Test  $n=6$  and 3,  $p=0.1556$ ). During good periods stock-raiders used significantly larger home-ranges than they did during lean periods (Wilcoxon Signed

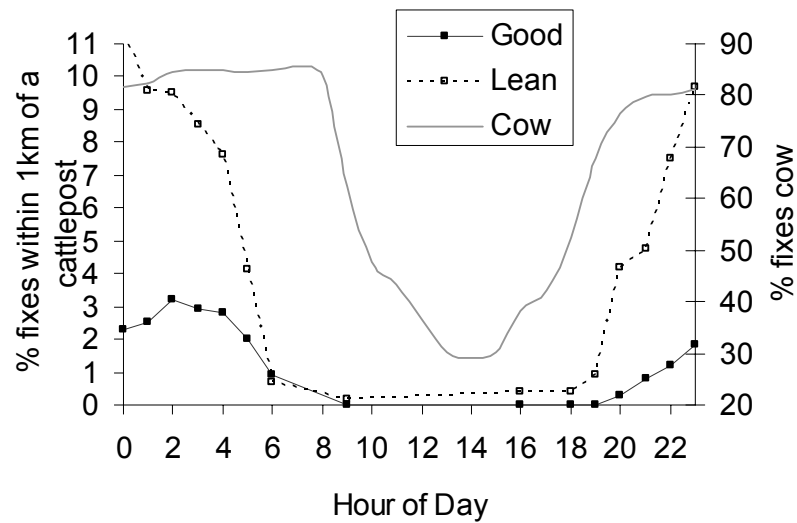
Rank Test,  $p = 0.018$  estimated median = +100.8%,  $n=6$ ). During good periods stock-raiding lionesses' 95% home-ranges overlapped less with the cattle buffer during both the day ( $p=0.018$   $n =6$ , estimated median -28.89%) and night ( $p=0.050$ ,  $n=4$ , estimated median -26.00%) than they did during lean periods.

All males in our sample were stock-raiders, and their home-ranges were significantly larger than those of stock-raiding lionesses (Mann-Whitney  $N = 6$  and  $3$ ,  $p = 0.0282$ ) but not significantly larger than those of non-stock-raiding lionesses (Mann-Whitney  $N = 6$  and  $3$ ,  $p= 0.3827$ ); each male overlapped with the ranges of lionesses from at least two prides and included at least one stock-raider. Night and day ranges and seasonal ranges of males were not significantly different.

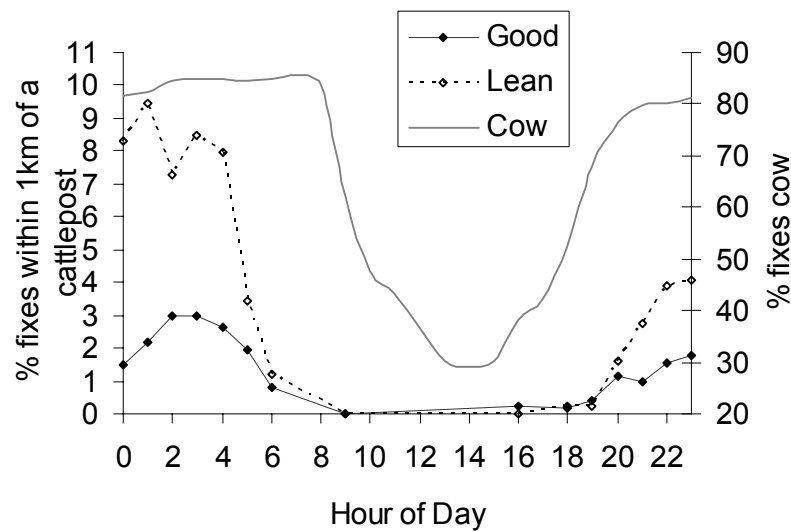
Although all lions spent considerably less time within 1km of cattleposts than did cattle, the pattern of movements of stock-raiding males and females relative to cattleposts during lean periods paralleled those of cattle more closely than during the good periods. In contrast the movements of non-stock-raiders did not mirror those of cattle (Figures 8a-c). Stock-raiders made most close approaches to cattleposts at night when 80% of cattle were at the cattleposts and most frequently between 22:00 and 04:00. By 06:00 less than 1% of stock-raider locations were within 1km of cattleposts. There is evidence that some non-stock-raiders did make a few close approaches between 22:00 and 04:00, however we could not correlate these approaches to livestock predation incidents. Anecdotal evidence suggests that not all close approaches relate to attempts to find and kill livestock as we have observed a lioness kill a zebra foal between the kraals at a cattlepost and interpretation of spoor suggests that lions sometimes use water sources associated with cattleposts.

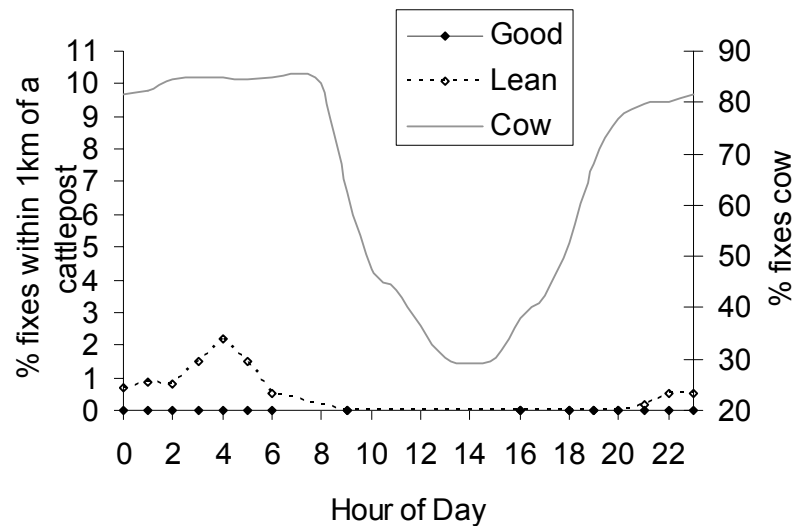
Figure 8a-c. The percentage of GPS-collar fixes at different hours of the day within 1km of cattleposts by season compared with percentage of cattle fixes within 1km (upper grey line and right hand y axis) for stock-raiding females (a), males (b) and non-stock-raiding females (c).

8a



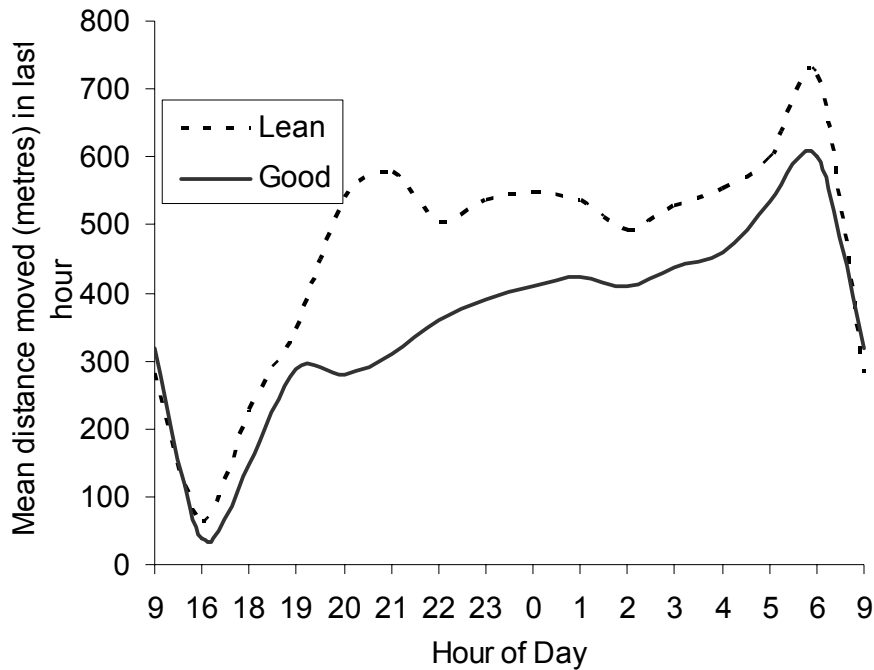
8b





All lions moved further per hour at night (mean 0.7 km/h) than during the day (0.2 km/h) and males moved twice as far at night than both stock-raiding and non-stock-raiding females; these seasonal means were not significantly different between the classes/sexes of lions. Stock-raiding lions moved furthest between 20:00 and 06:00, with peaks at 20:00 and 06:00 during the lean season (Figure 9). The latter peak occurs when the frequency of close approaches to cattle posts is declining (Figure 8a) suggesting that stock-raiders were moving rapidly away from cattleposts around sunrise. The earlier lesser peak occurs as lions are beginning to forage and move towards cattleposts. Good season movements appear to accelerate throughout the night with a similar peak around sunset. In this case, and possibly the former, it may be that this movement is away from open areas into shade and cover for the day. The upper lean season curve arose as stock-raiding lions may have to both approach and subsequently retreat from foraging areas near to cattleposts when predating upon livestock whilst they need not make these 'round trips' when hunting for wild prey.

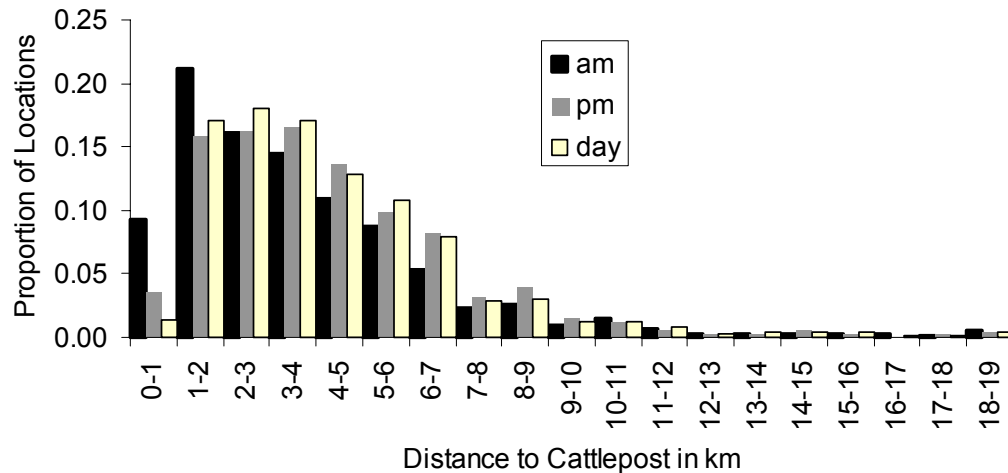
Figure 9. The mean hourly distance moved by stock-raiding lionesses at different times of the day and during different periods of prey abundance.



The modal radius from cattlepost for stock-raiding lion locations during lean periods changed slightly between different parts of the 24 hour period (Figure 10). During the late evening (19:00-23:00) (pm in figure 8) stock-raiders lions were most frequently located between 3-4 km from cattleposts while during the day (06:00-18:00) they were most often somewhat closer at 2-3 km. During the early morning (00:00-05:00) they were closest with a modal distance of 1-2 km. 78% of all GPS locations of stock-raiders were within 6km of cattleposts during lean periods. The mean distance of 66 livestock kills from the closest cattlepost was 3.6km (Mode 3.0 km and SD 3.2km).



Figure 10. The mean proportion of GPS locations of stock-raiding lions in successive radii from cattleposts between 00:00 and 05:00 (am), 19:00 and 23:00 (pm) and 06:00 and 18:00 (day).



## Habitat

Cattle locations within 3km of cattleposts at night were predominately in scrub (43%) and grassland (41%) with fewer locations in savannah (16%) and woods (1%). During the day, GPS-collared cattle were most often located in grassland (49%) with scrub (29%), savannah (19%) and woods (3%) making up the remainder. These proportions were calculated after locations inside the kraals had been removed. Of the 66 livestock kills for which we have reliable spatial data, most were located in grassland and scrub habitat types (Table 6). The occurrence of livestock kills in different habitats was most similar to the habitats in which cattle GPS locations were found during the day and significantly different from that expected from the frequency of cattle locations in different habitats at night ( $\chi^2_{[5]}$ ,  $p < 0.001$ ) suggesting livestock may be being killed during the day or that lions were preferentially hunting cattle that were in denser habitats.

Table 6: Percentage of all livestock kill incidents by habitat ( $n = 66$ ) and percentage of cow locations in different habitats by day and night and percentage similarity between data sets (Krebs, 1999).

Habitat	Percentage of Livestock Kills	Percentage of Cattle Locations during the day	Percentage of Cattle Locations during the night
<b>Saltpan</b>	3%	2%	16%
<b>Grassland</b>	41%	56%	72%
<b>Scrub</b>	32%	25%	7%
<b>Savannah</b>	17%	13%	5%
<b>Woodland</b>	8%	4%	0%
<b>Bare Earth</b>	0%	1%	1%
<i>Percentage Similarity</i>	100%	84%	55%

## **Discussion**

There is little convincing evidence for a change in niche breadth associated with changes in prey abundance. However, lions specialised on migratory prey and killed less livestock and resident prey when migrants were most abundant, as might be predicted by a simple rate maximising model (Krebs *et al.*, 1977; Pyke *et al.*, 1977). When migratory prey moved away lions killed resident wild prey more frequently than livestock despite livestock being most abundant. While lions did increase the frequency with which they killed livestock during lean periods, it was never killed more frequently than proportional to its abundance. In comparison wild migratory prey and resident prey was killed more frequently than proportional to abundance estimates during good and lean periods respectively. Even so, most kill incidents were still made up of livestock during lean periods, probably because of their preponderance within abundance estimates in the zones at these times. The impact of this predation on local herders would be exacerbated by an increased likelihood of livestock kill incidences involving surplus killing.

Lions in the Makgadikgadi changed their movement patterns with changes in wild prey distribution. Non stock-raiders did not move noticeably closer to cattleposts during periods when wild prey migrated away but tracked movements of the migratory ungulates and by doing so utilised larger areas than stock-raiding lionesses. In contrast stock-raiding lions (males and females) moved closer to cattleposts during lean periods; making more frequent and closer approaches, and spending more time within livestock areas than they did during good periods. These data indicate that observed changes in livestock predation rates resulted from both changes in prey abundance and changes in lion foraging behaviour in response to these changes. Night ranges of stock-raiding lions were significantly closer to cattleposts and livestock areas than they were during the day, revealing diurnal movements away from cattleposts and nocturnal movement towards them. As such we caution against the assumption that spatial data gathered during the day is necessarily representative of stock-raiding lion space use.

While we have measured abundance, we suggest that lion predation responds to abundance only in that it is a component of availability. Indeed availability is likely to be a combination of abundance, vigilance, speed, detectability and the degree to which finding, catching, killing or eating a prey item represents a risk to the predator. In practice it is difficult to measure or estimate different availabilities per unit abundance of ungulate species and currently impossible to adjust these values for different predator species (i.e. buffalo might be less available to cheetahs (*Acinonyx jubatus*) than to lions for example). As such an implicit assumption in studies where preference or selection is inferred from abundance e.g. (Honer *et al.*, 2002; Karanth & Sunquist, 1995) is that all wild prey is equally available per unit abundance. While this may be true, we have no specific data to suggest this is the case in this study.

While it is probably correctly assumed that livestock is inherently more available per unit abundance, being slower and less vigilant etc than wild prey (Kruuk, 1972), they are protected by people who present a risk to predators. We can make semi-quantitative estimates of how protection might influence availability from indirect measures;

- We estimated that 13-20% of cattle were stray at night (Hemson *et al.*, submitted-a)

- Only 20% of reported livestock predations occurred during the day when lion movements were also minimal and livestock was un-herded away from settlements (Hemson *et al.*, submitted-a)
- At least 8 of 10 adult lions that died during the study were stock-raiders killed by herders (the remaining two were also stock-raiders and died in suspicious circumstances).

However, we have no way of quantifying other contributions such as the spatial and temporal predictability of livestock movements and their increased vulnerability may have on availability. Any tests or predictions based on estimates of these values would be unsound and we feel it more informative to concentrate on the changes in predation frequency between periods of different prey abundances while availability per unit abundance remains constant. For example zebra availability may not be quantifiable but by assuming it is constant per unit abundance throughout the study (not unreasonable) we can use changes in predation frequency to imply changes in prey selection.

Livestock predation frequency changed between periods of different prey abundance whilst herding effort did not (Hemson *et. al.*, submitted-a), and we can thereby say that Makgadikgadi lions did select livestock more frequently when wild prey was relatively scarce than when it was very abundant. These results demonstrate that changes in the relative abundances of livestock and wild prey can alter the amount of livestock killed disproportionately to the magnitude of the changes in abundance. An increase in the relative abundance of livestock results in both an increase in the proportion of livestock in the environment, and an increase in the frequency of livestock kills per unit abundance (kill intensity) (an increase in RFR in figure 3). If a trebling of relative abundance of livestock causes the frequency of its use per unit abundance to increase by approximately 2.5 times, as in this study, then approximately 7.5 times as much livestock is then killed. Similarly increases in wild prey abundance result in an increase in the kill intensity on wild prey relative to livestock, resulting in a decline in livestock predation out of proportion to the relative increase in wild prey. Available data suggests that other predators may follow a similar pattern of livestock utilisation e.g. wolves (Meriggi & Lovari, 1996), tigers (Bagchi *et al.*, 2003) and cheetah (Marker *et al.*, Submitted).

Contrary to our hypothesis, stock-raiders had smaller home-ranges when wild prey was scarce than they did when wild prey was abundant. During lean periods non-stock-raiders temporarily emigrate, resulting, if anything, in a reduced potential for competition and arguing against the hypothesis that range contraction was a response to increased competition for space. Instead we suggest that by moving closer to cattleposts and predating more intensely upon livestock, stock-raiding lions use a resource (livestock) that is less temporally and spatially dispersed than wild prey.

Stock-raiding behaviour appeared to be a trade off between the need to find food and the risks associated with livestock predation. Similar to Laikipia, Kenya, where more predators were killed in areas of high livestock losses (Ogada *et al.*, 2003) all adult lion mortality recorded during this study were stock raiders. One died of unknown causes outside the park, another disappeared despite being fitted with a collar (we assume the lion was killed and the collar destroyed) and the remainder were all killed by herders. Lions were either trapped and the shot, shot without restraint or poisoned. Observations suggest that movements away from largely uneaten kills, occurred before lions were disturbed by herders; a strong indication that the lower consumption of livestock carcasses, compared with wild prey kills, may be a result of premature carcass abandonment to minimise human encounter rates.

Stock-raiding lions responded to both the movements (Figures 5a-5b) and distribution of livestock (Figure 7). They moved away from cattleposts before 06:00 (Figure 6) and rarely rested within 1km of them during the day, again suggesting that they respond to the risks of encounter with herders as well as livestock movements. Stock-raiders spend most of their days relatively close to human habitation (2km - 6km) during lean periods, apparently without being discovered by local people. It may be that they do this to increase the probability of encountering livestock. Indeed the habitats in which livestock kills were discovered were most similar to those used by cattle during the day. An alternative interpretation of these data is that these lions killed livestock during the night in habitats that cattle used most frequently during the day. However, 22% of 137 kill incidents reported by herders occurred during the day. Findings from Laikipia, Kenya, are similar in that a proportion of livestock kills are

made during the day (Frank, 1998a; Hemson *et al.*, submitted-a). It is probably reasonable to assume that while daytime predations do occur most still occur at night.

One view of stock herding in Botswana is of a “rather *laissez faire* system of livestock husbandry” with herds “allowed to roam free, with little, if any direct supervision” (Wint, 1997). This view resonates with our own data which indicate that 94% of a recent sample of 51 livestock herds were not attended by a herder and 97% of interview respondents stated that livestock was not tended during the day (Hemson *et al.*, submitted-a). This strategy similar to the approach adopted by the Ju/Hoan people of Namibia (Stander, 1997), would appear to explain the availability of livestock at night that we recorded.

Lions became most active at night. Stock-raiders spend most time between 1 and 6km from cattleposts within the radius that livestock used. The centre of this activity shifts from 3-4 km during the first part of the night (pm) to 1-2km in the early morning (am). Peak distance moved per hour was associated with a rapid increase in distance from cattleposts between 05:00 and 06:00. Taken together these data suggest most frequent approaches after midnight when it is most likely that cattleposts resident were asleep and a rapid retreat away from these areas before dawn when human activity would increase.

Our observations suggest a trade off between the risks of starvation and the risks of anthropogenic mortality. Unlike lions in Laikipia, that kill most livestock after stampeding them from kraals at night, Makgadikgadi lions behave more similarly to Kenyan spotted hyaenas, killing stock away from their enclosures (Frank, 1998a; Kruuk, 1980; Ogada *et al.*, 2003). Livestock kill data suggests that most kills do not occur within 1km of cattleposts, as they would be if predation occurred in or near the cattleposts. Instead they are further away in areas most frequently used by lions in the evening and day. Indeed, 84% of 139 kill incidents reported during interviews with herders were reported to have occurred away from the kraals (Hemson *et al.* submitted-a). Even this is likely to be a conservative estimate, as kills away from the kraal imply inadequate vigilance that herders would probably try to hide from us. Why then do the habits of Makgadikgadi lions differ from those in Laikipia?

Makgadikgadi lions probably do not approach human habitation as frequently as Kenyan lions, as livestock are available in areas where the risks of human disturbance are reduced. If they cannot find stray livestock in areas away from centres of human activity, it seems likely that lions would only then have to approach cattleposts and expose themselves to anthropogenic risks. Even then it seems likely that they would hunt unenclosed stock adjacent to kraals in preference to those in kraals. On occasion we observed lions visiting several cattleposts in quite rapid succession before killing livestock unenclosed in kraals. The higher frequency of approaches in the early morning during lean periods may reflect attempts to locate livestock that have returned too late to be enclosed. Our findings do not imply that static defences are not important generally but that in Botswana at least, herding practices need to be examined before or alongside reinforcement of static defences (Hemson *et al.*, submitted-a).

It does not seem unreasonable to suggest that each prey type has a perceived profitability associated with it (equation 1).

*Equation 1: Perceived Prey Profitability, where  $E_i$  = potential energy gain,  $p_i$  is the proportion of  $E_i$  that can be consumed,  $S_i$  is energy used searching for the prey,  $K_i$  is the energy used killing it and  $R_i$  is a measure of the probability and consequences of the risk associated with foraging for the  $i$ th prey type.*

$$\text{Perceived Profitability}_i = (E_i p_i) - (S_i + K_i) - R_i$$

We can speculate that while altering abundance will affect the energy used locating prey, it may also be altered in other ways (Stephens & Krebs, 1986). Increases in the number of herders per unit abundance and the vigilance of these herders would decrease the proportion of stock wandering untended, and will increase  $S_{\text{livestock}}$  by increasing time spent searching for or waiting for untended livestock and may also increase the risk of anthropogenic mortality associated with livestock predation ( $R_{\text{livestock}}$ ) (assuming that the risk associated with killing stock is from retaliation by stock owners/herders (Ogada *et al.*, 2003)). That livestock kills are abandoned faster than wild prey kills and that the amount of a kill consumed is positively correlated

with distance from cattle posts suggests that lions may be reacting to the risks associated with killing livestock and proximity to people (see also (Kerley *et al.*, 2002). The risk of retaliation should not change in absolute terms as a lion's risk of starvation increases, we would thus expect the risk of being killed would decrease relative to the risk of starvation and that lions would take more anthropogenic risks. While not conclusive the movement data from GPS-collared lions suggests stock-raiding lions use a strategy which minimises human encounter rates during good periods but trades increased chance of livestock stock encounter with minimising the chance of human encounter during lean periods. That Makgadikgadi lions appear to take more risks by killing livestock more frequently when food is scarcer, appears to bare out the predictions of this speculative qualitative model.

To reduce livestock loss, the availability of livestock relative to the availability of wild prey should be reduced. Methods of achieving this can logically be separated into at least three overlapping causes;

- 1) Decreasing availability of livestock through the physical separation of lions and livestock in space and time.
- 2) Increasing the risks associated with predating upon livestock to discourage lions.
- 3) Reducing the absolute abundance of livestock in an area by reducing stocking levels.

The first category might be attained by improving static defences at the cattleposts to keep lions away from enclosed livestock at night (Ogada *et al.*, 2003) and/or improving herder vigilance while the animals are grazing. Both may in turn increase the risk that lions may perceive as associated with livestock and reduce the probability that a lion will kill livestock when encountered. However a less direct approach may also help.

Data from Botswana suggests that while smaller ungulates may persist in fairly close proximity to human habitation, larger species most often preyed by lions may not, and that hunting/poaching may play a role in this (East, 1999; Thouless, 1998; Verlinden *et al.*, 1998). Large wild herbivores, including large grazers, can coexist alongside livestock production (Homewood & Rogers, 1991) and it seems probable that browsers such as kudu could do better yet if not killed by people and domestic



dogs (*Canis familiaris*)(Fritz *et al.*, 1996). Kudu diet suggest they would not compete directly with predominately grazing livestock and that they could benefit from browse species associated with bush encroachment commonly linked with livestock production in Botswana (Fritz *et al.*, 1996; Perkins & Thomas, 1993; Ringrose *et al.*, 1996; Smithers, 1983; Verlinden *et al.*, 1998). If so, reducing hunting pressure on populations of these species in areas of high human/lion conflict may yield significant reductions in livestock predation rates. It should be pointed out that an overall increase in total prey availability may also result in a longer term increase in the predator population that might otherwise negate any short-term improvement stock predation rates. As such any rises in resident wild prey abundance should ultimately be matched by reductions in livestock availability.

In certain circumstances where reducing the availability of stock is not possible due to political, and/or sociological limitations; it is conceivable that encouraging local people not to kill wild prey species that might otherwise compete for the attentions of potential livestock predators may make an effective alternative. This would require community complicity in implementation and more importantly policing to avoid a tragedy of the commons type scenario (Hardin, 1968). If these efforts proved successful in reducing stock loss in the eyes of the local community, conservation implementers may find interventions that might require more active community participation, received with more enthusiasm. We argue that if a method is not likely to reduce the availability of livestock relative to alternative wild prey or increase the relative availability of resident wild prey then it will not directly address the cause of livestock predation.

### **Males & Females; Movements and Vulnerability**

It has been reasoned that species with large ranges have a significantly higher probability of going extinct in a protected area of a given size (Brashares, 2003; Woodroffe & Ginsberg, 1998, 2000). To explain this we suggest that there are positive correlations between range size and the probability of encountering stock and between the frequency of livestock encounter and the probability of becoming a stock-raider. Ultimately these stock-raiders suffer higher mortality than non-stock-raiders (Frank, 1998a; Ogada *et al.*, 2003; Rabinowitz, 1986) and lion populations are

reduced. While our data show that stock-raiders have smaller ranges than non-raiders, we argue that the ranges we observed were smaller because these animals were already stock-raiders. As stock-raider ranges periodically become vacant when lions are destroyed, other lions may move in and also become stock-raiders. To test the hypothesis one would have to measure an animal's range size before and after it moved into one of these vacant ranges and became a stock-raider. As an example a pride exterminated for stock-raiding in 2000 has subsequently been replaced with lions that appear to have moved out from the core of the park and have now been observed to kill livestock.

We propose that this same logic might well be extended to the widest ranging sex within a species, usually males, e.g. black bears (*Ursus americanus*), jaguars (*Panthera onca*), leopards (*Panthera pardus*), tigers (*Panthera tigris*) and lions (Clutton-Brock, 1989; Dahle & Swenson, 2003; Nowell & Jackson, 1996; Powell *et al.*, 1997; Rabinowitz & Nottingham, 1986; Stander *et al.*, 1997). In the Makgadikgadi, adult males occurred at a lower density (1/1000km<sup>2</sup>) than females (1/250km<sup>2</sup>), moved twice as far as females and despite being stock-raiders had significantly larger home-ranges than stock-raiding females and slightly larger ranges than non-stock-raiding females. Adult males were three times as likely as adult females to be problem animals in Etosha (Stander, 1990). In the Makgadikgadi, all adult males (n=7 in three coalitions) were stock-raiders and had home-ranges that overlapped with cattleposts and as such were exposed to a risk of being killed by people (n=3 killed during study).

It seems possible, therefore that males (which generally have larger ranges and occur in smaller groups), may be more likely to become stock-raiders and be killed than females. Male mortality should reduce inter-male competition for space and females, potentially resulting in range expansion and access to more groups of females for the remaining males (Adams, 2001; Yamazaki, 1996). That large ranges may result in mortality which may in turn result in further range expansions would seem to constitute the basis of a positive feedback loop that could result in disruption of lion society. Indeed it has been reasoned that a high turnover of adult males will result in increased juvenile mortality and male bias in cub sex-ratio (Anthony & Blumstein, 2000; Pusey & Packer, 1987; Whitman & Packer, 1997). In the Makgadikgadi 10 of

14 known cub mortalities were due to abandonment or infanticide following a pride take over and cub sex ratio was 1♀:1.75♂ (n=22).

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## **Chapter 2: Socio-economic aspects of lion-human conflict in Botswana.**

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“Socio-economic aspects of lion-human conflict in Botswana.”

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### **Summary**

Lions (*Panthera leo*) are a considerable problem for livestock owning people living near protected areas throughout Africa. Around the Makgadikgadi Pans National Park in Botswana, people nearest the park had the highest losses and the most negative attitudes towards wildlife, conservation and particularly lions. Losses did not appear correlated with the size or structure of livestock enclosures, numbers of dogs or herders. Rather, relaxed herding resulted in a high proportion of strays at night that reduced the need for stock raiding lions to approach habitation thereby circumventing any potential role of static defences in limiting stock loss. Although four tourist camps were operating in the area, benefits from these operations were largely limited to employees who made up a small sub-section of the adult population. In contrast the costs of livestock loss were spread across many livestock owners. Consequently few people felt that they or their community benefited from tourism but stated that government was the main beneficiary. It appeared that this belief was so strong that they were not prepared to act independently to improve stock care, but instead implied they would do so only if the government assisted them.

### **Introduction**

In many parts of the world predation of livestock by large carnivores (>10kg) and crop damage by herbivores causes considerable conflict between people and wildlife

(Kangwana & Mako, 2001; Mills, 1991; Newmark *et al.*, 1993; O'Connell-Rodwell *et al.*, 2000; Weber & Rabinowitz, 1996). Conflict between carnivores and man is a threat to local carnivore populations, a factor limiting carnivore meta-population viability and a cause of anti-wildlife/conservation sentiment that can undermine other, potentially unrelated conservation initiatives (Kiss, 1990; Sillero-Zubiri & Laurenson, 2001).

Many wildlife/conservation institutions are looking towards increasing the area over which local people are able to coexist with large carnivores, through reducing conflict, increasing tolerance of conflict and/or making wildlife management and enforcement institutions more effective (Linnell *et al.*, 2001; Mills, 1991; Sillero-Zubiri & Laurenson, 2001). By doing so, animal populations separated by land utilized predominately for livestock or agriculture may be able to establish contiguities thereby minimizing the probability of being affected by the deleterious consequences of population isolation such as inbreeding (Maehr & Caddick, 1995; Maehr *et al.*, 2002; Mansfield & Land, 2002; Michalski *et al.*, 2001) and vulnerability to stochastic disaster events e.g. (RoelkeParker *et al.*, 1996).

Whilst addressing the patterns and causes of livestock predation, with the aim of reducing its frequency, is one approach to reducing this conflict e.g. (Frank, 1998; Hemson *et al.*, submitted-a; Hemson *et al.*, submitted-b; Marker *et al.*, Submitted; Stander, 1990), conservation efforts have increasingly been directed into the human dimension. By doing so conservation hopes to explore and increase community tolerance for large carnivores and encourage communities to reduce their losses to carnivores without unsustainable offtake from carnivore populations (Baker & Macdonald, 2000; Macdonald & Sillero-Zubiri, In press; Marker *et al.*, 2003; Sillero-Zubiri & Laurenson, 2001). By stressing the potential for revenues generated from wildlife to contribute to local economies it is hoped that these economic incentives will create or increase a desire to manage local wildlife sustainably (Giannecchini, 1993; Hackel, 1999; Kiss, 1990; Shogren *et al.*, 1999). This approach, synonymous with the phrase “if it pays it stays”, is both logical and appealing, particularly to donor agencies and NGO's, stung into change by accusations of neo-imperialism that often go hand-in-hand with the dismissal of preservationist approaches known colloquially as “Fortress Conservation” (Brockington, 2002; Hulme & Murphee, 2001b). Indeed

“the success of any community-based wildlife utilisation plan will depend on ensuring that individuals derive benefits from conservation and sustainable management of the resource”(Kiss, 1990).

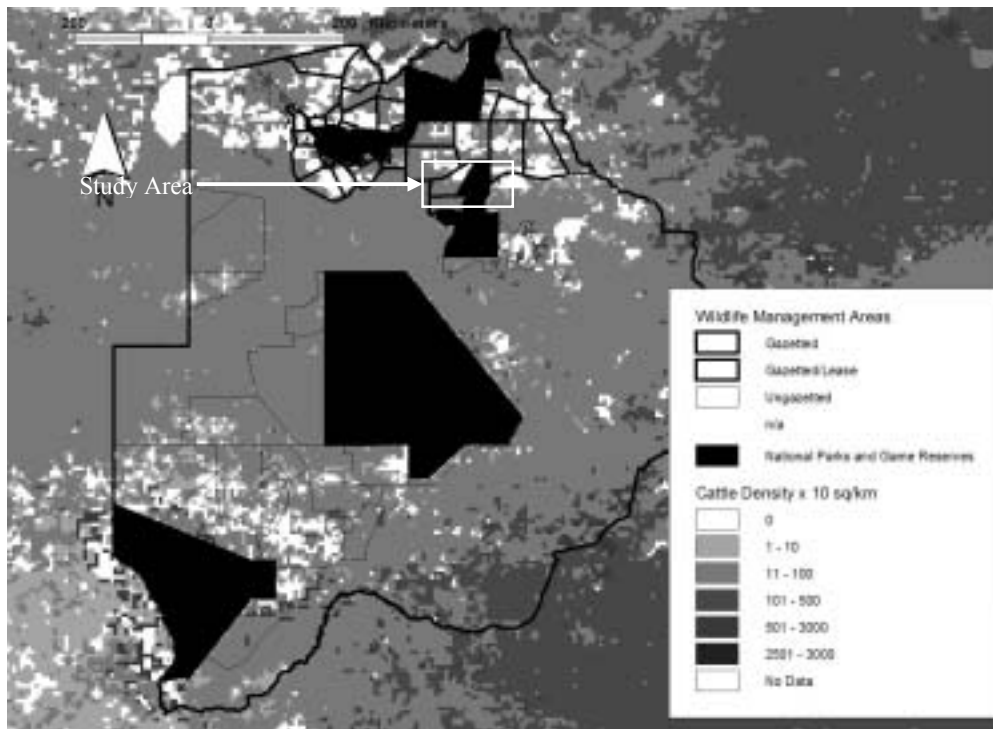
Botswana has impressive conservation credentials, with over 18% of its surface set aside as protected area, and a further 21% gazetted as wildlife management areas (WMA) and controlled hunting areas (CHA) (multiple use areas often buffering formal protected areas)(Lawson & Mafela, 1990). Nationally, population density is low (2.8 people km<sup>2</sup>) and lower still in the settled areas within the study area (1 person/km<sup>2</sup>) (Botswana Central Statistics Office Data); suggesting there is potential for larger species of wildlife to coexist with people (Newmark *et al.*, 1994). However, livestock have a high traditional and economic value to most rural citizens of Botswana (Batswana) (Twyman, 2001) and are widespread throughout the country (Figure 1). Unusually, livestock outnumber people in Botswana with approximately two tropical livestock units for every person in the country (Botswana Central Statistics Office Data).

In the east of the country, rural livelihoods are derived almost entirely from livestock and agriculture. In the west, where wildlife is most abundant (Wint, 1997), alternatives such as sport hunting, game ranching, veld products and photographic tourism within the WMA network (Fig 1), are being promoted by the government to diversify rural economies in an attempt to bring conservation and development into a more synergistic coexistence (Lawson & Mafela, 1990; Rozemeijer, 2003).

Despite state support and a healthy tourism industry, conservation success of the community based natural resource management program (CBNRM) in Botswana has been limited. Although revenues derived by some communities have been considerable e.g. (Bolaane, 2000; Rozemeijer, 2003), conservation goals do not appear to have been universally advanced. Indeed one observer suggests that “there is no substantial evidence that poaching in community-managed areas has diminished and that land use patterns in resource-rich areas have changed to the benefit of wildlife” (Rozemeijer, 2003). While globally, community conservation can boast some successes e.g. (Western, 1989)(see also (Lyndsay, 1989)), substantial proof of

the successes of community conservation have proved elusive even within projects synonymous with the approach, such as CAMPFIRE (Hulme & Murphee, 2001a).

*Figure 1: The study area, cattle distribution, protected areas and wildlife management areas in Botswana.*



We studied both patterns and causes of livestock predation in the Makgadikgadi Pans area of Botswana (an area well known within Botswana as a conflict hotspot) (Hemson *et al.*, in prep-a; Hemson *et al.*, in prep-b) and investigated the attitudes of local herders, villagers and tourism employees towards wildlife, lions, conservation and the current efforts to control stock loss. We wanted to see how kraal structure, numbers of herders and other static defences affected livestock predation, and assess how local tourism ventures, livestock predation, park regulations and government policies affected attitudes and perceptions of the costs and benefits associated with living near the Makgadikgadi Pans National Park. We anticipated that tourism would act, through revenue and opportunity generation within the community, to increase the incentives to tolerate the presence of valuable problem species, in this case lions, and the local protected area as a reservoir of economic potential.

## **Methods**

The study was conducted in and around the 4,900 km<sup>2</sup> Makgadikgadi Pans National Park in Northern Central Botswana (centred on South 20° 26' East 24° 45') between January 1999 and October 2003 and interviewed people between May 2001 and September 2003. The study area is semi-arid, falling between the 250mm and 450mm rainfall isohyets, with rainfall predominately during the summer, or hot-wet season, between November and April (Thomas & Shaw, 1991). The park is surrounded on approximately 75% of its boundary by controlled hunting areas predominately used for livestock rearing by local people (over 100 cattle posts (small family livestock farms) and 4 villages) (Hemson *et al.*, in prep-a). The remaining boundary area borders on very open uninhabited salt pan in the south and east, or joins with the Nxai Pan National Park to the north. The western boundary of the national park follows the course of a dry riverbed (Boteti) with scattered permanent pools concentrated in the northern half of its adjacent length. Inside the study area were four photographic safari operations; two in the east and two in the west and commercial big game hunting was not allowed in any part of the study area. The lion population in the area was small (32-41 adults and sub-adults) and subject to seasonal bouts of persecution associated with movements of migratory prey. As an example during the wet season of 2000 while migratory wild prey had moved east, 8 lions were killed by stock owners or their employees in the west.

Cattleposts, safari camps, larger villages, and the national park and the wildlife department (DWNP) camps in the study area were mapped into a GIS with which spatial information such as distances of cattlepost from nearest village; safari camps and national park were calculated using ArcView 3.2 (ESRI 1992). Cattleposts, villages and safari camps were visited and people living therein interviewed. Where possible, the head person of a cattlepost (defined here as the person in charge of the cattlepost) was interviewed, to best represent the most influential opinion at that location. The interviewee was asked if he/she was willing to take part in the survey and if he/she agreed, a series of scripted questions were asked and answers recorded verbatim using a Setswana translator. As questions were generally quite specific e.g. "Do you like living near the national park?" "Do you think lions are an important tourism resource?" it was possible to classify answers into similar or identical groups

of answers which could then be given numeric states (e.g. 1= yes and 2 = no) to facilitate statistical analysis. Often a simple yes/no answer was followed by a question requesting qualification of this answer e.g. “Why do you (not) like living with lions?” and answers grouped into similar classes of answer e.g. 1 = answers relating to livestock loss, 2= answers relating to the tourism value of lions, 3 =answers relating to the aesthetic or existence value of lions etc. Quantitative data on details of livestock ownership, sales and losses and other socio-economic data were also collected. Numbers of livestock, structure and construction of kraals, numbers of dogs, herding techniques, numbers and ages of herders and other factors were measured so that we might model the effects of various strategies on reducing predation rates. Answers that demonstrated the respondent did not comprehend the intended meaning of the question were excluded from the analysis as were questions which individuals did not want or feel comfortable answering or those irrelevant to the respondent e.g Q, “Do you like living near lions?” A, “I don’t live near lions”. While we did interview expatriot staff working in the camps, we did not feel their views were reflective of the local community’s and the sample size was very small (n=7). Detailed questions relating to livestock husbandry were limited to cattlepost residents.

Local and national population sizes, economic and demographic trends were extracted from the Botswana government’s Central Statistics Organisation website (<http://www.cso.gov.bw/cso/index.html>) and correspondences with statisticians within that institute. All statistical analyses were undertaken using Minitab 13.31 (Minitab Inc 2000).

2001 census data indicated that the local populations of Gweta, Moreomato and Khumaga (the three main villages) and surrounds were 6,653, 671 and 1,252 respectively (8,576 total) with an annual population growth estimated at between 2% and 3.1% (national average = 2.39%) Approximately 42% of rural Batswana are under the age of 14 and 55 % below the age of 19 (Botswana Central Statistics Organisation). As such the adult (over 16 years of age) population in the study area is probably close to 4,200. We estimated that 80-100 Batswana staff worked in the camps, the majority of which were from the local community.



## Results

An average cattlepost in the Makgadikgadi was 5.1 km from the national park (range 0.2km-22km) and had 3.9 people (1.9 children, 1.4 other family and 0.5 employees), 63.5 cows, 23.2 goats, 1.5 horses, 4.1 donkeys, 17.2 calves and 3.2 dogs living at it. 85 cattlepost residents (each from a different cattlepost), 55 tourism employees, and 76 villagers were interviewed.

There was considerable variation in the value of livestock owned per cattlepost. The majority of herds were less valuable than the mean due to the influence of a few very large herds. Of 86 cattleposts visited and interviewed 7% had no livestock. Of the remainder 69% sold livestock, 24% lost livestock to disease, 55% had livestock stolen and 65% lost livestock to lions in the past year (Table 1). If cattleposts without losses were excluded from calculations to establish the mean values of losses actually experienced by those that incurred losses, the mean value of livestock lost to lions was US\$ 647.0, disease US\$ 847.3 and US\$ 848.5. The perhaps surprisingly high cost of disease was skewed by a single loss of US\$ 13,112.8. Losses to lions were most widespread and totalled approximately US\$ 24,000 per annum as compared to \$62,000 in sales, US\$ 40,000 from disease and US\$ 14,000 through theft.

*Table 1: The value of livestock owned, sold and lost to theft, disease and lions per annum and the distribution of these losses across the community.*

Value of	Mean (StDev)	Median (Range)	Of 86 cattleposts
Livestock Owned	US\$ 14,119 (21,617)	US\$ 7,061 (634,650 - 0)	6 no livestock
Stock Sold	US\$ 716 (1555)	US\$ 176 (8815 - 0)	31 no sales
Losses to Disease	US\$ 482 (1,523)	US\$ 47 (13,113 - 0)	67 no losses
Losses to Theft	US\$ 172 (430)	US\$ 0 (2,435 - 0)	42 no losses
<b>Losses to Lions</b>	US\$ 283 (592)	US\$ 95 (4,528 - 0)	34 no losses

We attempted to predict the value of livestock lost to predation from lions from a series of continuous attributes of cattleposts that might contribute towards static defence (number of herders, number of dogs, distance from national park, value of stock owned etc) using principal components analysis and a multivariate GLM. None of the principal components from the PCA predicted stock loss with any reliability. In the final GLM, loss to predators was significantly negatively correlated with distance to national park (Coef -US\$82 per km further from the national park  $p=0.024$ ) and positively correlated with the value of stock owned (Coef US\$0.09 per US\$ stock owned  $p=0.024$ ). The final model however, explained only 14% of the variation observed. Sales were significantly correlated with total value of stock ( $r^2=42.0\%$   $p<0.0001$ , US\$ Sales =  $20 + 0.0493$  US\$ Stock Owned).

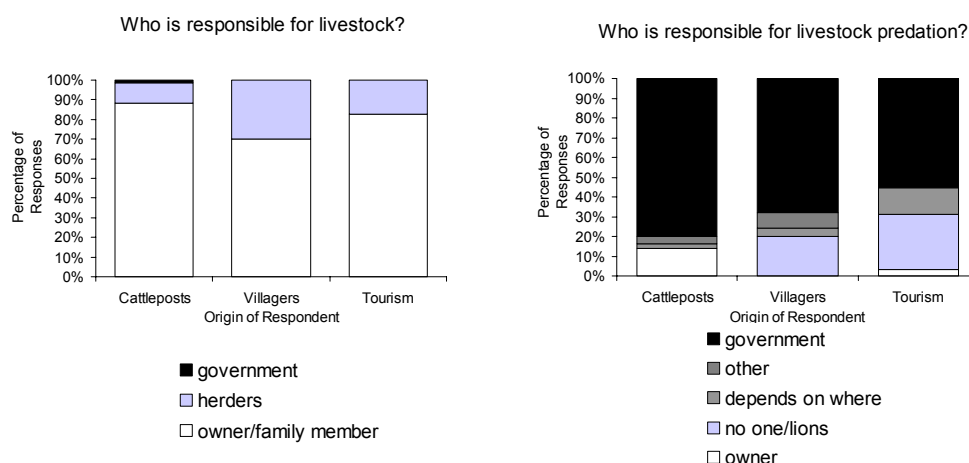
97% of all respondents ( $n=168$ ) stated that livestock was let out from the kraals in the morning and left untended all day. 81% of respondents that gave further detail on herding practices ( $n=84$ ) stated that they did not fetch stock in the evening but waited for it to return to the cattlepost in the evening. Only 3% reported that they herded their livestock throughout the day. The mean amount of livestock left out at night as estimated by respondents ( $n=173$ ) was 13%. Losses to lions were predominately reported as occurring away from the cattleposts (117 stock kills occurred away from the kraals and 22 inside) and at night (107 at night and 30 during the day). The mean time that cattleposts residents thought it took them to notice that an animal was missing was 1.1 days (SD 3.4 days). Subsequent to noticing 73% would search on foot, 6% on a donkey, 20% on a horse and only 1% using a car.

Only 15% of cattlepost respondents ( $n=85$ ), 22% of village respondents ( $n=49$ ) and 53% of tourism respondents ( $n=51$ ) stated that they wanted to improve their herding methods to reduce stock loss. However, 56% of cattlepost respondents ( $n=85$ ) thought that building a sturdy kraal for livestock to use at night would help. 86% stated that if increased compensation payments were linked to DWNP evaluations of their own herding vigilance and static defences that they could improve these, and 85% said they could improve herding vigilance and kraal structure if the government would invest in improvements with them.

A bigger proportion of staff of safari camps said that they did like living near the national park than both cattlepost ( $\chi^2_{[1]}= 12.51$   $p<0.0001$ ) and village residents ( $\chi^2_{[1]}= 4.23$   $p=0.04$ ) and less cattleposts respondents than village respondents said the same ( $\chi^2_{[1]}= 12.51$   $p<0.0001$ ) (table 1). 132 respondents could tell us why they did not like living near the park (2 did not know). Of these 101 cited stock losses to predators as their reason, 14 grazing restrictions and competition and 10 restrictions on access. 43 said they liked living near the park because they valued the park's aesthetic qualities and only 16 respondents said that they liked living near the park because of the improved chances of employment in tourism.

Whilst most respondents in all groups stated that owners, family or employed herders were responsible for livestock (Figure 2), they generally assumed that the government or DWNP was responsible for controlling livestock predation (Figure 3) with 65% of all respondents ( $n=152$ ) stating this was because the government was responsible for wildlife and problem animals. Suggestively, 5% stated that by banning them from killing lions, the government had incurred this responsibility. Tourism employees blamed the government least often and cattlepost respondents most often. Tourism employees were the only group to regularly state that stock, killed inside the park, was the owner's/herder's responsibility for letting it stray ("depends on where" response in figure 2).

*Figure 2a and 2b: Proportions of respondents from each category and responses to the question of "who was responsible for livestock?" and "who was responsible for livestock loss?"*



While we expected a negative correlation between distance to national park and frequency of dislike for living with lions; the very high frequency of this attitude among cattlepost residents precluded us from being able to test for this (Table 1). Dislike of living alongside lions was less common in tourism employees than in both villagers ( $\chi^2_{[1]} = 13.048$ ,  $p < 0.001$ ) and cattleposts residents ( $\chi^2_{[1]} = 27.804$ ,  $p < 0.001$ ) and non-significantly less common in villagers than cattlepost residents ( $\chi^2_{[1]} = 1.805$ ,  $p = 0.179$ ).

There was no statistical evidence that people in any group of respondents were more likely to say they did not like lions if they had lost stock in the last two years or vice versa. Tourism employees were least likely and cattlepost residents most likely to say that they had tried to kill lions. Of 171 respondents from all backgrounds, 65% had lost livestock to lions in the last two years and 21 stated that they had attempted to kill lions and several more added later that they were willing to try, but that they presently did not have the guns or traps to do so. Of those that had tried 67% said they had using a gun and 33% using traps; poisoning was not mentioned despite one and possibly two incidences during the study (pers obs). Despite widespread losses only 19 respondents (n=208) said they had killed lions in the past. It should be stressed that respondents were probably less likely to say they had attempted to kill lions as they may have known that we were lion researchers and because the killing of lions had been banned shortly before the questions were asked.

*Table 2: A comparison of some key answers provided by different groups in the study area.*

Question	Respondent	N	$\chi^2$	% Yes	%No	%Don't Know
Do you like living near the national park?	Cattleposts	85	$\chi^2_{[2]}=29.27$ P<0.001	<b>15.3</b>	<b>84.7</b>	<b>0</b>
	Villagers	69		<b>39.1</b>	<b>56.5</b>	<b>4.3</b>
	Tourism	52		<b>59.6</b>	<b>40.4</b>	<b>0</b>
Do you like living with lions?	Cattleposts	85	$\chi^2_{[2]}=34.73$ P<0.001	<b>5.9</b>	<b>94.1</b>	<b>0</b>
	Villagers	57		<b>12.3</b>	<b>87.7</b>	<b>0</b>
	Tourism	51		<b>43.1</b>	<b>56.9</b>	<b>0</b>
Have you ever attempted to kill a lion?	Cattleposts	85	$\chi^2_{[2]}=9.2$ P=0.010	<b>17.6</b>	<b>82.4</b>	<b>0</b>
	Villagers	71		<b>7.0</b>	<b>93.0</b>	<b>0</b>
	Tourism	50		<b>1.9</b>	<b>98.1</b>	<b>0</b>
Are lions valuable to the tourism industry?	Cattleposts	85	$\chi^2_{[2]}=9.0$ P=0.011	<b>80.0</b>	<b>18.8</b>	<b>1.2</b>
	Villagers	48		<b>89.6</b>	<b>8.3</b>	<b>2.1</b>
	Tourism	55		<b>96.4</b>	<b>1.8</b>	<b>1.8</b>
Does Botswana benefit from tourism?	Cattleposts	84	$\chi^2_{[4]}=9.71$ P=0.046	<b>84.5</b>	<b>11.9</b>	<b>3.6</b>
	Villagers	47		<b>80.9</b>	<b>2.1</b>	<b>17.0</b>
	Tourism	41		<b>82.9</b>	<b>7.3</b>	<b>9.8</b>
Does your community benefit from tourism?	Cattleposts	85	$\chi^2_{[4]}=20.59$ P<0.001	<b>25.9</b>	<b>67.1</b>	<b>7.1</b>
	Villagers	43		<b>36.7</b>	<b>36.7</b>	<b>26.5</b>
	Tourism	49		<b>48.8</b>	<b>32.6</b>	<b>18.6</b>
Do you benefit from tourism?	Cattleposts	85	$\chi^2_{[4]}=36.15$ P<0.001	<b>12.9</b>	<b>84.7</b>	<b>2.4</b>
	Villagers	50		<b>6.0</b>	<b>90.0</b>	<b>4.0</b>
	Tourism	42		<b>52.4</b>	<b>45.2</b>	<b>2.4</b>

When asked what the government could do to reduce livestock loss the most frequent reply (61% of 173 respondents) were that they could erect a fence between their grazing areas and the national park to prevent predators from mixing with livestock. Most of the remainder asked that they killed lions (16%) although this was suggested least frequently by tourism employees. Cattleposts respondents (n=83) were frequently (82%) not happy with the existing compensation scheme and of these (n=67) 94%, perhaps predictably, wanted more money, 3% replacement livestock instead of money and 3% the system speeded up. Compensation for losses of pedigree animals in Botswana is based on 80% of the market value of that animal. While livestock value is affected by inter animal, seasonal and market variations it appears

that non pedigree animals are compensated at a similar rate. 33% of incidents reported by cattlepost respondents had not been reported for compensation and 21% of those that were, were unsuccessful. Farmers often did not claim for compensation as livestock were killed inside the national park and legislation restricts compensation to losses occurring outside protected areas (DWNP, 1998; Sechele & Nzehengwa, 2002). Indeed despite being illegal a few farmers admitted that the park had better grazing than the area adjacent to it and that they allowed their livestock to graze there. We estimate that each cattlepost only recoups approximately 42% of the value of stock that is lost to lions and each cattlepost is therefore losing, on average US\$ 168 per annum to lions alone. As losses are not spread homogenously across the population some lose more while others will not lose at all.

Other suggestions included translocation of lions to other areas, herding or kraaling lions and government investment in better kraals or water provision for livestock (animals in the west frequently drank at water holes shared with wildlife in the river bed (some containing large crocodiles (pers obs)). Despite the popularity of the fence there was some acknowledgement that it would reduce grazing for some people (46% of 85 cattlepost respondents) and would probably be broken by elephants (81% of 83 cattlepost respondents). Despite this cattlepost respondents were generally convinced that the fence would entirely solve the problem of livestock loss (72%, n=85).

Despite rarely liking living with lions, the majority of respondents in each group did feel that lions were valuable to the tourist industry (Table 1). This view was most prevalent among tourism employees, and least frequent among cattleposts residents although cattlepost respondents living closer to safari camps were significantly more likely to view lions as valuable to tourism (Binary Logistic Regression probability of “no” increased with distance  $p < 0.000$  that slope  $\neq 0$ ).

Perhaps surprisingly, the frequency of cattlepost respondents (n=86) with relatives working in tourism (n=21) viewing lions as a valuable tourism resource was the same as those without relatives employed in the industry ( $\chi^2_{[1]}=0.149$ ,  $p=0.7$ ) and a significantly higher proportion of cattlepost respondents living in the west of the study area thought lions were a valuable tourism resource, compared with the east ( $\chi^2_{[1]}=14.25$ ,  $p < 0.001$ ). Interestingly people living in the west were significantly more

likely to have lost livestock in the last two years than respondents from the east ( $\chi^2_{[1]}=19.357$ ,  $p<0.001$ ) and there were more lions living along the western boundary than the east. One interpretation of this is that ample evidence of a local lion population (roaring, tracks and sightings) was enough to convince people that lions could be valuable to local tourism. In the east, where lions were harder to find and/or hear, people were less inclined to believe they could be an asset.

While most respondents thought that Botswana benefited from tourism, many stated that they did not think they benefited directly and that their local community did not benefit at all (Table 1). While people were pretty clear as to whether they benefited directly there were much higher levels of uncertainty as to whether the community or the country benefited. We queried why so many tourism employees did not feel they benefited from tourism. Our understanding is that many of those who did not regularly interact with tourists did not feel they were part of tourism as they understood it. Respondents with relatives working in tourism were significantly more likely to think that they benefited directly ( $\chi^2_{[1]}$ ,  $p = 0.003$ ). Binary logistic regressions suggested that there was no significant difference in the probability of a respondent perceiving that the community as a whole benefited from tourism, with distance to nearest village (the administrative/tribal centre of the local community) (binary logistic regression  $p= 0.3$  that slope  $\neq 0$ ) or nearest safari camp (binary logistic regression  $p = 0.9$  that slope  $\neq 0$ ).

## ***Discussion***

Stockholders living closest to the park were most likely to experience losses to lions, and these losses were correlated with numbers of livestock owned but not to factors associated with protection of livestock at the cattleposts (static defences). As livestock ownership is associated with status in Botswana it may be important that people with more stock are both influential (local councillors, headmen and chiefs) and more likely to lose stock. Their influences coloured by their own losses may affect the opinions of others beyond their own separate experiences. We caution against the interpretation that static defences may not play a significant role in reducing stock loss. Lion/livestock conflict is dependent upon many local ecological, sociological and economic conditions (Loveridge *et al.*, 2002) and one should not seek to

generalize too broadly from any one study. Evidence from East Africa suggests that static defences are important when, as appears to be the case, all livestock are enclosed at night (L. G. Frank pers comm) (Kruuk, 1980; Ogada *et al.*, 2003). In Botswana the *laissez faire* herding strategy ensures that many un-herded livestock are available to lions away from the kraals (also see (Hemson *et al.*, in prep-a), thus circumventing any role that static defences may play (Ogada *et al.*, 2003). Data from lion movements and diet suggest that lions exploit this system to minimize the chances of contact with people and the costs of locating and accessing livestock as a food resource (Hemson *et al.*, submitted-a; Hemson *et al.*, submitted-b). We suggest this method of livestock husbandry is unsuitable where large predators and livestock coexist and could be a target of efforts to reduce stock loss in Botswana and similar areas.

While we do not have data to infer why herding is so relaxed it appears that government policy and the rarity of livestock theft may reduce the costs of not herding in Botswana. In Laikipia, Kenya, livestock is herded closely at considerable expense, however this investment deters both predators and thieves in an area where stock rustling is common (Frank, 1998). Botswana has a state service to find and care for stray livestock, known as Matimela. Matimela officials receive and care for stray animals and broadcast the brands of their wards on national radio every Sunday evening so that farmers can then claim livestock. As such although the costs of losses to predators may be higher the overall cost of not herding in Botswana are probably less when compared to countries like Kenya where theft is a common threat and straying is more likely to result in loss. As lions currently have limited value to livestock owners it is more cost effective to eliminate the predators using bear or gin traps etc than it is to invest in herding.

The community's perception appeared to be that government and tourism operators are the main beneficiaries of wildlife and are thus responsible for limiting its costs. This limits development of community based initiatives aimed at reducing stock loss. Conversations with operators suggested they feel that they already give enough money to the government. As such the onus of responsibility as perceived by both operators and community appears to lie with the government. The government's main actions are compensation payouts, patrolling to try and keep lions away from stock



and a planned fence to separate wildlife from livestock (very popular with respondents).

While it is likely that the fence will reduce stock losses considerably it is possible that the community have been (possibly unwittingly) oversold the idea. Experiences of fences in Etosha, Kruger and Kalahari Transfrontier Park (Funston, 2001; Mills, 2003; Stander, 1990) suggest they are rarely impermeable and that the design, frequency of breakages (perhaps correlated with density and distribution of elephants and large burrowing mammals) and investment in surveillance and repairs are likely to be important in determining the fences effectiveness. Local people have very high expectations of this fence.

In general the community wanted; fewer lions (unlike ranchers in Laikipia (Frank, 1998), the right to kill them, the government to increase compensation, the national park fenced, lions removed or reduced and the removal (lethally or otherwise) of lions from the surrounding area. They did not appear willing to take action, other than killing lions, to address the problem of livestock loss. Rather they viewed the government as responsible for the costs of wildlife incurred by the community. One recent development that had particularly colored local attitudes appeared to have been a recent national ban (2001) on the killing of lions by herders and hunters. The government introduced the ban, after growing concerns (not all necessarily scientifically justified) in specific locations that the killing of lions was having a significant negative impact upon their populations. Conversations with people after they had been interviewed gave us the impression that many blamed the government for the feeling of helplessness associated with the loss of a right to protect their own property. Whilst the intervention does appear to have reduced the rate of lion killings in the Makgadikgadi (pers obs), it seems probable that it has also inflamed anti-lion/wildlife sentiment and increased beliefs that the government is responsible for stock loss.

Indeed many respondents indicated they would be willing to improve their own preventative measures only if assisted by the government. We suggest that this willingness to participate is important and that the state or operators need to capitalize on it through:-

1. Education in the realistic values, potentials and costs of wildlife and giving the community an informed option to take both the benefits and the responsibility for dealing with the costs.
2. Exploring the potential for joint investment in herding collectives, more secure kraals and encouraging/tolerating local populations of resident wild prey species (Hemson *et al.*, submitted-a)
3. Linking the payment of compensation to the implementation of approved and effective preventative measures by herders (assessed by DWNP currently engaged in chasing lions (Sechele & Nzehengwa, 2002)) e.g. (Swenson & Andren, in press).

Practices such as 2 & 3, aimed at reducing the availability of livestock or increasing the availability of alternative wild prey (Hemson *et al.*, in prep-b) can only be implemented with local community complicity or legislation. It is often assumed that the incentive via which complicity is to be achieved is economic benefit from tourism (Arntzen, 2002; Lawson & Mafela, 1990; Meynell & Parry, 2002; Rozemeijer, 2003).

While it is tempting to conclude that employment in tourism affects peoples attitudes towards wildlife, we cannot reliably differentiate between this hypothesis and another, that it may be that people with an interest in wildlife, are more likely to seek employment within wildlife tourism and an interaction between these factors. However, experience of the first author (who worked in a safari camp for four years and maintained close contact with all tourism operators and many staff in the area during the study) suggested that Batswana employees initially had the same attitudes as those of cattlepost and village interviewees and were more interested in money than the existence or aesthetic value of wildlife. As such it does seem likely that tourism employment acts as a catalyst for pro-wildlife attitudes in the Makgadikgadi but predominately only for employees. Tourism in the area does not seem to be having a wider effect on community attitudes towards lions and wildlife. It would seem there is a need to clarify to the community the ways in which it benefits and the amounts involved. However, it may be that they are already aware and are not satisfied with the amounts.

We have estimated that livestock losses to lions cost an average cattlepost US\$ 168 per annum. However, this does not include costs of filing for and receiving a claim

(transport etc), finding and buying a replacement animal and less quantifiable costs of sharing space with and losing livestock to large carnivores such as lions (Loveridge *et al.*, 2002). This figure is also only an estimate for lions, one observer suggests that 50% of wildlife caused damage in the Makgadikgadi is due to lions (Meynell & Parry, 2002). As such it may be that the real cost of coexisting with wildlife at present may be at least double if not treble our initial estimate, and cost the communities US\$ 50-75,000 per annum.

Currently revenue from tourism in the study area is divided among the operators, the government and the local community. From one operator we could obtain data from, the central government received US\$ 150,000 VAT per annum and the Central District Council US\$ 55,000 as a resource rental. The local community organization obtained a set lease fee (US\$ 6,600 per annum) and members of the local community receive total salaries roughly equal to US\$ 105,600 per annum (likely to be a generous estimate as some employees are not local residents). Similar results have been suggested for other WMA's in Botswana with Arntzen (2003) suggesting that "community benefits are highest from commercial tourism mostly in the form of local wages and royalty payments". While wages plus lease fee is larger than a crude estimate of the costs of living with wildlife we wonder if it is appropriate to view wages as a community benefit per se. They accrue to a sub-section of the population which is not necessarily the same sub-section that loses stock to predators. The extent to which wages influence a community's attitude is likely to depend upon how poor the average member of the community is, how large the wages are, how widely they are passed on beyond the employee, what proportion of the adult population is engaged in employment in the sector and how well the importance of wildlife to tourism, and tourism to the community are understood.

Although national CBNRM figures are impressive (46 community based organisations serving 130 villages and covering 40,000 people and generating US\$ 1,400,000 per annum in 2001) (Arntzen, 2002), these people potentially receive only \$US 35 per annum (it is not clear if wages are included in this value) and those living closest to wildlife may still lose more than they gain. While there may be further existence value associated with wildlife our data suggests that this may not always be substantial and it is human nature to appreciate something's value only once it has

gone. The significance of creating local employment should not be dismissed but it is important that suggestions that it will have a dramatic influence on local attitudes to wildlife, are evaluated critically (Bookbinder *et al.*, 1998; Giannecchini, 1993).

A limitation of using tourism to offset the costs of wildlife conservation globally may be the scope for local tourism to generate enough revenue in enough places (Walpole & Thouless, in press). A viable tourism operation requires a marketable, and ideally, unique appeal that must be transmitted effectively to the target market that expects value for money and an unforgettable (and pleasurable) experience. How much of the world's threatened species, live in areas of sufficient tourism potential to generate enough revenue to create or preserve positive attitudes and galvanize these into community conservation action? How many of these areas are in politically stable countries with good access for tourists this year; and will these be the same areas in twenty years time? Whilst Southern and Eastern Africa have between them captured 47% and 35% of Sub-Saharan Africa's tourism market, West and Central Africa cater for only 16% and 3% (Cleverdon, 2002); what scope is there for tourism to add enough value to wildlife in these areas to meet conservation objectives. Whilst these questions might appear glib and dismissive of the potential for tourism to power local conservation initiatives, they need to be addressed openly so that conservationists and communities living with wildlife can assess the pros and cons of wildlife based tourism.

Whilst there is potential for tourism based conservation/development programs to work, the approach has limitations that need to be locally assessed before implementation is attempted (Walpole & Thouless, in press). In some cases where tourism may not be viable sport hunting may be better suited e.g. (Lewis & Alpert, 1996; Wilkie & Carpenter, 1999), although many of the same limitations may still apply. It is too easy to fall back on the logic of community conservation rhetoric when trying to explain away failure and justify renewed investment. We owe it to local and international communities alike to be as ruthless in assessing the failures and limitations of the approach as we are quick to point out success.

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## **Chapter 3: Some ecological correlates of lion density and space use revisited.**

### ***Summary***

Lion density has been shown to have a positive linear correlation with prey abundance (Carbone & Gittleman, 2002) and a positive correlation with prey abundance during periods of prey scarcity (lean season prey density or LSB) (Van Orsdol *et al.*, 1985). Home-range size has been negatively correlated with LSB between studies (Van Orsdol *et al.*, 1985). Although home-range size within studies are generally inversely proportional to prey abundance (Packer, 1986; Viljoen, 1993) they may also respond to spatio-temporal aspects of prey dispersion (Hemson *et al.*, submitted-a). Using data collated from studies which used improved and standardised techniques, more advanced technology and encompassed a wider range of ecological settings than were previously available I revisit previous meta-analyses. I suggest that lion home-range size is negatively exponentially correlated, and lion density positively exponentially correlated, with lean season prey density. The exponents of these curves are similar to the exponent of a curve of the number of herds (resource patches) per unit area plotted against LSB as calculated from a separate data set using aerial and spoor census data from Botswana and South Africa. While there are still limitations in the approach they are less severe than those of previous meta-analyses. It appears that while lion range size and density does vary with prey density it may be that the dispersal and aggregation of prey that explains the demonstrated departure from linear relationships. These results are suggestive that aspects of resource dispersion may play roles in regulating the social ecology of lions and merit further investigation.

### ***Introduction***

Inter-specific meta-analyses have demonstrated positive correlations between home-range sizes and the metabolic needs (individual mass and group size) of different species of carnivore (Gittleman & Harvey, 1982; Kelt & Van Vuren, 2001; Mace *et al.*, 1982; Swihart *et al.*, 1988). Large carnivorous species that often consume large prey (Carbone *et al.*, 1999) have the largest home-ranges, and the lowest densities relative to their metabolic needs (Gittleman, 1986; Kelt & Van Vuren, 2001; Swihart

*et al.*, 1988). Comparatively little attention has been given to intra-specific variation relative to resource abundance. Data on species' home-range sizes are generally treated as points rather than as clines and intra-specific variation overlooked to simplify analyses e.g. (Gittleman & Harvey, 1982). Lions are a model species with which to examine intra-specific variation as they are found across a considerable ecological diversity for which data on their ecology is now available e.g. (Stander & Hanssen, 2003; Van Orsdol, 1982). Furthermore, there have been considerable efforts made to record the abundance of ungulates in many of these habitats e.g. (Coe *et al.*, 1976; Dunham, 2001; East, 1984; Wint, 2000). As such there is an excellent cross section of the range of ecological variation reflected in the literature.

Across many taxonomic groups, food abundance and availability is thought to be a major factor governing home range and territory size and consequently density, although this relationship may be complicated by factors such as the competitive quality of territorial neighbours, interspecific competition and/or access to specific resources (Adams, 2001). Lion home range size is negatively correlated with measures of prey abundance made during periods of prey scarcity (Van Orsdol *et al.*, 1985) and lion density has been positively correlated with LSB (Van Orsdol *et al.*, 1985). Carbone and Gittleman (2002) suggest that this relationship is linear. Within study areas, long term increases in resident prey density (analogous to lean season prey biomass) have been correlated with increased lion density and causality inferred (Hanby & Bygott, 1979). Seasonal increases in wild prey abundance can result in reductions in home range size and effect local seasonal increase in lion density in the Savuti marsh in Botswana (Viljoen, 1993) and the Serengeti Plains (Packer, 1986; Schaller, 1972). However in some areas seasonal increases in 'preferred' but dispersed prey (zebra (*Equus burchelli*) and wildebeest (*Connachaetes taurinus*) may lead to switching from more aggregated prey (livestock) to the more dispersed prey resulting in increases in home range size with increases in prey abundance (Hemson *et al.*, submitted-a).

I re-addressed Van Orsdol *et al* (1985) and Carbone and Gittleman's (2002) findings using data gathered from improved and standardised study methods over a wider ecological range. In particular, advances in radio telemetry have made studies of lions living in habitats like the Kalahari and Namib deserts possible and have led to several

detailed studies across the lion's ecological range. By removing pseudo-replicated data points (Hurlbert, 1984) used in Van Orsdol's original analysis (1985) (two points for each of Ngorongoro, Serengeti Plains and Serengeti Woodlands), and by limiting the effects of using different home range estimation techniques (which can significantly alter the outcomes of analyses (Kenward, 2001; Powell, 2000) e.g. (Hemson *et al.*, submitted-a)) I hoped to remove significant sources of noise in the data.

More accurate descriptions of the relationships between aspects of lion social and spatial ecology may be useful in predicting lion densities using data on prey abundance or rainfall only (Coe *et al.*, 1976; East, 1984). Predictions such as these may help us in understanding the impacts of factors such as disease, hunting and retaliatory killing on lion populations and be useful for planning reintroductions, and meta-population and protected area management. Furthermore it may improve our understanding of lion social ecology and perhaps contribute to the debate on lion sociality.

Lion sociality was initially described in terms of an improved ability to hunt large prey when in groups (Caraco & Wolf, 1975; Schaller, 1972; Van Orsdol, 1982). While this hypothesis is intuitively appealing, detailed analysis of data from the Serengeti suggests that lions do not forage in groups of sizes that optimize foraging success (Packer *et al.*, 1990) and that cooperative hunting is a consequence rather than a cause of sociality (Packer & Rutten, 1988). Alternatively it has been suggested that it may be the size, dispersion and renewal rate of resource patches that facilitates the formation of groups at pre-existing high densities of ancestral lions. These patches may be aggregations of ungulates at waterholes (Macdonald, 1983) or large easily detectable carcasses (Packer, 1986). These descriptions are consistent with the Resource Dispersion Hypothesis (RDH) (Macdonald, 1983). Broadly speaking RDH suggests that where resources are distributed heterogeneously in large or rapidly renewing patches such that the minimum defensible territory size for one animal also contains enough resources to support more conspecifics; then the pre-requisites of group formation have been met (Carr & Macdonald, 1986; Macdonald, 1983). As such, a resident occupying a defensible territory large enough for its own needs may, due to the dispersion of aggregations (patches) of resources within that territory have

sole access to enough resources for several conspecifics. If the costs of tolerating these conspecifics would be lower than the potential benefits then there is the potential for groups to form (Macdonald, 1983). These benefits might include cooperative hunting, group territorial defence, interspecific competitive advantage and defence of young (Packer *et al.*, 1990) whereas the costs may be limited to increased intra-specific competition at kills. However, although it is an appealing hypothesis, there is little quantitative support to suggest that RDH explanations may be applicable to lion sociality.

Resource dispersion has already been suggested as playing a role in sociality in feral domestic cats (Liberg & Sandell, 1988; Macdonald, 1983), where very large resource patches led to formation of groups even at low population densities (6 cats/km<sup>2</sup>) and male cheetah, where seasonal aggregations of nomadic females (the resource) create conditions in which the costs of tolerating more mating competition are outweighed by the benefits of improved ability to defend many females from solitary males (Caro, 1994). In contrast domestic cats feeding on more homogeneously dispersed prey tend to be solitary even at high densities (20-50 cats/km<sup>2</sup>) (Liberg & Sandell, 1988). A potential intermediate stage is the sharing of space by felids in response to temporary aggregations of resources. Female mountain lions (*Puma concolor*) in Idaho had almost entirely overlapping ranges when prey was concentrated in a single area but redistributed themselves into more exclusive home-ranges when prey were more homogeneously dispersed (Seidensticker *et al.*, 1973).

RDH (Johnson *et al.*, 2002) predicts that:

1. Territory/home-range size does not correlate with group size.
2. Territory/home-range size is determined by the dispersion of resources
3. Group size is determined by the heterogeneity and total richness of resources.

## **Methods**

Data were gathered via an extensive literature search including both peer reviewed papers, and the so called 'grey literature'. Data from previous meta-analyses were evaluated and studies in which methodologies for estimating lion numbers or ecology

could not be ascertained, or are now viewed as unreliable e.g. transects (Geerling & Bokdam, 1973) or discussions with fishermen and chance encounters (Green, 1979), both in (East, 1984) used as only source for lion data in (Carbone & Gittleman, 2002), were rejected. I assumed that advances in telemetry and lessons learned from prior studies, would improve the accuracy of estimates of prey density and lion ecology (although being mindful that good technology alone does not equate to good science). As such, if there were sequential studies from an area then only the latest study was used and pseudo-replication thereby avoided (Hurlbert, 1984). As a consequence all studies used in (Carbone & Gittleman, 2002) and several from (Van Orsdol *et al.*, 1985) were excluded from the analysis.

Home-range sizes of females estimated using the 100% minimum convex polygon methods (Kenward, 2001) are used to minimise dimorphic bias from potentially wider ranging males and variation from different home range estimators (Hemson *et al.*, submitted-a; Loveridge *et al.*, 2002; Powell, 2000; Yamazaki, 1996). To establish lean season biomasses the lowest available prey abundance estimate for an area was used. Data on prey abundance were gathered from the lion studies themselves, calculated using Botswana's aerial survey data or obtained from independent prey ungulate surveys (Coe *et al.*, 1976; Dunham, 2001; East, 1984). Using older prey estimates e.g.(Coe *et al.*, 1976; East, 1984) and more contemporary lion data clearly risks error insofar as circumstances may have changed between the studies. It is felt that this risk is outweighed by the considerable improvements in lion range and density estimation techniques used in later studies. Elephants (*Loxodonta africana*), rhinoceros (*Ceratotherium simum* and *Diceros bicornis*) and hippos (*Hippopotamus amphibius*) were excluded from the analysis as they are rarely preyed upon by lions and would otherwise considerably bias the prey biomass data. Giraffe (*Giraffa camelopardalis*) were also excluded to conform to medium sized (61-450kg) ungulate data presented by Coe et al (1976). Pride size was calculated as the number of adult females per pride. By using this definition I minimised the transient influence of cubs and variation in male coalition size. All statistics were performed using Minitab 13.31 (Minitab, 2000).

For several areas in Botswana I calculated the lean season prey biomass excluding elephants, giraffe and hippos from aerial survey data using BASIS (Botswana Aerial Survey Information System) (Wint, 2000). I then imported the raw aerial survey transect data into Arcview 3.2 (ESRI, 1992-1999), excised the section relevant to the study area, and exported the data from that area to a spread sheet. The raw data are made up of a series of observations from a low flying aircraft. Each observation consists of a time, a coordinate, the species seen and the number of animals in a group. From this, I was able to calculate the mean size of the herds spotted in that area during the lean season and relate these to lean season biomass and calculate the number of herds per unit area. Lean seasons were defined by study area as patterns of ungulate movements vary between areas and lean seasons in different areas could be wet or dry depending upon these movements. Herd size data were also calculated from a spoor transect study in the Southern Kalahari (Funston, 2001). Paul Funston also supplied herd size data calculated from two study areas in Kruger National Park (Funston pers comm).

## Results

*Table 1: Data on lion ecology and prey biomass used in this study prey data calculated by myself using the Botswana Aerial Survey Information System (Wint, 2000) is indicated as BASIS.*

Study	Source	Density (lions/100sq/km)	Pride Size	Home Range (km <sup>2</sup> )	Lean Season Prey Biomass (kg/km <sup>2</sup> )
Makgadikgadi	(Hemson <i>et al.</i> , in prep)	0.74	2	725	111 (BASIS)
CKGR	(Thouless, 2000)	0.6	-	-	118 (BASIS)
Kunene	(Stander & Hanssen, 2003)	0.6	4	1628	200 (calculated from data on Namibian MET website and (Coe <i>et al.</i> , 1976; East, 1984)
Dune Savannah Southern Kalahari	(Funston, 2001)	0.77	-	2823	200 (Funston, 2001)

Etosha	(Stander, 1991)	1.8	4.8	962	283 (Coe <i>et al.</i> , 1976; East, 1984)
Tree Savannah	(Funston, 2001)	1.63	-	707	349 (Funston, 2001)
Southern Kalahari	Funston	-	-	249	419 (Funston pers comm)
Northern Plains (Kruger)	pers comm				
Hwange	Loveridge pers comm	2.7	2.7	345	454 (Dunham, 2001)
Manovo	(Ruggiero, 1991)	9.3	3.25	-	651 (Ruggiero, 1991)
Moremi, Okavango	(Harvey & Kat, 2000)	-	5.25	-	677 (BASIS)
Savuti	(Viljoen, 1993)	17	-	424	730 (Viljoen, 1993)
Khudum, Okavango	(Winterbach & Winterbach, 2002)	18.8	5.6	69	950 (BASIS)
Serengeti plains	(Hanby & Bygott, 1987)	10	4.7	226	1000 (Hanby & Bygott, 1987)
Kruger	(Funston <i>et al.</i> , 2003)	13	4.2	150	1014 (Coe <i>et al.</i> , 1976; East, 1984)
Matetsi	(Van der Meulen, 1976)	6.2	-	1693	1693 (Van der Meulen, 1976)
Selous	(Creel & Creel, 1997)	10.5	-	-	1874 (Caro <i>et al.</i> , 1998)
Nairobi	(Rudnai, 1973)	26	3	26	2656 (Coe <i>et al.</i> , 1976; East, 1984)
Lower Sabie, Kruger	Funston pers comm	-	-	76	3559 (Funston pers comm)
Umfolozi-Hluhluwe	(Anderson, 1981)	9.21	-	-	3919 (Anderson, 1981)
Serengeti woodland	(Schaller, 1972)	25	6.1	65	8224 (Van Orsdol <i>et al.</i> , 1985)
Lake Manyara	(Makacha & Schaller, 1969)	40	3.3	-	9368 (Coe <i>et al.</i> , 1976; East, 1984)



Luangwa	(Yamazaki, 1996)	13.18	3.5	58	10003 (Ndhlovu & Balakrishnan, 1991)
Masai Mara	(Ogutu & Dublin, 2002)	30	9.2	71	10335 (Ogutu & Dublin, 2002)
Ngorongoro	(Hanby <i>et al.</i> , 1995)	40	5.9	45	11217 (Hanby <i>et al.</i> , 1995)
Queen Elizabeth (Rwenzori)	(Van Orsdol <i>et al.</i> , 1985)	30	7	39	13346 (Van Orsdol <i>et al.</i> , 1985)
Laikipia	(Frank & Woodroffe, 2002)	1.8	-	-	-
Mana Pools	(Dunham, 1992)	4.25	-	-	

While home range size was negatively correlated with lean season prey biomass the relationship was not linear (Figure 1) but exponential (Figure 2). Log home range size was significantly ( $p < 0.0001$ ) linearly negatively correlated with log lean season prey biomass (figure 2). The relationship explained the majority of the variation in home range size ( $r^2 = 75.9\%$ ) and the slope was significantly less than one ( $P < 0.0001$  slope  $\neq 0$ ,  $p = 0.045$   $t_{[16]} = 2.17$ , slope  $\neq 1$ ) indicating that lion home-range size increased faster than proportional to lean season prey biomass at low prey densities.

Figure 1: Mean home-range size plotted against lean season prey biomass per km<sup>2</sup>.

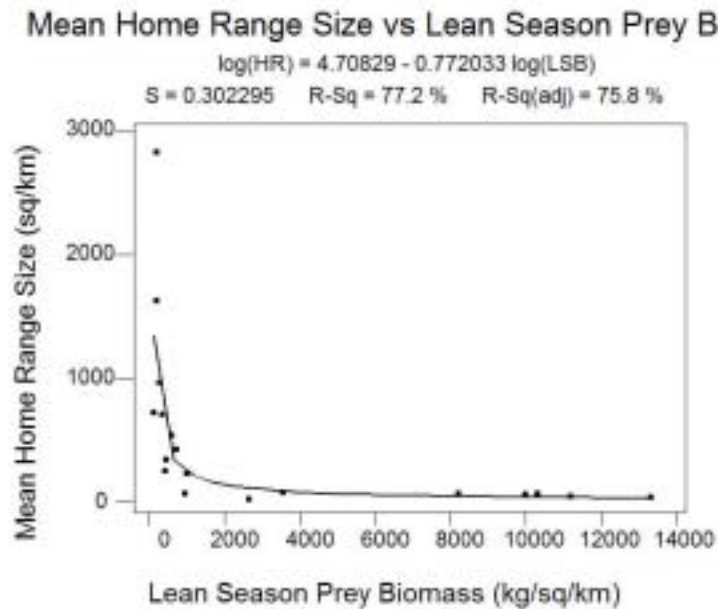
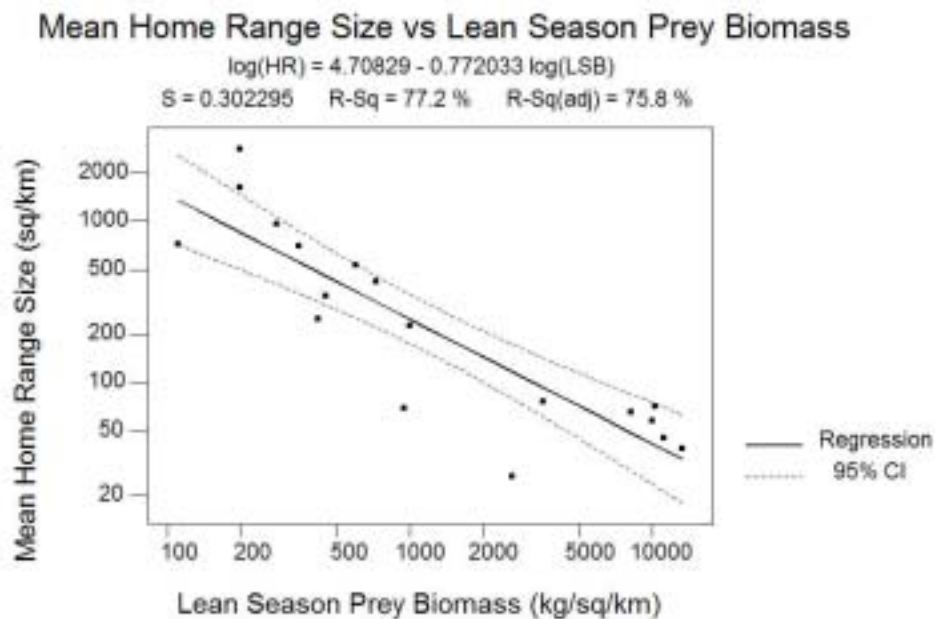
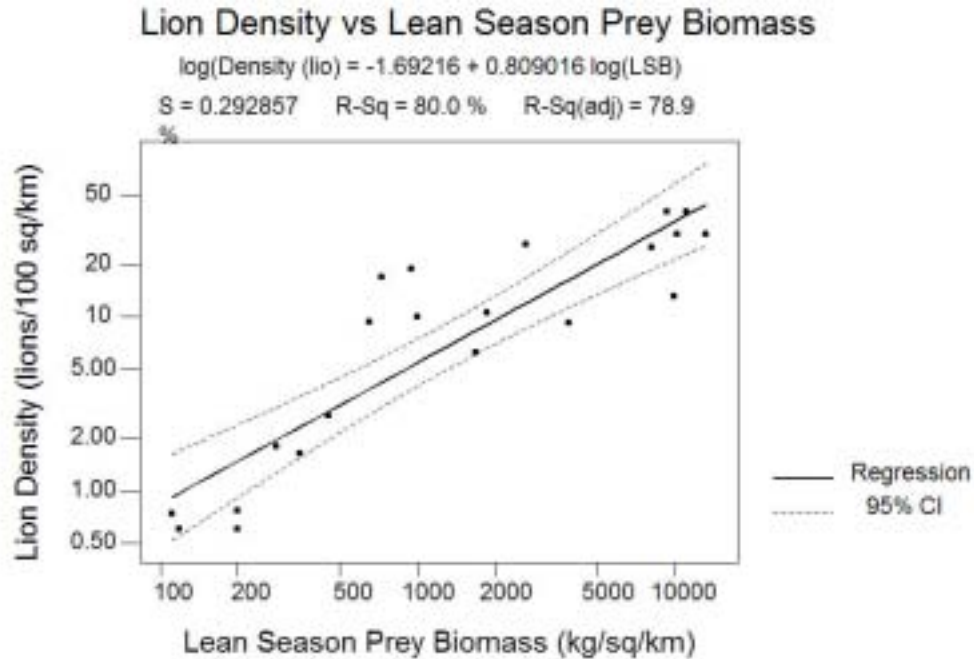


Figure 2. Mean home-range sizes and lean season prey biomass (log-log scale,  $P < 0.0001$  slope  $\neq 0$ ,  $p = 0.045$   $t_{[16]} = 2.17$ , slope  $\neq 1$ ).



Lion density was best explained by an exponential relationship with lean season prey biomass ( $p < 0.0001$  slope  $\neq 0$ ,  $p = 0.054$   $t_{[19]} = 2.06$  slope  $\neq 1$ ) (Figure 3), the slope of which ( $+ 0.81 \log(\text{LSB})$ ) was opposite in direction, but of a similar gradient to that describing the relationship between home range and prey density ( $-0.77 \log(\text{LSB})$ ) (Figure 2).

Figure 3: Overall lion density and lean season prey biomass density on a log-log scale ( $p < 0.0001$  slope  $\neq 0$ ,  $p = 0.054$   $t_{[19]} = 2.06$  slope  $\neq 1$ ).



There was a weak but significant ( $p = 0.024$ ) positive linear correlation between pride size as measured by number of adult females per pride and lean season prey biomass with pride size increasing by 0.1 of a member for every 1000 kg increase in LSB (Figure 4). Considerable variation in pride size was not accounted for in this regression ( $r^2 = 23.2\%$ ) but a better fit was not obtained by log transformation. Mean pride size was not significantly correlated with mean home-range size (Pearson's Correlation Coefficient  $-0.348$ ,  $p = 0.268$ ) or lion density (Pearson's Correlation Coefficient  $0.496$ ,  $p = 0.072$ ).

There was a positive correlation between the numbers of herds per unit area (herd density) and lean season prey biomass density ( $p < 0.0001$  slope  $\neq 0$ ,  $p = 0.02$   $t_{[10]} = 2.70$  slope  $\neq 1$ ) (Figure 5). Again the relationship was exponential with a similar exponent function to that of the preceding regressions of lion home-range size and density. Note that the range of lean season prey biomass densities is restricted to the lower end of the cline of lion data presented in this study (Table 1).

Figure 4: Mean pride size (adult females per pride) and lean season prey biomass density ( $p=0.024$  slope  $\neq 0$ ).

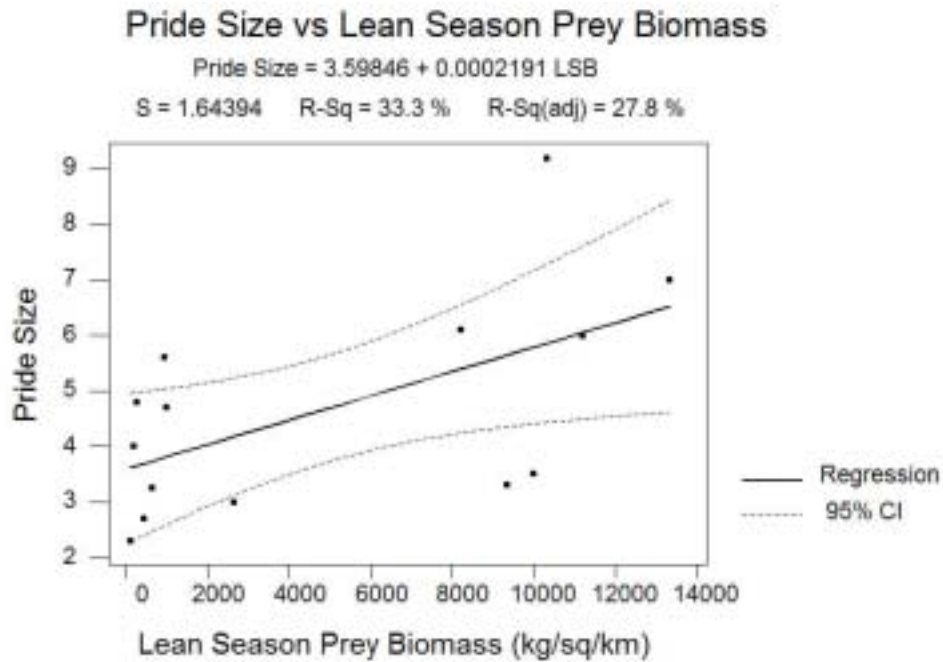


Table 2: Lean Season Prey Biomass, Mean Herd Mass and Herd Densities for 11 areas in Southern Africa.

Area	LSB (kg/km <sup>2</sup> )	mean herd mass (KG)	Herd Density (herds/100km <sup>2</sup> )
Nxai Pan	67	262	25
Chobe	82	1143	7
Khutse	105	1122	9
Makgadikgadi	110	1353	8
Central Kalahari	117	502	23
Dune Savannah, Southern Kalahari	200	556	35
Tree Savannah, Southern Kalahari	348	553	65
Northern Plains, Kruger	419	1448	26
Santawani, Okavango	677	1015	66
Khudum, Okavango	950	1512	62
Moremi, Okavango	1077	2570	41
Sabie, Kruger	2965	5429	136

Mean patch size (mean herd mass) also increased with lean season prey biomass although not as rapidly ( $p=0.004$  slope  $\neq 0$ ,  $p=0.005$   $t_{[13]}=3.59$  slope  $\neq 1$ ), exponent  $+0.492 \log(\text{LSB})$ ). This relatively slow increase in patch size with prey biomass accounts for the deviation of the patch density changes from proportionality with changes in prey biomass.

*Figure 5: Herd density plotted against lean season prey biomass density for several study areas in Southern Africa ( $p<0.0001$  slope  $\neq 0$ ,  $p=0.02$   $t_{[10]}=2.70$  slope  $\neq 1$ ).*

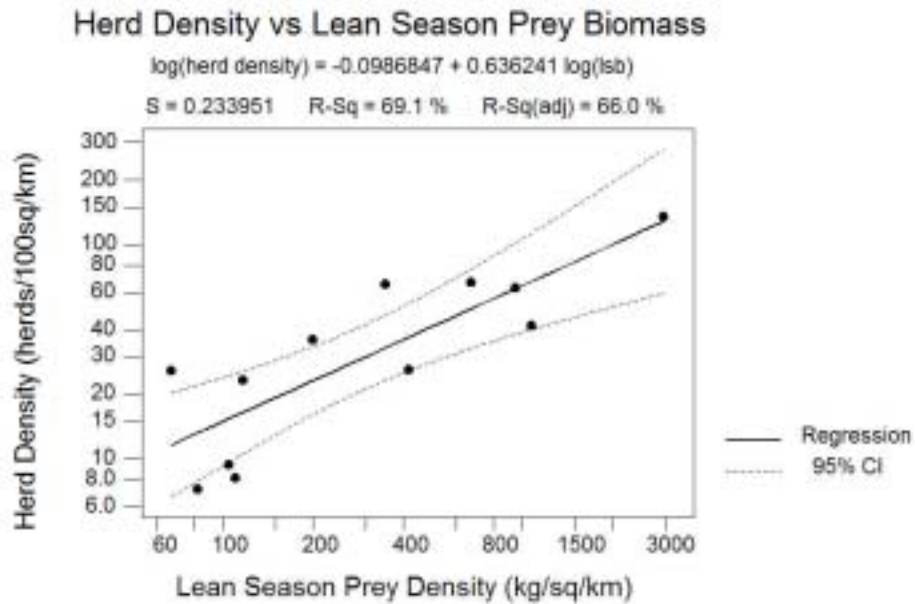
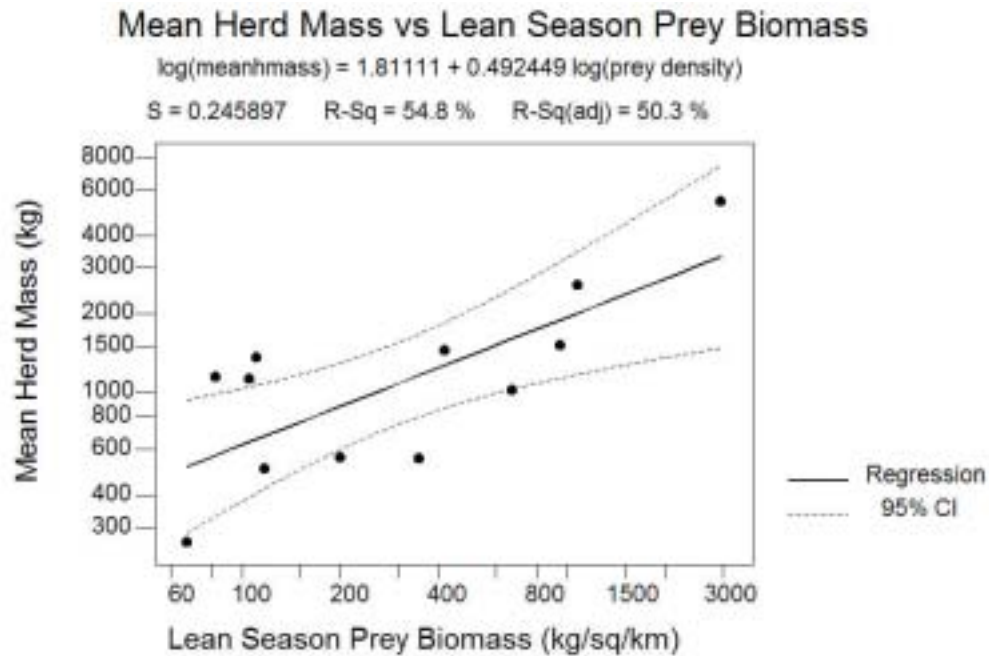


Figure 6: Mean herd mass (patch size) and lean season prey biomass plotted on a log-log scale ( $p=0.004$  slope  $\neq 0$ ,  $p=0.005$   $t_{[10]}=3.59$  slope  $\neq 1$ ).



## Discussion

If lion home-range size and density were influenced by the overall density of prey alone then I would expect to have seen linear correlations between both home-range size and lion density, and lean season prey biomass. It is clear that these relationships are not linear as previously described (Carbone & Gittleman, 2002) and there is strong evidence that both vary exponentially with prey density (Figures 2 & 3). Pride size does increase with lean season prey density although pride size increased less than proportionally with prey abundance (Figure 4) and was not correlated with home range size or lion density. While it is not immediately apparent why these trends might occur, it appears that the dispersion and the size of patches of resources (here defined in terms of herds of ungulates) may be a significant influence on lion social ecology (Johnson *et al.*, 2002; Macdonald, 1983).

If prey were homogenously distributed throughout each study area (in that ungulates did not form herds or aggregate at certain locations (waterholes, grazing areas etc) and distributed themselves evenly across the study areas) we would expect positive linear relationships between lion density and home-range, and prey density e.g. (Carbone &

Gittleman, 2002). Lion density would scale to prey density. However this is not the case and lion prey is not homogenously distributed. The majority of prey are ungulates between (50-600kg) living in relatively open habitats; typically savannah, open woodland or grassland (Mills & Biggs, 1993; Schaller, 1972; Scheel & Packer, 1993). These ungulates are generally more gregarious than forest or other closed habitat species and most form herds (Estes, 1991; Jarman, 1974). Herds can be thought of as mobile resource patches; aggregations of resources whose formation is an increase in the heterogeneity of resource dispersion in an area. The spatial and temporal distribution of these herds is already known to correlate with lion home-range size changes between seasons (Hemson *et al.*, submitted-a; Packer, 1986; Viljoen, 1993).

For each species of prey there is likely to be a minimum herd size (typically of females), and indeed solitary female (50-800kg) ungulates are rare in geographic areas where lions occur (Brashares *et al.*, 2000; Estes, 1991; Jarman, 1974; Smithers, 1983). Many gregarious prey species form stable groups of 5-50 individuals) from which larger aggregations are made up at certain times or in certain habitats e.g. plains zebra (*Equus burchelli*), topi (*Damaliscus lunatus*) and buffalo (*Syncerus caffra*) (Brashares, pers comm; Estes, 1991; Jarman, 1974); these units are effectively indivisible resource patches. Some species common in the lower density habitats in this study such as gemsbok (*Oryx gazella*) actually occur in slightly larger mixed sex herds than analogous species in more mesic areas e.g. greater kudu (*Tragelaphus strepciceros*) (Estes, 1991; Jarman, 1974). As such prey may become increasingly dispersed at lower prey densities as the distance between these patches (herds) increases rather than further division of these patches below the minimum herd size. As this occurs the density of herds per unit area may decline more rapidly than the density of prey overall. Indeed my own data does suggest that herd density may tail off more rapidly below 1000 kg/km<sup>2</sup> lending some support to this hypothesis.

This data from Southern Africa also suggests that increasing the numbers of animals per unit area results in larger herds. One prediction of RDH is that as the size of heterogeneous resource patches increase the size of groups of consumer will also increase. While this appears true from my data I cannot distinguish between this and an alternative hypothesis that increases in overall prey abundance drive group size

increases. However, both pride size and herd size do not scale proportionally with prey abundance but are significantly less than proportional. This is also the case in plains zebra where herd size does increase with zebra density but not proportionally, inferring that both herd density and herd size increases with overall density (Rubenstein & Hack, 2004). As such the dispersion of these herds should vary with overall density. It is also suggested in the literature that ungulates in open areas tend to form larger herds at higher densities possibly as a way of increasing group vigilance and maximising foraging times (Bednekoff & Ritter, 1994; Childress & Lung, 2003; Dehn, 1990). However I could not find robust empirical support that this trend might extend across the ecological diversity from which the lion data originates as it does not appear that anyone has previously attempted to quantify herd dispersion (Brashares, pers comm; Brashares & Arcese, 2002; Coe *et al.*, 1976; East, 1984; Estes, 1991; Jarman, 1974; Leuthold, 1977; Sinclair, 1985).

A further possibility is that there is an increasing tendency for herds to aggregate around points of attraction in low density habitats and that the dispersion of these resources might further increase resource heterogeneity. The lowest prey density habitats in this study are typically environments in which the resources limiting ungulate density (typically forage and water (Coe *et al.*, 1976; East, 1984)) may also become increasingly scarce and/or heterogeneously distributed. Water and cover are limited to scattered waterholes and river beds in the Kunene region of Namibia (pers. obs.) and productive grassland areas and water (mainly pumped) restricted to pan and river bed areas in the Makgadikgadi, Southern Kalahari, Etosha and Central Kalahari (Funston, 2001; Hemson, pers obs; Stander, 1991). It follows that prey are not only aggregated into herds but these herds may be aggregated in response to resources vital to their own survival and reproduction at certain times of the day or year, further increasing the heterogeneity of prey dispersal. Hence there may be potential for these, often xeric, habitats to contain more heterogeneous distributions of prey than more mesic habitats in which water and fodder may be distributed more homogeneously throughout the habitat. Indeed I suggest that it is both the mean size of herds and density of these herds in the landscape and the distribution of these herds about geographic features that may ultimately best describe the non linear relationship between both home range size and density and prey abundance. However at present we do not have access to the data required to establish the existence of this complex



relationship (see below). However, while my description of ungulate dispersion is certainly an oversimplification of ungulate sociality e.g. (Rubenstein & Hack, 2004) ignoring different species compositions and influence of herbivore resource dispersion, it is intriguing that the lion density and herd density curves are similar.

This analysis lends support to the hypothesis that it is the dispersion of herds as well as the abundance of prey during periods of prey scarcity (Van Orsdol *et al.*, 1985) that are the major determinants of lion social ecology. However, there are limitations to these data and analyses. Variation from other sources may complicate my analysis. Lion socio-ecological data may be influenced by anthropogenic offtake and the presence of livestock as a potential prey source. For example it is possible that anthropogenic offtake may reduce pride sizes and lion density and livestock may reduce home-range sizes in the Makgadikgadi (Hemson *et al.*, submitted-a; Hemson *et al.*, submitted-b; Stander, 1997). To investigate this possibility I re-analysed the dataset without the data from the Makgadikgadi to investigate what affect this might have. I found that the Makgadikgadi points fell comfortably within the 95% confidence intervals and that the relationships had not changed significantly without its inclusion. While the influence of these biases was not large enough to invalidate or significantly influence the results, I am mindful that I have encompassed variation not factored for in the experimental design. Some areas used in the analysis of herd density were less than 1000 km<sup>2</sup>. As such the prey estimates therein had large confidence intervals associated with them (typical when using quite coarse aerial survey data designed to produce ungulate abundance estimates for larger areas). Some of my assumptions regarding the exclusion of larger species, particularly giraffe and elephant may not be correct. Both giraffe and elephant may be important prey species for lions in some areas (Hwange National Park, Zimbabwe, A. Loveridge pers. comm.). It may be that larger groups of lions may be better able to kill these larger prey and/or that in certain ecological situations the vulnerability of these species may increase (e.g. droughts). Presently I am unable to add species to density estimates made by Coe (1976) and cannot therefore explore the effect of introducing these species to the analysis or introduce concepts such as increased vulnerability of sex/age classes. While adding elephants and other very large species to analyses en masse would probably not be desirable (their masses inflating prey abundance estimates with largely unavailable biomass) it would be advantageous to use elephant population

structure data and add only that component of their population that may be vulnerable to lions i.e. the young of elephants may be the only age class available to lions (A. Loveridge pers comm). The overall range of prey dispersion data used presently does not cover the geographic or ecological range covered in the analysis of lion data and comes from a relatively homogenous ecological range, predominately semi-arid and arid savannah.

Despite these limitations the relationships presented thus far are, I believe, sufficiently interesting to merit the consideration that it is possible to test RDH predictions of lion socio-ecology more robustly using ungulate survey data. Future work based on this initial analysis has been planned whereby raw ungulate census data for the same areas and periods as the lion studies used in the first analysis is being sought. By doing so we (Dr. David Macdonald, Dr. Andrew Loveridge and I) would be able to correlate the social ecology of lions with the corresponding measures of herd dispersion and prey density. Such data may enable us to quantify patterns of dispersion of these patches possibly in relation to spatial and temporal patterns of water or forage availability.

Without attempting to interpret the causes of the observed relationships the implications remain important for interpreting the results of inter specific meta-analyses (Carbone & Gittleman, 2002; Mace *et al.*, 1982). The recent additions of studies in the low density tail of lion range (Funston & Hermann, 2002; Stander & Hanssen, 2003) might suggest that mean range size values may be underestimated and densities over estimated. In studies using a single mean point for species such as lions to search for allometric scaling across species this may create problems and data presented as lines might better be presented as surfaces. Similarly the shape of the relationships between these variables, at least for lions, has been misinterpreted (Carbone & Gittleman, 2002).

This study suggests that both the abundance and dispersion of prey may explain much of the variation in lion home-range size and density observed and hints that the formation of groups in large social predators like lions, might yet be explained in terms of the Resource Dispersion Hypothesis (Macdonald, 1983). It demonstrates the potential to refine models using correlates of primary productivity such as rainfall and

soil quality to predict lion density and social ecology that may be useful in conservation planning at larger scales (Carbone & Gittleman, 2002; East, 1984). It also highlights that lions in low density populations may have larger home ranges than would otherwise be predicted and as such predators in arid areas may be more vulnerable to persecution than might otherwise be predicted by linear correlations between prey abundance lion home-range size and density (Brashares, 2003; Hemson *et al.*, submitted-a; Woodroffe & Ginsberg, 1998, 2000).

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## **Chapter 4: Are kernels the mustard? Data from GPS collars suggest problems for kernel home range analyses with least squares cross-validation.**

### ***Summary***

1. Kernel density estimation has become one of the most widely used home range estimators in ecology. The recommended implementation of the method uses least squares cross-validation to estimate the appropriate smoothing factor ( $h$ ) used. The smoothing factor has a significant and considerable influence on the size and shape of the contours produced by the method.
2. We tested the performance of least squares cross-validated kernel density estimation (LSCV KDE) using data from GPS-collared lions sub-sampled to simulate the effects of several alternative radio tracking strategies.
3. LSCV produced variable results and a 7% failure rate for fewer than 100 locations ( $n=2069$ ) and a 61% failure rate above 100 points ( $n=1220$ ). Patterns of failure and variation were not consistent among lions, reflecting different individual space use patterns.
4. Intensive use of core areas and site fidelity by animals caused LSCV to fail more often than anticipated from similar previous studies that used computer simulated radio tracking data.
5. LSCV failures at large sample sizes and variation at lower ones limits the applicability of LSCV kernels to fewer situations than the literature suggests, and casts doubts over the method's reliability and comparability as a home range estimator.

Key words: kernel, home range, least squares cross validation, sample size

### ***Introduction***

Home range is the fundamental measure of space use by an animal, defined as: 'That area traversed by an individual in its normal activities of food gathering, mating and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered part of the home range' (Burt 1943). Burt's definition has persisted in the literature despite inquiries as to "what are normal activities?" (White and Garrott 1990) and "how to quantify occasional sallies and identify the area from

which the sallies are made” (Powell 2000). The home range concept is important in determining habitat preferences (Aebischer et al. 1993), carrying capacities and aspects of species extinction susceptibility (Woodroffe and Ginsberg 2000; Brashares 2003) and underpins several ecological theories including allometric scaling correlations (e.g. Mace et al. 1982; Carbone and Gittleman 2002). Whilst advances in improving definitions of home range have been few (e.g. Kernohan et al. 2001), advances in the methods used to estimate this elusive concept have been considerable (reviews in Macdonald et al. 1980; Harris et al. 1990; Powell 2000; Kenward 2001 and Kernohan et al. 2001).

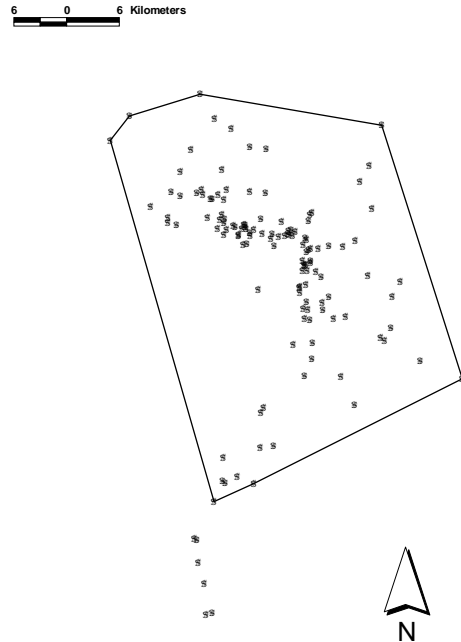
Increases in available computing power have allowed ecologists to use increasingly sophisticated methods to estimate home-range use, culminating in the use of contouring methods for estimating complex probability density distributions (Dixon and Chapman 1980; Worton 1989). Contouring methods have considerable advantages over other popular home range estimation methods such as the minimum convex polygon. They do not assume an animal has a single focus of activity and thereby allow the user to accommodate multiple centres of activity and, as they do not rely on outlying points to anchor their corners, are also less influenced by distant outliers and exclude considerable proportions of unused home range leading to a more accurate depictions of space use (Fig 1).

Kernel density estimation (KDE) is widely viewed as the most reliable contouring method currently used in ecology (Kernohan et al. 2001; Powell 2000) and was first adapted for animal home range analysis by Bruce Worton (Worton 1989) from a technique devised to estimate complex distributions from small samples (Silverman 1986). KDE creates isopleths of intensity of home-range utilization (e.g. 95%) by calculating the mean influence of data points at a series of grid intersections. An isopleth contains a fixed percentage of the utilization density indicative of the amount of time that the animal spends within the contour. A critical component of this calculation is the distance over which a data point (location) can influence the grid intersections; this value is known as the smoothing factor or  $h$ . The larger the value of  $h$  the larger and more smoothed the home range estimate and the less detail is apparent in the final probability density isopleths (Silverman 1986; Worton 1989) (Fig 1 b-f). Conversely small values of  $h$  reveal more of the internal structure of a

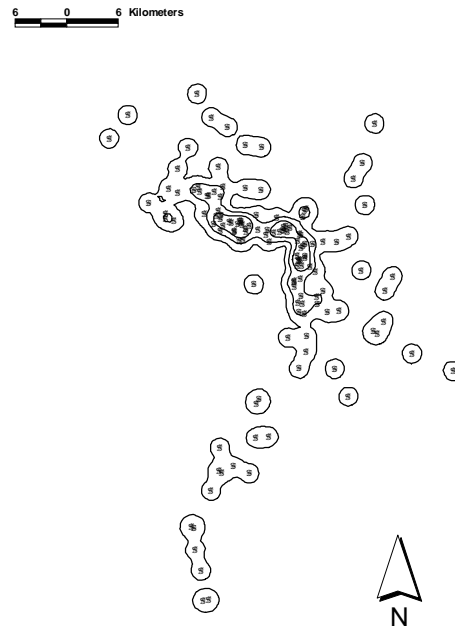
home range but under-smooth in the tail of the density (outer density isopleths) leading to smaller home range estimates and often creating discontinuous outer contours and “islands” of utilization e.g. Figure 1d. As KDE is sensitive to different values of  $h$  the size and shape of KDE home range estimates are consequently dependent upon the methods used to calculate  $h$  (Silverman 1986; Wand and Jones 1995). This raises the possibility that variation in  $h$  may introduce systemic variation into home-range utilisation and size calculations that may complicate or invalidate some inter- and intra-study comparisons.

*Figure 1: The influence of  $h$  on home range size and shape. 1b-f show 95%, 75% and 50% kernel density isopleths for data from a single lion (UG) sampled once every two days. Values of  $h$  were chosen rather than calculated from the data. 1a shows the raw data with a 95% minimum convex polygon fitted (points excluded by the harmonic mean method).*

*1a) Raw data ( $n=134$ ) and 95% MCP*

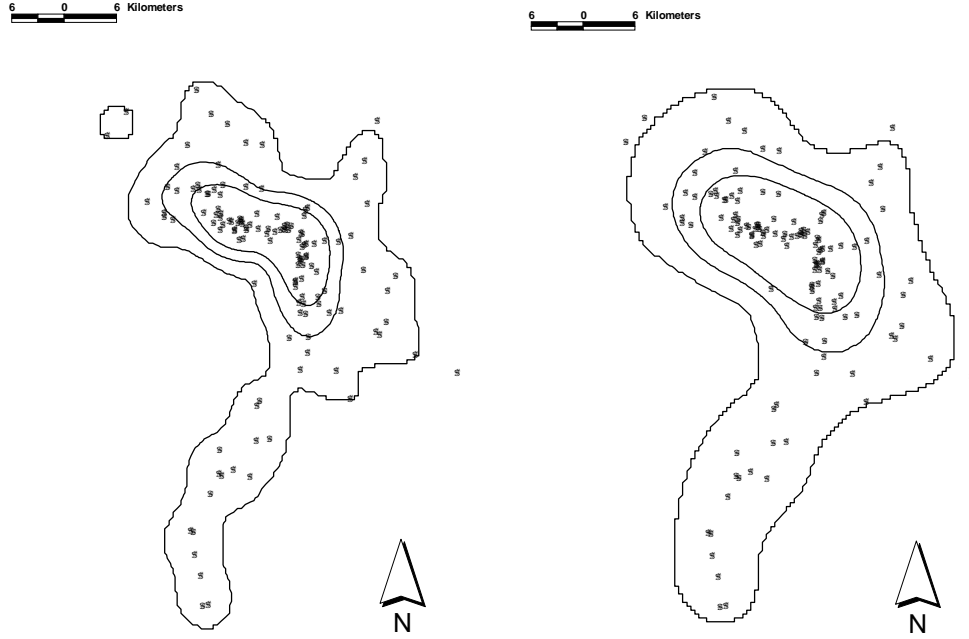


*1b)  $h = 1000m$*



1c)  $h = 3000m$

1d)  $h = 5000m$



The two most frequently used methods of calculating  $h$  in home range analysis are the reference smoothing factor (Equation 1) and Least Squares Cross Validation (LSCV) (Equation 2).

*Equation 1: The Reference Smoothing Parameter Function.  $n$  is the number of locations and  $\sigma$  is the standard deviation of the  $x$  coordinates, with  $y$  coordinates transformed throughout the calculations to have the same standard deviation (Worton 1989).*

$$h_{ref} = \sigma n^{-1/6}$$

*Equation 2: The Least Squares Cross Validation Function.*

$$h_{lscv} = \frac{1}{\pi h^2 n} + \frac{1}{4\pi h^2 n^2} \cdot \sum_{i=j}^n \sum_{j=l}^n \left( \exp \left[ -\frac{d_{ij}^2}{4h^2} \right] - 4 \exp \left[ -\frac{d_{ij}^2}{2h^2} \right] \right)$$

Where  $d_{ij}$  is the distance between the  $i$ th and  $j$ th points.

LSCV allows  $h$  to be chosen so as to minimize the squared distance between the fitted surface and the target surface, integrated over the area. It creates an estimate of this by a formula (Equation 2) which is derived from the difference between the predicted value at each data point based on a surface fitted using all the data and on one fitted after excluding the data point. This estimate of the error is then minimized by varying the bandwidth (Silverman 1986).

Computer simulation studies have been unanimous in their recommendation of KDE as a reliable estimator of range use by animals and of LSCV as the best method of calculating the best values of  $h$  and that  $h_{ref}$  results in over-smoothing and home range overestimates (Worton 1995; Seaman and Powell 1996; Seaman et al. 1999; Powell 2000). However, these tests of LSCV KDE have been based on simulation of animal locations, not on field data.

Worton (1995) expanded on analyses by Boulanger and White (1990) using simulated data to test the performance of home range estimators. These studies used 1000 data sets of 50 and 150 points taken from a normal distribution with one centre of activity, a composite of two normal distributions, a uniform distribution confined within a square or a uniform distribution confined within a right angled U shape. Worton concluded that kernels were more reliable and accurate than the Harmonic Mean method approved by Boulanger and White (1990) but cautioned that the choice of smoothing factor had a profound effect on the bias observed in the final estimates.

Seaman et al. (1999) expanded on Worton's analysis. They used simulated data of between 10 and 200 points from more complicated distributions of 4-16 merged bivariate normal distributions, designed to mimic animal movements more closely, to test the influence of sample size and different methods of choosing  $h$  on kernel home range estimates. The precision of KDE improved to an asymptote of 5-20 percent bias as sample size increased to 50 data points for simple distributions and 200 with complex distributions. They concluded that  $h$  values chosen using LSCV produced the most reliable estimators of the distributions, by giving the lowest frequency of poor estimates when compared to the reference smoothing parameter ( $h_{ref}$ ) at sample sizes between 20 and 200 points.

Despite concerns over the superiority of kernels (Robertson et al. 1998), LSCV fixed kernels have gained in popularity (Powell 2000) and are viewed as applicable in all but a few specific situations (Blundell et al. 2001). Perhaps worryingly for advocates of LSCV KDE the method's performance has been reviewed more critically by statisticians (Sain et al. 1994; Wand and Jones 1995; Jones et al. 1996). They point out that LSCV may seriously underestimate the value of  $h$  appropriate for a given distribution and that variation in values of  $h$  chosen by LSCV ( $h_{lscv}$ ) may be considerable compared to methods such as the "Solve-the-Equation Plug In" which have as yet not been adapted to home range analysis (Wand and Jones 1995; Jones et al. 1996; Kernohan et al. 2001).

A recent study used GPS data from moose (*Alces alces*) to test LSCV KDE (Girard et al. 2002). Comparing kernels made from fewer locations to those estimated from using the majority of the data, they concluded that up to 300 locations were required for the home range estimates to become accurate; slight improvements were noted up to sample sizes as large as 850. As the apparent accuracy of LSCV KDE improved with increasing size of already-large samples, they advocated the use of GPS telemetry as a method for obtaining adequate sample sizes.

We extended these tests to a different species and to individuals with markedly different home range use patterns in order to explore the relationship of sampling intensity with home range size and stability in more detail. We used 4 large data sets (>3,000 points) spanning 9-12 months, collected from lions (*Panthera leo*) with Global Positioning System (GPS) collars.

## **Methods**

Ten Televilt Simplex Predator 2D collars were placed on lions in the Makgadikgadi Pans National Park in Botswana, between May 2001 and January 2002. The collars were scheduled to take 15 positions in every 24 hour period and made 94.5% of fixes attempted. Data were retrieved via a coded VHF transmission and lions were located by radio tracking (Telonics TR-4 receiver and 4 element Yagi antenna (Powerserv, Maun Botswana). The data were received and stored with a 4 element Yagi antenna

(Televilt Y4-FL) and a receiver/data logger (Televilt RX-900). Data were decoded using Televilt SPM software. Due to a considerable failure rate (70% of collars failed within 30-200 days (Hemson 2002)) continuous data were available from only four lions: two males and two females.

UG and SP were territorial males yielding 3968 and 4624 positions respectively. 5069 positions were recorded for NI; a solitary adult female, who denned during the study period. AR was an adult female who left her natal pride shortly after tagging; 5073 locations were downloaded from the collar showed a range split into two overlapping seasonal areas.

Data were converted to the Universal Transverse Mercator coordinate system and sub-sampled to simulate radio tracking strategies using code written for the SAS system (SAS Institute Inc. 1989). Fixes were drawn twice a day (without replacement), once a day, or at intervals of two, four, seven, 14, 21 and 28 days for each animal. The start point for each sub-sample was a random day within the first 30. The tracking strategy for each animal contained 100 sub-samples.

LSCV 95% contours were created for all sub-samples on a 40 x 40 grid using Ranges6 (Kenward et al. 2002). LSCV begins at  $1.51 * h_{ref}$  and works downwards in steps of 0.02 to  $0.09 * h_{ref}$  and stops if it reaches an inflection, at which a decreasing downward slope becomes an upward slope (indicating a local minimum) or increases again in a downward direction (indicating that a local minimum would have been likely with a smaller step size than 0.02). This method was preferred over local and global minimum options as it was most sensitive to changes in the gradient of the function and less likely to fail. If it was unable to find an inflection we used the Ranges6 default substitution of  $h_{lscv}$  with  $h_{ref}$ . Therefore  $h_{used} = h_{lscv}$  if  $h_{used} \neq h_{ref}$  and if  $h_{used} = h_{ref}$ , LSCV has failed.

Plots of variation of  $h_{used}$ ,  $h_{lscv}$  and  $h_{ref}$  were examined to compare the trends in variability of these estimates between sampling intervals and animals:

- 1) The value of  $h$  used ( $h_{used}$ ) to create the contour using the LSCV algorithm (accepting that LSCV failure would cause substitution with the reference smoothing parameter).

- 2) Only those values created from an inflection point in the LSCV function ( $h_{lscv}$ ).
- 3) The value of  $h$  calculated by the reference method ( $h_{ref}$ ).

If the home range estimator used is perfect then all sub sampled home range estimates within each animal should be identical, having been sampled from the same source distribution. As such we used variation of home range estimates within a particular tracking strategy as an index of home range performance. Stability of home range estimates was assessed using overlap analysis in Ranges6 home range analysis software (Kenward et al 2000). The percentage overlap of each range with each other within a sub-sample was calculated, and a matrix created. If all home range estimates were identical, all values in the matrix would be 100%. The mean and standard deviation of the values were used as indices of stability for each sampling interval.

To test whether the performance of LSCV or the value of  $h$  could be predicted from characteristics of the utilization distribution, descriptive statistics were calculated for each sub-sample using the harmonic mean routine (Spencer and Barrett 1984). These statistics describe features of the distribution without circularity in our analysis. Analogous statistics from KDE were not used (e.g. Kenward et al. 2001) because these are dependent upon the value of  $h$ .

1. The dispersion of the data or “the peak density value (at the range centre location) divided by the standard deviation of the density value across all the locations”.
2. The “Value” or probability density score at the peak of this density.
3. Skew. Estimated by measuring the distance between the arithmetic centre and the location with the peak density and dividing by the standard deviation of the density across all locations. A measure of the tendency for fixes to be distributed asymmetrically about this mean.
4. Kurtosis. An assessment of the size of the tails of the distribution as compared to a normal distribution of the location distribution (Kenward et al. 2001).

We investigated the output statistically addressing three issues.

- 1) We used GLM to ascertain how influential  $h$  is in predicting the size of the range.



- 2) We used a binary logistic regression to try and investigate what attributes of the distribution of the data cause failure of the LSCV algorithm.
- 3) We explored which attributes affected the multiple of  $h_{ref}$  equivalent to values of  $h_{lscv}$  used when LSCV was successful with a forward stepwise general linear model (Minitab GLM procedure).

## Results

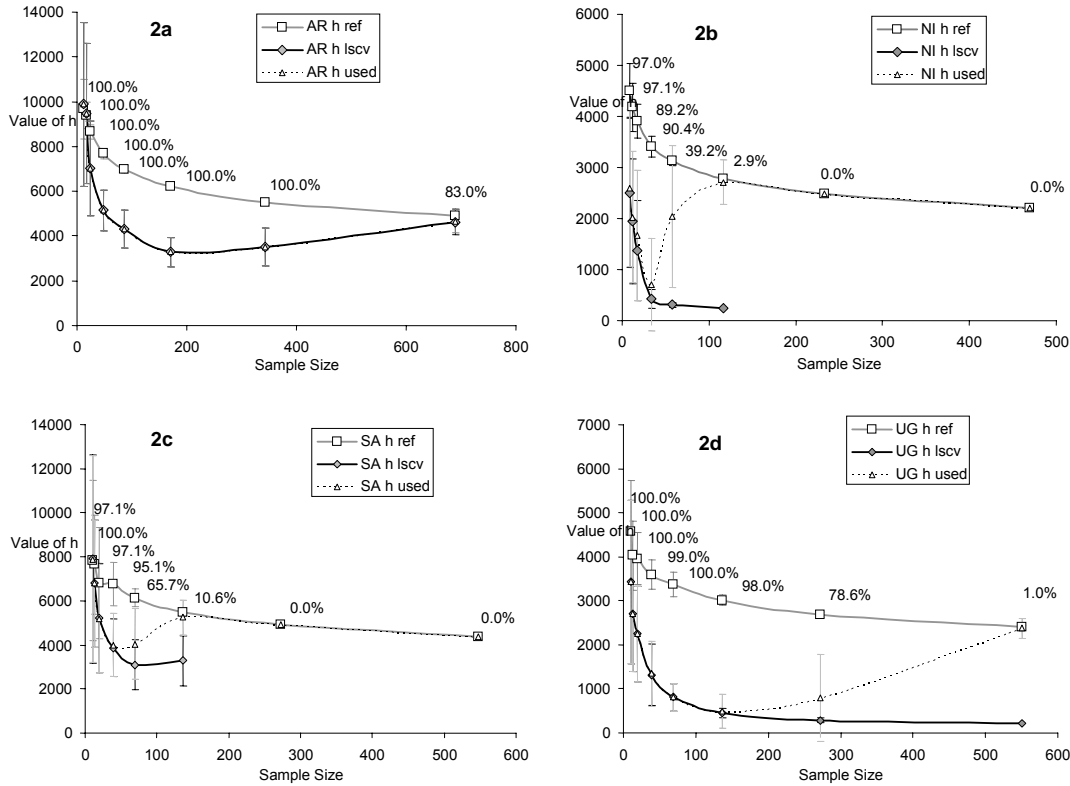
The value of  $h$  used has a significant influence over the size of range as estimated by KDE using our sample data sets. The predicted 95% area using  $h$ , sample size and the individual animal as predictors was strongly positively correlated with the value of  $h_{used}$  (Coef = 6.13 m<sup>2</sup> per unit smoothing factor,  $F_{1, 3283} = 4167.70$ , partial  $r^2 = 35.4\%$   $P < 0.001$ ).

The divergence of the  $h_{used}$  line from the  $h_{lscv}$  line in (Figures 2a-d) represents failure of LSCV to find an appropriate value of  $h$  and replacement of  $h_{lscv}$  with  $h_{ref}$  (% success also shown). If the failure rate is 0% then mean  $h_{used} = \text{mean } h_{lscv}$  and if it is 100% then mean  $h_{used} = h_{ref}$ . Thus for animals NI and SA, LSCV starts failing at sample sizes below 100 and produced no values at sample sizes larger than 150. With UG the LSCV algorithm begins to fail at sample sizes of 300 or more and has a 99% failure at 550 points. AR is successful throughout the range tested with only 13% failure at nearly 700 locations.

If the relationship between  $h$  and sample size is inspected only for those samples where the algorithm succeeded (i.e. the  $h_{lscv}$  lines in figures 1a-d), the values and variation of  $h_{lscv}$  initially tended to decline with increasing sample size. UG and AR both produced  $h_{lscv}$  values up to quite large sample sizes and AR showed signs of an increase in the mean value of  $h_{lscv}$  at samples larger than 200, converging towards the mean value of  $h_{ref}$  at around 700 points. Mean  $h_{lscv}$  values for UG appear to reach an asymptote at around 120 and did not converge on  $h_{ref}$ . The decline in variation of  $h_{lscv}$  at larger samples is in part an artefact of declining numbers of values of  $h_{lscv}$  as LSCV failures become more frequent, as is the increased conformity of  $h_{used}$  with  $h_{ref}$ . The results for AR (Figure 1a), which had the highest success at high sample sizes,

suggests that actual variation in  $h_{lscv}$  remained fairly constant at sample sizes larger than 180 fixes.

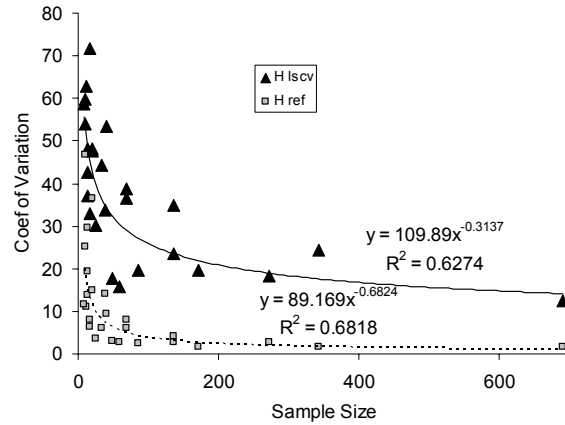
Figure 2a-d: The mean and standard deviation in the values of  $h_{used}$ ,  $h_{lscv}$  and  $h_{ref}$  produced with changes in mean sample size per sub sample and the percentage of lscv success within each sub-sample for AR, NI, SA and UG (lines are smoothed interpolations and not fits).



The trend in  $h_{ref}$  with sampling size was more stable and predictable than that observed for  $h_{lscv}$  and variability of  $h_{ref}$  declined with increasing sample size (figures 1a-d). Variation in  $h_{ref}$  was considerably less than in  $h_{lscv}$  and approached an asymptote at around 100 locations (Figure 3). Both are to be expected since  $h_{ref}$  is a function of the standard deviation and sample size, and estimates of the standard deviation will become less variable as sample size increases. The mean value of  $h_{used}$  reflects the percentage of LSCV success and the proportion  $h_{ref}$  or  $h_{lscv}$  used. All animals showed a tendency for an initial steep decline in the value at lower sample sizes whilst LSCV is still successful. At higher samples sizes for SA, NI and UG,

mean  $h_{used}$  increases towards  $h_{ref}$  as LSCV success rate declined and  $h_{lscv}$  was replaced more frequently and in AR,  $h_{used}$  tracks  $h_{lscv}$  very closely as LSCV failure is minimal.

Figure 3. Plot of the coefficient of variation in  $h_{ref}$  and  $h_{lscv}$  against sample size.



The 95% core range estimates were highly variable at low sample sizes tracking the variation in  $h_{used}$  (Figure 4). Our index of range estimate stability (mean percentage home range overlap) increased, and the standard deviation around this mean decreased, as sample size increased. Mean percentage overlap tended towards asymptote at between 100 and 150 data points for 3 of the 4 animals, but at closer to 500 points for UG. (The asymptote for NI and SA is an artefact of the failure of LSCV at sample sizes greater than c 100).

Given, the strong dependence of the estimated area on whether the LSCV algorithm succeeded or not, it was of some interest to investigate the attributes of samples which affected the likelihood of LSCV success. Binary logistic regression was used to predict the probability of success or failure of LSCV using kurtosis, value, sample size and skew of the utilisation distributions. Predictors were standardized (expressed in SD units) to compare the relative contribution of each predictor over the range of observed values (the large sample sizes generated statistically significant  $P$  values throughout).

Figure 4: The relationship between mean and standard deviation percentage overlap, as indices of stability, with increasing sample size for 95% cores calculated using the Ranges6 LSCV routine.

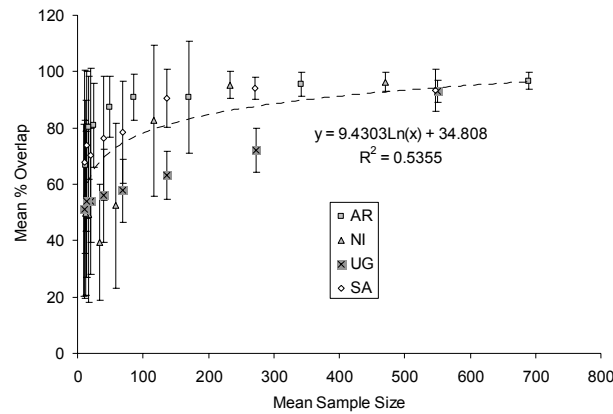


Table 1: Pearson's  $r$  for correlations between sample size and various range use statistics calculated using the harmonic mean routine in Ranges6.

	Sample Size	Value	Spread	Dispersion	Skew
Value	0.778				
Spread	0.991	0.827			
Dispersion	0.758	0.971	0.805		
Skew	-0.439	-0.527	-0.460	-0.584	
Kurtosis	0.822	0.366	0.771	0.398	-0.301

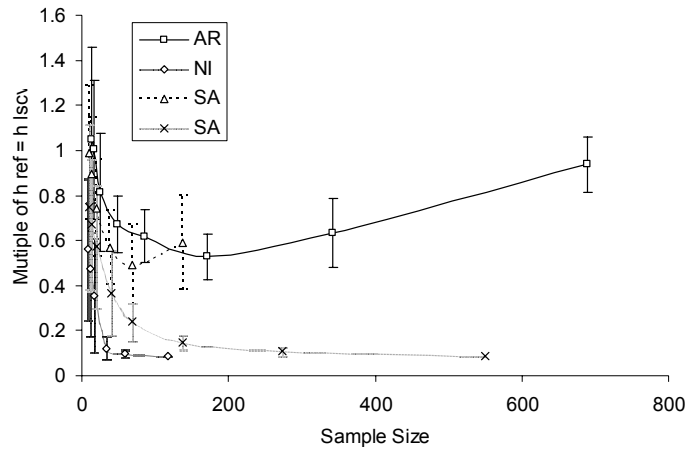
Dispersion and spread were very strongly correlated with value and sample size respectively (table 1) and were therefore not included in the final model (table 2). Sample Size was the best predictor of LSCV failure (Table 2), though correlations among the variables complicate interpretation. Value and Kurtosis and Sample Size were all negatively correlated with the probability of LSCV success.

Table 2: Outcome of the binary logistic regression modelling LSCV success. Odds ratio (reciprocals in brackets for values lower than 1) signifies size of effect based on standardized values of predictors (all  $P < 0.001$ ). 97.6% LSCV successes and 85.5% of LSCV failures were correctly predicted by the model ( $> 0.5$  = success and  $< 0.5$  = failure)

Predictor	Coefficient	Odds Ratio	Lower 95% CI	Upper 95% CI
Value	-0.9985	0.37 (2.7)	0.17	0.79
Skew	1.0752	2.93	1.74	4.92
Kurtosis	-1.2995	0.27 (3.7)	0.15	0.51
Sample Size	-4.1972	0.02 (50.0)	0.0	0.10

We investigated whether sample size could be used to predict the mean value of  $h_{lscv}$  expressed as a multiple of  $h_{ref}$ , among the four lions. However, there was no consistent pattern in the multiple of  $h_{ref}$  calculated as  $h_{lscv}$  versus sampling interval (figure 5). There is some negative correlation between sample size and the multiple of  $h_{ref}$  used at small sample sizes, although it does not appear consistent between animals and variation is considerable.

Figure 5: The relationship between multiple of  $h_{ref}$  used as  $h_{lscv}$  when LSCV was successful and sample size.



A GLM modelling the influence of the measures of the shape of the utilisation distribution on values of  $h_{ref}$  equivalent to values of  $h_{lscv}$  when LSCV succeeded, left

considerable variation unexplained (Table 3). “Value” was significantly negatively correlated with the multiple of  $h_{ref}$  used and had the most explanatory power. Sample size, skew (both positively associated with use of LSCV), as well as kurtosis (negatively associated) were all statistically significant but of relatively minor effect size. Comparison of the adjusted and sequential sums of squares suggests that collinearity among predictors does not affect conclusions to an important extent, with the exception of sample size, which was a more useful predictor in a model adjusting for the other predictors. Quadratic functions resulted in relatively minor improvements in the predictive power of the model and were therefore not retained in the final model. A similar observation applies to second order interaction terms between main effects.

*Table 3: General linear model, using a forward stepwise approach, predicting the multiple of  $h_{ref}$  used by LSCV against standardised measurements of value, skew, kurtosis and sample size based on harmonic mean calculations (all  $p < 0.001$ ).*

	Sequential Sums of Squares	% Variation Explained	Adjusted Sums of Squares	Coefficient
Lion ID	85.51	27.78%	91.43	-
Value	39.1	12.7%	33.74	-0.38
Sample Size	12.32	4.00%	18.60	0.53
Kurtosis	13.39	4.34%	9.91	-0.31
Skew	3.60	1.17%	3.60	0.06
Error	153.99	50.02%	153.99	
Total	307.86			

## **Discussion**

The value of  $h$  used to calculate KDE home ranges is an important determinant of the end result (e.g. Figures 1b-d). In GPS data from 3 of 4 lions LSCV was only consistently successful for deriving values of  $h$  at sample sizes less than 100 locations (Figures 2a-d) However despite this “success” the variation in values of  $h_{lscv}$  created were also highest at sample sizes less than 100 suggesting that systematic variation of LSCV at lower sample sizes is considerable (Figure 3). Indeed, stability of LSCV KDE estimates, as indicated by mutual overlap, was poor for samples of fewer than

200 points (Figure 4) for all lions and up to samples of 500 locations for UG. The encouraging subsequent improvement in stability beyond these sample sizes is an artefact of the increasing substitution of  $h_{LSCV}$  with the less variable  $h_{ref}$  caused by increased failure rates of LSCV at larger sample sizes. Whilst this substitution is one method of coping with LSCV failure, there does not appear to be consistent relationships between  $h_{LSCV}$  or  $h_{ref}$  with any measure of the utilisation distribution that might make a basis for an alternative to this method (Table 3 and Figure 5). Only 39% of LSCV attempts on samples above 100 locations were successful (Figure 2a-d) most of them from AR.

Failure of LSCV is caused either by a large number of identical points (Silverman 1986) or a high proportion of points that are very close, relative to  $h_{ref}$ , in the latter situation LSCV would select a value below the range searched. The probability of these occurring increases considerably with increasing sample size and peak density (Value) (table 2) that result from an animal repeatedly visiting restricted areas of its range. Rising failure rate with increasingly leptokurtic distributions reflects a decrease in the standard deviation of the estimated distribution indicative of a narrower and therefore denser peak density value. Intense peaks of density such as that observed with NI (actually caused by a denning period) also lead to low values of  $h$  (table 3) and therefore undersmoothing across much of the range. LSCV is most likely to work with more platykurtic or homogenous spatial distributions such as that exhibited by AR, with no areas of repeated high intensity use and low relative peaks of density. However, it is unclear how prevalent uniform use may be in animals and as such a home range estimator relying on this property may have limited applicability.

That previous studies using computer modelled distributions have returned results at odds with our own findings warrants explanation. It appears that there have been no attempts made to model the repeated use of focal sites (such as dens, leks, resource patches, roosts, territorial boundaries etc) by animals. One recent study stated that “there are few identical points or very tight clusters within our simulated points (in this case multimodal combinations of normal distributions), so LSCV rarely failed” (Gitzen and Millspaugh 2003) and it is inferred from the paper that this data was similar to that used in previous studies (Seaman and Powell 1996; Seaman et al. 1999). This suggests that computer simulated data used were unlike the data from

three of the four lions in this study which had very close or identical points and clusters of locations around favoured sites.

While the properties of simulated data drawn from known distributions may be well understood, such data may not generally mimic the inevitable irregularities exhibited by real data-sets. If simulated data sets are to be used to test home range estimators they should be representative of animal range use.

In the one other study of LSCV based on GPS data (Girard et al. 2002), there was an apparent improvement in precision of fit with the total data set up to very large sample sizes. This was also the case in our study for  $h_{used}$ , but the effect was mainly an artefact of increasing substitution of  $h_{lscv}$  with the less variable  $h_{ref}$  caused by failure of LSCV at larger sample sizes. As the Girard et al. (2002) estimates were created with RangesV which uses  $h_{ref}$  as a substitute value (Kenward and Hodder 1996), a similar explanation may apply in their case especially as the reference ranges used to estimate accuracy of home range estimates made with varying sample sizes were those calculated using 3 locations per day (mean 1559 locations).

Increasing sample size may be considered desirable for increasing the precision of a range estimate, but it also increases the probability of recording returns to favoured areas of the range, thus reducing the likelihood of LSCV success and of obtaining a representative home range. Thus we caution the use of LSCV KDE on large samples such as those generated by GPS-collars. Despite suggestions that KDE does not require serial independence (De Solla et al 1999) it seems likely from our analysis that problems should be anticipated for data with very short sampling intervals (i.e. highly auto-correlated), although in our examples there was more than one location per day only when sample size exceeded 400.

In previous studies, kernels created with  $h_{ref}$  for sample sizes over 100 points, had much higher area bias (20-60%) than LSCV (0-20%), and consistently overestimated the area of the home range or distribution (Sain et al. 1994; Worton 1995; Wand and Jones 1995; Seaman and Powell 1996; Seaman et al. 1999; Kernohan et al. 2001; Gitzen and Millsaugh 2003). As such we investigated whether it might be possible to use a smaller multiple of  $h_{ref}$  as an appropriate  $h$  but could see no evidence of stable



relationships between multiples of  $h_{ref}$  and sample size or other range use parameters. We conclude that spatial features specific to individual lions and related to environmental variables (e.g. cubs, prey distribution, hard and soft edges to the ranges and socio-ecological range use requirements etc.) account for the variation unexplained by the GLM and the considerable variation between individuals. We therefore consider that substitution of  $h_{lscv}$  with a multiple of  $h_{ref}$  is an unsatisfactory method of coping with LSCV failure although a better method is elusive.

One recent study shows that differences exist between different methods of LSCV implementations (Gitzen and Millspaugh 2003). Different interpretations of these methods may create even greater variation depending on the scale over which the algorithm is allowed to search, use of global or local minima and absolute or gradient inflections, the direction of search and the programming language used. An experimental implementation that attempted LSCV with larger increments of  $h_{ref}$  (0.1) and started with  $1 \times h_{ref}$  yielded poorer results with only 22% of LSCV attempts successful with samples larger than 100 but with similar patterns of variation in  $h$  values. The Ranges6 implementation we used (it can also search for global and local minima) should fail less often than others by searching over a larger range of values ( $1.51-0.09 h_{ref}$ ), in smaller increments ( $0.02 h_{ref}$ ) and stopping at a gradient inflection rather than a global minimum. Our results may be influenced by our choice of software implementation but are consistent with the mathematical theory and we are confident that higher failure rates would be expected from other LSCV implementations particularly those that search for global minima. All publications based on LSCV KDE should indicate the methods used for LSCV, failure rate and the treatment of failures.

Explorations of less variable alternatives to LSCV, such as Solve-the-Equation Plug-in methods, (Wand and Jones 1995; Jones, Marron et al. 1996) need to be made for bivariate data, and alternatives to kernel density estimation such as those using local polynomials explored (Loader 1996; Loader 1999). Whilst the science of home range estimation will develop and new methods be devised, a concerted effort must be made to reach some consensus of which methods perform best in which situations and for which ends (e.g. Powell 2000; Kernohan et al. 2001; Kenward et al. 2001).

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## Chapter 5: Final Discussion

As set out in the introduction, my goals in this study have been to address aspects of the ecology and behaviour of lions relevant to challenges to their conservation in the Makgadikadi Pans National Park, and to do so in the wider context of the human community surrounding the park.

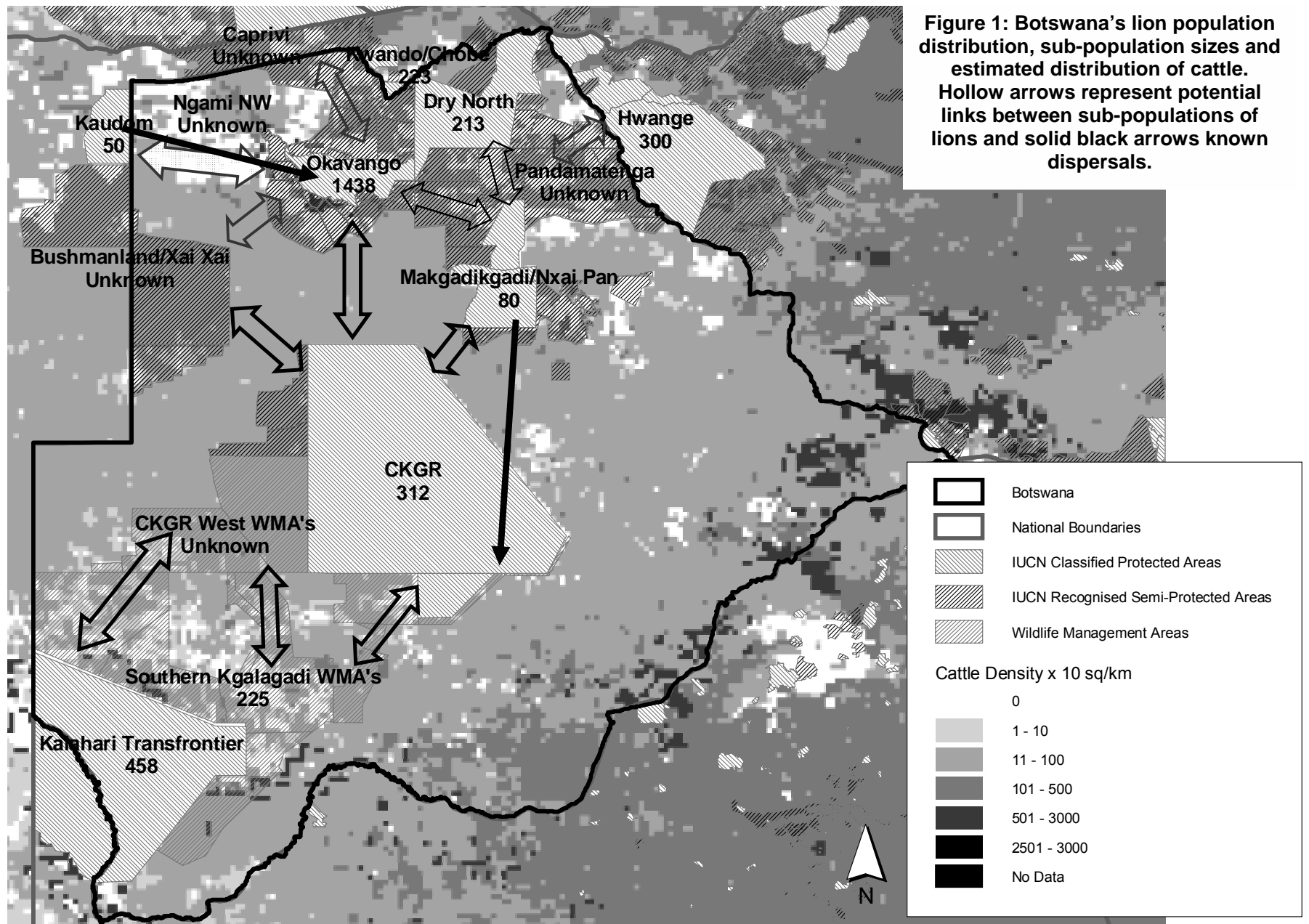
In particular, my hope has been to use science to underpin and inform policies aimed at conserving viable populations of lions in Botswana and especially at mitigating conflict between livestock owners and the species. The Makgadikgadi made an ideal setting for this work: the combination of several factors, a national human-lion conflict hotspot (Meynell & Parry, 2002; Nagafela & Kalikawe, 1993; Wint, 1997), surveyed populations of migratory and resident wild prey (Wint, 2000), several safari camps, and a traditional livestock owning community provided me with a natural laboratory and a microcosm of several important aspects human-lion conflict. While no single study can realistically hope to provide definitive answers to a problem whose complexity is evident when mapped out (Loveridge *et al.*, 2002) I hope these results will be useful both locally, regionally and internationally as a contribution to the growing body of data in this field.

In this final chapter I will summarise the key findings of my study and try to relate them to wider issues in conservation and ecology; specifically, I will ask what lessons for lion management might be drawn from my findings, and what questions now emerge as priorities for future work.

### ***Lions in Botswana***

I shall begin by revisiting the context for this thesis with a brief exploration of some key issues pertinent to species survival in the country. Botswana hosts Southern Africa's largest lion population (approximately 3,000 lions). The northern populations live at high densities in a large matrix of protected and semi-protected areas. Lions living in the arid central and southern parts of the country occur at lower population densities ( $\pm 1$  lion per 100km<sup>2</sup>). These populations are potentially connected to each other, and to the larger northern populations, across areas designated as wildlife management or livestock grazing areas (Figure 1). While long distance dispersals

have been recorded across these areas (a collared sub-adult male from this study and another branded in Namibia (Stander & Wintebach pers. comm.)) it is currently unknown how many animals move between these populations. The results of viability studies are frequently equivocal and often disputed, however at least one recent study suggests we should be considering populations of thousands of animals to ensure species survival into perpetuity (Reed *et al.*, 2003) see also (Creel, 1998; Reed & Bryant, 2000). In the light of these predictions it becomes important that the contiguity of Botswana's lion population and its connections to populations in neighbouring countries are retained or expanded. If this is to occur then lions will need to be able to move through or live in areas in which livestock farming is a major or sole land use option.



## ***Key findings***

### **1. Lion predation on livestock is influenced by the relative abundance of wild prey and livestock**

- Increases in wild prey abundance result in decreases in the frequency of livestock predation disproportionate to the changes in abundance.
- Foraging theory suggests that, while we can measure abundance, it is likely that lions respond to the availability of prey, of which abundance is only one component.

### **2. Lions changed their movement patterns according to whether they were predating predominately upon wild prey or upon livestock**

- When wild prey was scarce they moved closer to human habitation and spent more time in areas where livestock were likely to be encountered.
- These movements appeared to be limited by the probability of encounter with humans and lions spent less time near habitation during the day than they did at night.
- Livestock were frequently left out at night, increasing the probability that it would be killed.
- Despite there being less prey overall stock-raiding lions used smaller areas when predating on livestock, a predictable and aggregated resource.

### **3. Static defences did not have a significant affect on reducing livestock predation by lions in the Makgadikgadi**

- Livestock owners confirmed that livestock were frequently left out at night and as such are vulnerable to lions away from the protection of static defences.



- 4. The benefits from tourism did affect attitudes towards lions and wildlife, but these effects were largely limited to tourism employees who constituted a minority in the community**
- A large proportion of the economic benefits from tourism was accrued as wages and did not appear to influence the attitudes of people not linked directly with the industry.
- 5. Most people viewed the problem of livestock predation as one which the government was responsible for resolving**
- Livestock owners indicated that they would be prepared to take measures aimed at reducing livestock availability if the government also invested.
- 6. Lion home-range size and population density are exponentially correlated with prey abundance during times of prey scarcity**
- This exponential function *may* be explained by the pattern of aggregation of animals in herds and of those herds at points of attraction.
  - If so it is possible that resource dispersion plays an important role in defining lion social ecology.
- 7. Kernel home-range estimation is flawed**
- The least squares cross validation technique (LSCV) recommended for kernel home-range analysis introduces systemic variation that it is difficult if not impossible to control for, especially with data from animals that revisit locations.
  - Computer simulated animal movement data have not yet captured all the significant elements of the movements of animals.
  - With GPS-collars it is possible to produce comparable volumes of data to that hitherto more characteristic of computer simulations.

- I have presented methods by which accuracy of a home-range estimator may be inferred in the absence of knowing from what distribution the data are drawn.
- 

## ***Implications of this study's key findings***

### **1. The role of prey availability in limiting livestock predation**

There has been speculation in the literature that adequate wild prey abundance may reduce livestock predation by large carnivores. The few data that exist outside this study are equivocal (Cozza *et al.*, 1996; Hoogestein, 2000; Mizutani, 1999; Novaro *et al.*, 2000; Polisar *et al.*, 2003; Rudnai, 1979; Sidorovich *et al.*, 2003; Weber & Rabinowitz, 1996), and in at least one case (Stahl *et al.*, 2002) livestock losses appeared higher in areas of the highest wild prey density. Perhaps as a result of the poor quality of available evidence, the potential for wild prey to mitigate livestock loss conflicts is not emphasised in IUCN conservation action plans (e.g. Mills, 1998; Nowell & Jackson, 1996).

I have provided empirical evidence that wild prey abundance can buffer livestock owners against losses. Lions in the Makgadikgadi take wild prey more frequently per unit abundance than they take livestock. As such wild prey may play a role in reducing livestock predation disproportionate to the relative abundance of livestock and wild prey. By exploring predation in terms of hypothetical costs and benefits it appears that decreasing the availability and abundance of livestock relative to wild prey may also reduce livestock losses. Livestock availability could be reduced by building enclosures for livestock that did not allow lions to enter or livestock to escape when panicked, increasing the numbers of guard dogs at the cattlepost, ensuring there are people available to respond to the alerts provided by guard dogs, herding livestock closely during the day and ensuring it is enclosed at night (Frank, 1998; Kruuk, 1980; Ogada *et al.*, 2003; Stander, 1997).

## **2. The implications of least squares cross-validation limitations**

The LSCV component of kernel home-range estimation imposes considerable limitations on the distributions of data to which the method can usefully be applied. There is no clear alternative to LSCV and no way of transforming data to conform to requirements of LSCV without affecting the biological value of the data. Great care should be taken when both using kernels as a home-range estimator and interpreting analyses that used the method; system error may introduce bias into results that is difficult to control for. The interpretation and use of kernels and indeed other home-range estimators may be further complicated by variation in implementations between software packages (Gallerani Lawson & Rodgers, 1997; Larkin & Halkin, 1994). While kernels may produce variable results as to home-range size and shape, they may still be useful in describing the internal structure of home-ranges, as long as the analysis can be planned to avoid the limitations I have exposed.

## **3. How knowing the movements of livestock and lions can contribute towards reducing livestock losses**

The understanding of the spatial and temporal aspects of space use by problem carnivores is largely limited to locations of livestock kills e.g. (Mazzolli *et al.*, 2002), the location of conflict hot spots or seasons (Jackson, 1996; Odden *et al.*, 2002; Oli *et al.*, 1993; Polisar *et al.*, 2003; Stahl *et al.*, 2001) and a handful of radio-tracking studies (Rabinowitz, 1986; Stahl *et al.*, 2002). By using GPS-collars I was able to explore the movements of stock-raiding lions in unusual detail and relate these to patterns of human habitation and movements of livestock. The movements of stock-raiding lions suggest that there is a trade-off between the risks associated with going hungry and those associated with encountering people, (see also Mazzolli *et al.*, 2002). As such they seem to be compelled to approach cattleposts at night and predominately after midnight, when the probability of encountering herders is lowest. Stock-raiding lions spent most foraging time away from cattleposts, and I suggest that they may be searching for stray livestock, which are fairly common in the study area (20% of GPS-collared cattle locations were away from cattleposts at night). These findings support the prediction that improving static defences alone may not significantly reduce livestock predation, as most such predation appears to occur in

areas where these defences would have no influence. A similar situation in Namibia (Stander, 1997) and quite different situations in Kenya (Frank, 1998; Frank & Woodroffe, 2002; Kruuk, 1980; Ogada *et al.*, 2003) suggest that it is important not to jump to conclusions about a particular situation prevailing in a given locality and propose interventions aimed at reducing livestock loss, without first investigating local conditions.

#### **4. The role of herding in reducing livestock predation**

The lack of close herding in Botswana and Namibia creates conditions in which controlling livestock predation without killing predators becomes difficult (Stander, 1997; Wint, 1997). The result of these conditions may be an unsustainable level of predator removal (Stander, 1997) which may compromise populations of predators considered protected by reserves and parks (Brashares, 2003; Woodroffe & Ginsberg, 1998, 2000). I have hypothesised that in Botswana, the comparative rarity of stock theft and the State policies of care for stray animals may reduce the costs of poor livestock control, in comparison to circumstances prevailing in east Africa (Frank, 1998; Ogada *et al.*, 2003). Reducing the number of strays at night and developing static defences simultaneously would appear a promising way of reducing livestock losses in the Makgadikgadi, while implementing one without the other may not have a significant effect. Unless the cost-benefit ratio to livestock owners, of herding or not herding can be changed there seems little prospect for recommended changes to herding practices to occur.

#### **5. The impacts of benefits from wildlife utilisation**

A considerable portion of the economic benefit from tourism in the Makgadikgadi accrues to tourism employees. As tourism employees are not drawn selectively from the portion of the population that loses most livestock, the result is a mismatch between the distribution patterns of tourism revenue and of livestock predation costs. Consequently, the current situation does not provide much incentive for increased tolerance for large carnivores amongst livestock owners, nor does it encourage herding practices likely to limit livestock loss. There remains a considerable need to introduce incentives beyond those presently in place or to introduce legislation which

makes up for this economic deficit, if recommended interventions are to be implemented.

## **6. The potential for state intervention**

It appeared that most people understood that both improved herding would reduce livestock losses, and that lions were valuable assets to the local and national tourism industry. However their stated impression overall was that the government benefited more than they did from the industry (an impression borne out by my calculations). This imbalance created a belief amongst many people that the Government was responsible for wildlife, and that livestock predation was an issue that the Government should address. Although livestock owners perceived that killing problem predators could constitute the loss of an asset to some sectors of their community, the benefit to themselves of the lions' presence was perceived as minimal, whereas the costs could be high. While revenue distribution might be thought of as a logical partitioning of tourism benefits between different sectors of the community, it should be restructured to redress the cost-benefit mismatch currently observed. Any revenue distribution plan should also accommodate the stochasticity in livestock predation patterns and it may be necessary to devise methods whereby benefit distribution is flexible enough to accommodate variation in losses, to minimise the probability that large losses (which are occasional and unpredictable) might spur disgruntled individuals to kill problem predators.

Under the current conditions, costs to livestock owners can probably be limited most cheaply using traps, poison and guns to kill problem predators. However, most people expressed a preparedness to try different methods of herding if the government would bear some of the costs of implementation. This attitude indicates an opportunity to implement changes to livestock husbandry, but it also indicates a negation of personal responsibility, and this may need to be addressed in order for any distribution system to be welcomed and maintained at a local level without constant intervention.

## 7. Resource Dispersion

I have provided a basis for the future exploration of the relationships between resource dispersion and lion spatial and social ecology, and highlighted the potential for ungulate herds to act as a potentially important factor influencing lion resource dispersion.

### ***Towards the mitigation of lion-human conflict in Botswana.***

Mitigation of conflict between livestock predators and livestock owners can be broken down into interventions that reduce the amount of livestock lost and those that increase tolerance for those losses (Macdonald & Sillero-Zubiri, in press). An optimal solution would be an approach that simultaneously achieves both.

The probability that an intervention will succeed in reducing livestock losses will, I have argued, depend on its ability to affect the cost-benefit ratio to the predator of predation on livestock relative to alternative wild prey sources. In Botswana, the larger ungulates that make up the bulk of lion prey occur at lower densities outside protected areas than they do inside them (Thouless, 1998; Verlinden *et al.*, 1998; Wint, 1997). Studies in Tanzania suggest that livestock and many large ungulates are able to coexist outside protected areas, even at quite high densities (Homewood & Rogers, 1991; Serneels & Lambin, 2001) and it has been argued that it is illegal hunting, and not a fundamental incompatibility of livestock and wild ungulates, which may have caused ungulate declines and prevented post drought population recoveries in Botswana (Thouless, 1998). This raises the possibility that if game hunting could be controlled, wild prey populations, particularly of those species that do not compete for grazing with livestock such as kudu (*Tragelaphus strepciceros*), might flourish in livestock grazing areas without detriment to the livelihoods of livestock owners. If the inferences derived in this study (Chapter 1) from the frequency of kills and degree of carcass utilisation for wild prey are correct, any increase in wild prey should result in a disproportionate decrease in livestock predation per lion. A caveat to this line of thought is that increases in wild prey might act in an additive rather than compensatory way, in that a net increase in lion prey could result in an increase in lion density (Van Orsdol *et al.*, 1985; Viljoen, 1993) contributing to a rise in livestock loss even if predation per lion were less. To maximise the chances of success, any

increase in wild prey abundance should be twinned with a decrease in livestock availability, to attempt to manage prey availability at more constant level and limit the potential for local lion populations to expand.

Decreasing livestock availability has been identified as a key component in many strategies directed at reducing losses to large carnivores (Conover, 2002; Jackson, 1996; Macdonald & Sillero-Zubiri, 2002; Marker *et al.*, submitted; Mills, 1998; Nowell & Jackson, 1996; Ogada *et al.*, 2003; Sillero-Zubiri & Laurenson, 2001; Stahl *et al.*, 2002). In some cases promising results have been obtained from slight improvements or intensification of traditional herding strategies e.g. (Butler, 2000; Jackson, 1996; Ogada *et al.*, 2003). However while some methods may be conceptually simple, and there is some agreement that predator proof enclosures and increased herder vigilance and presence will limit livestock loss, there is less clarity on how these changes might be implemented. African conservation efforts have shifted away from purely protectionist strategies, towards providing education, incentives and encouragement to communities, to increase participation in conservation action (Hulme & Murphee, 2001a; Kiss, 1990). However in some areas these interventions are proving inadequately rapid or failing outright (Hackel, 1999; Hulme & Murphee, 2001b). Indeed there is evidence that in areas of more marginal tourism potential in Botswana, community conservation is failing to deliver results in a timescale appropriate for conservation objectives to be realised (Rozemeijer, 2003). While it may be true that problems of revenue distribution and management may be overcome in some situations, and that considerable potential remains for this approach (Hulme & Murphee, 2001b; Rozemeijer, 2003), there are also concerns that the economic incentive of revenue generation may not be as widely applicable as some have hoped (Walpole & Thouless, in press).

Botswana currently deploys Problem Animal Control (PAC) teams to conflict hotspots in an attempt to scare problem animals away from vulnerable property, to collect and validate compensation claims, and to encourage farmers to introduce strategies to reduce damage, such as improved static defences and herding (Sechele & Nzehengwa, 2002). Partial compensation (+/-80% replacement value) is paid to reduce the financial cost of property loss and damage. In situations where problems are not sufficiently mitigated by these interventions, PAC teams may attempt to

translocate or destroy problem animals. While 75% of respondents (n=134) thought the PAC teams did a good job in the Makgadikgadi, they remained willing to kill lions and felt compensation was inadequate. It appeared that whilst they appreciated the effort, the results were not yet sufficient for them to tolerate the presence of lions. Although previously recommended as management tool in Southern Africa (Funston, 2001; Stander, 1990) translocation of problem animals has been shown to be ineffective or inhumane in some circumstances (Frank & Woodroffe, 2002; Linnell *et al.*, 1997), and killing the problem animal may prove a temporary solution unless the causes of livestock predation are also addressed (e.g. Stahl *et al.*, 2002). In a tacit admission of the failure of efforts to reduce lion killings to a level acceptable to the state, in 2001 the government introduced a ban on lion killing which it concedes has been unpopular with livestock owners, hunters and some conservationists (<http://allafrica.com/stories/200311250120.html>). Despite shortcomings as a national scheme, elements of the approach could make a greater contribution toward conservation goals if they were drawn together into a more coherent unified approach.

Compensation is a widely recommended and often used technique to reduce the economic impact of losses to wildlife in an effort to buy tolerance of problem species (Madhusudan, 2003; Nyhus *et al.*, 2003; Reiter *et al.*, 1999). However, it does not provide an explicit incentive to encourage better livestock care and some argue that it can result in the neglect of preventative measures (Dyar & Wagner, 2003). Swenson and colleagues provide an illuminating account of how different approaches to compensation in neighbouring Sweden and Norway have resulted in quite different end results (Swenson & Andren, in press). Both countries have compensation schemes; Norway pays unconditionally but pays below the market value of the loss (similar to Botswana) whereas Sweden pays over the market value but only pays farmers who have implemented state approved preventative measures. Despite higher costs per unit loss, Sweden pays substantially less in compensation per carnivore than does Norway. Sweden's sheep losses per carnivore are considerably lower and the status of its large carnivore populations is far healthier (Swenson & Andren, in press). Others have called for this approach to be instigated in the United States (Fritts *et al.*, 1992) and some have taken the concept further. In a detailed economic analysis of the problems created by the reintroduction and recovery of wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*) in the United States, Dyar and Wagner (2003) suggest



that whilst linking compensation for losses to ranchers' implementation of effective animal husbandry might be effective, the optimum solution is to compensate people for their precautionary efforts rather than for their losses. Indeed this agrees with my own findings that many livestock owners would be prepared to improve their herding techniques if the government were to assist them.

These approaches provide potential to break the deadlock between the conservation community, wildlife managers and the livestock owning community in Botswana, that will otherwise retard the implementation of potentially effective interventions such as those suggested herein.

### ***Further Work***

Alternatives to least squares cross validation should be explored.

“Solve-the-equation” plug-ins have been suggested as alternatives to LSCV in the mathematical and biological literature (Jones *et al.*, 1996; Kernohan *et al.*, 2001; Sain *et al.*, 1994). Further explorations of the performance of these methods with real animal movement data, similar to that used in Chapter 2, but from a wider range of species, could yield insights into the applicability of alternatives to LSCV. This problem of analysis is not trivial: with the advent of GPS-collars, fieldworkers are increasingly finding themselves facing a welcome, but potentially overwhelming volume of data. These data will demand more rigorous thinking, shifting the focus of how to tackle problems stemming from a paucity of data to how to tackle the right question from overwhelming data abundance.

The investigation of the role of resource dispersion in regulating lion ecology should be continued.

The value of the resource dispersion hypothesis in explaining the observed variation in lion social and spatial ecology has yet to be fully explored (Macdonald, 1983; Packer, 1986). Gathering detailed aerial census data concurrent with published data on lion ecology will allow a more direct test of RDH predictions (Johnson *et al.*, 2002). As more data on lion ecology becomes available these should also be added to

this analysis. While this topic has not been the main focus of my research, my findings have convinced me that it is a topic that could prove exceptionally rewarding.

## Improving the quality and availability of data to wildlife managers in Botswana

Despite a growing volume of data on conflict between wildlife and people, it may be some time before conservation decisions can be based solely or even largely on empirical data, as there is often a need to make changes to avert impending conservation disasters. These changes may not be as effective as anticipated and/or create problems not foreseen at their inception. As an example, Botswana banned the killing of lions by farmers in response to concerns that lion populations were declining in the country (<http://allafrica.com/stories/200311250120.html>). Faced with criticism from livestock owners that overseas tourists could still kill lions, the government expanded this ban to cover the sport hunting. In the absence of a system for assessing the impact of the ban on rural development, lion populations or human-lion conflict, the effects of the ban can only be guessed at. Some parties believe lion killings to have declined (my own evidence suggests this has been the case in the Makgadikgadi) but others that incidences of poisoning have risen, that hunting of lions in Botswana is ecologically unsustainable ([http://www.lionaid.org/new\\_sci.htm](http://www.lionaid.org/new_sci.htm)), that community conservation initiatives have been undermined (ULG, 2001), or that the killing of stock-raiding lions does not represent a threat to lion conservation anyway (Thomson, 2003). In all this there is a conspicuous absence of hard data.

The DWNP has considerable wildlife management and research capacity both in human resource and financial terms. It has a well developed network of camps and head quarters and a compensation system that with minor adjustments (recording GPS locations) could be used to monitor conflict trends in Botswana. The state has invested considerably in nationwide ungulate and livestock surveys, several large carnivore surveys, a regular national human population census, and has supported several independent research projects.

A GIS database incorporating these data layers would be a useful decision support tool with which wildlife and conflict trends could be monitored and the impacts of

local or regional interventions quantified and related to socio-economic and ecological conditions. Such a system of data gathering and collation would enable the DWNP to base management decisions on real trends and not perceptions.

### A systematic review of lion-human conflict across Africa

A considerable proportion of conservation implementation and decision-making is 'experience based', i.e. undertaken on the experiences and opinions of experts or advisory bodies, often without adequate data or other evidence. While this may be a necessity in the absence of data and in the face of pressing conservation emergencies, it is technique predisposed to high failure rates (Pullin & Knight, 2001). In the context of lion-human conflict it may yet prove not to be a necessity. It has been argued that analogous situations in medical treatment applicability have blighted health care decisions in the past. The medical community has responded to this decision making inadequacy with the concept of the systematic review (Pullin & Knight, 2001). During such an exercise all available evidence is collated and evaluated based on the quality of this evidence (ranging from strong experimental evidence, to inadequate experimental evidence and to the opinions of respected authorities) to produce an overview of the potential solutions to a problem.

It is clear that a similar "systematic review" of lion-human conflict experiences in Africa is long overdue. Every country that has populations of lions is likely to have experienced the dilemma of resolving conflict between lions and livestock owners, and to have implemented interventions targeted at increasing tolerance and/or reducing the volume of the problem. Many of these experiences and data may have been written up in internal reports and memoranda containing data of various qualities, or may exist only as the recollections of individuals tasked with resolving these problems. It has been my experience, whilst carrying out the present research, that a dedicated effort to unearth reports and experiences from previous wildlife management projects can yield unexpected and valuable information, and that a wealth of such useful information remains which is not easily accessible to decision makers due to its age or low level of circulation . These "hidden data" represent a considerable body of evidence for judging the success of many of the strategies used to mitigate conflict, and could therefore be of great value to conservation practitioners

and wildlife management organisations. The proposed systematic review would focus these experiences in a single source and perhaps relate successes and failures to ecological, economic, sociological and political factors. Future decision makers could draw from this existing body of evidence encompassing a wide range of settings rather than, as is often the case, the experiences of experts familiar with narrow subsection of the full range of settings and interventions applicable to the problem. I judge that a meticulous and exhaustive search for existing insights, and their synthesis, would be the most cost-effective, and fastest, way to reach sensible proposals for resolving conflict between lions and livestock owners.

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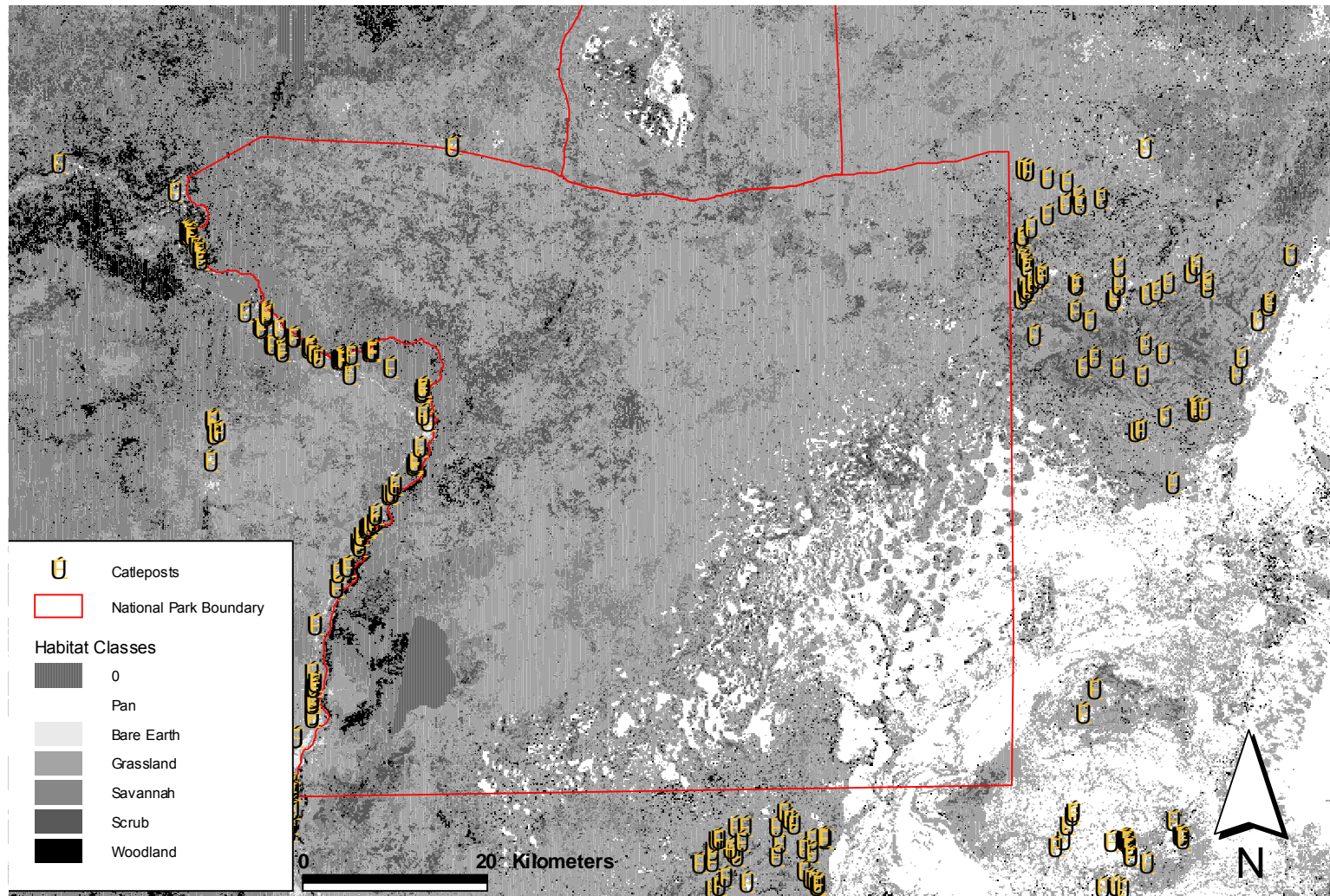
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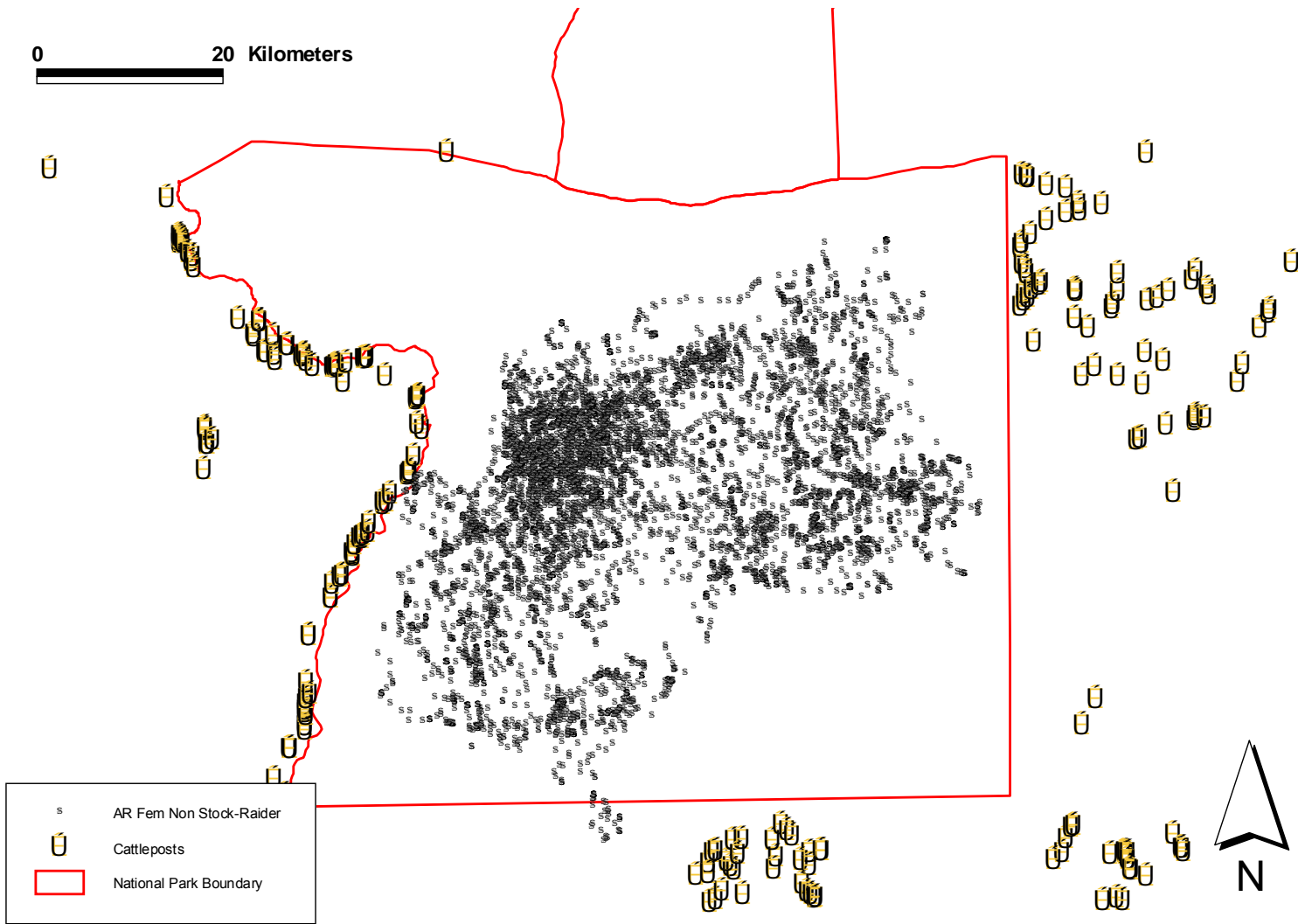
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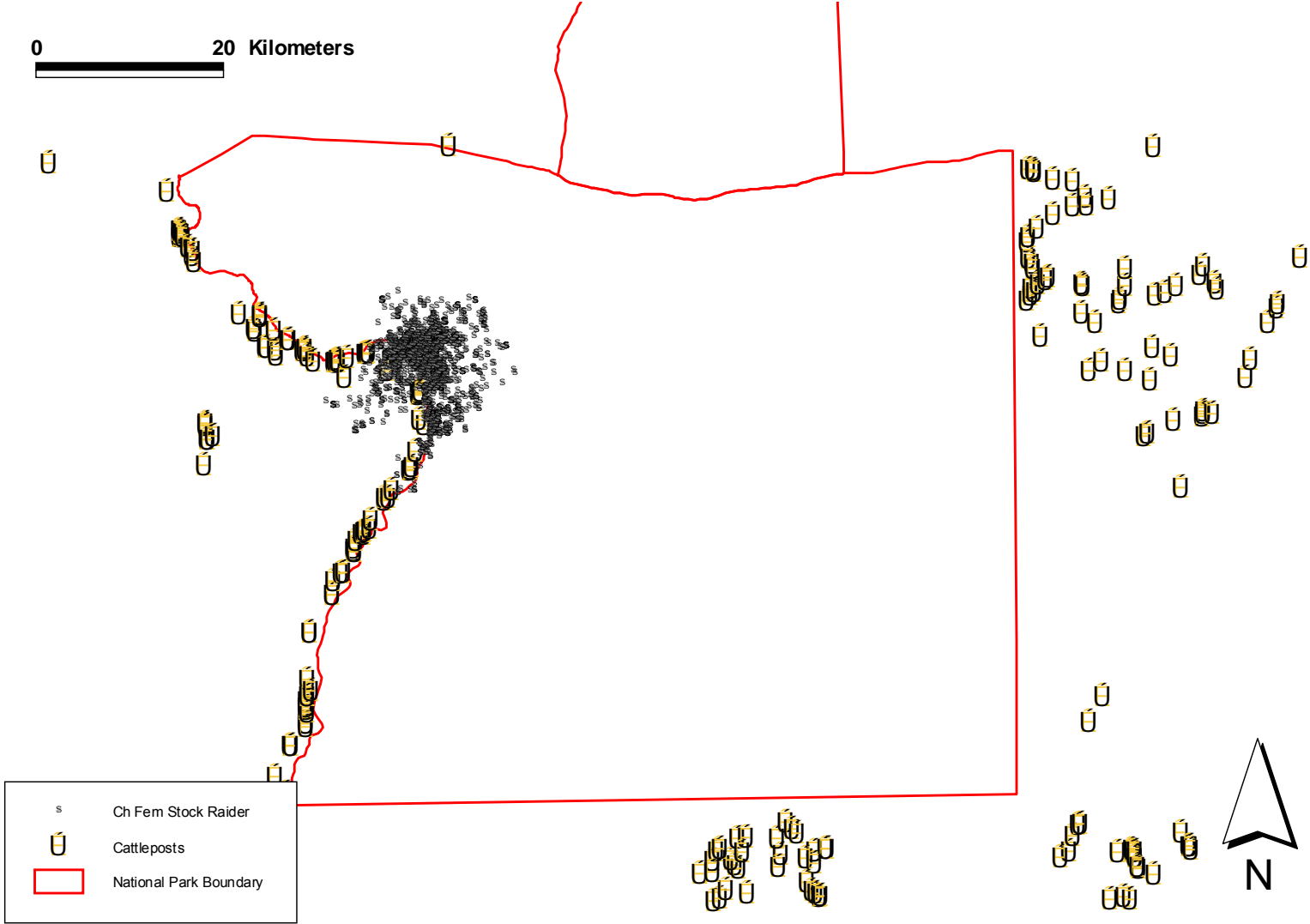
**Appendix 1: Habitat Map of the study area. For methods used see Chapter 1.**



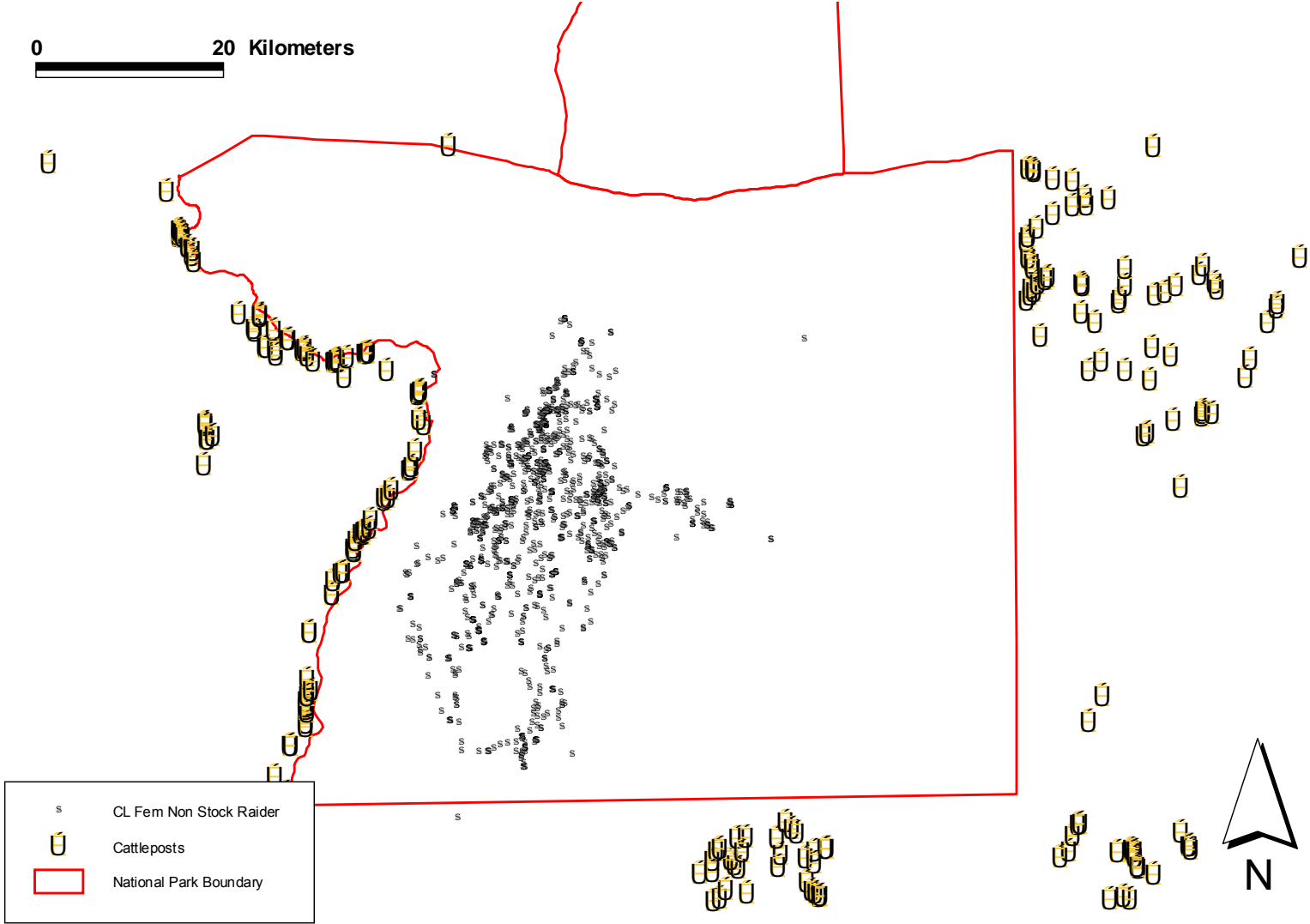
**Appendix 2a-n: The study area showing lion locations recorded from GPS and radio collars and used in this study.**



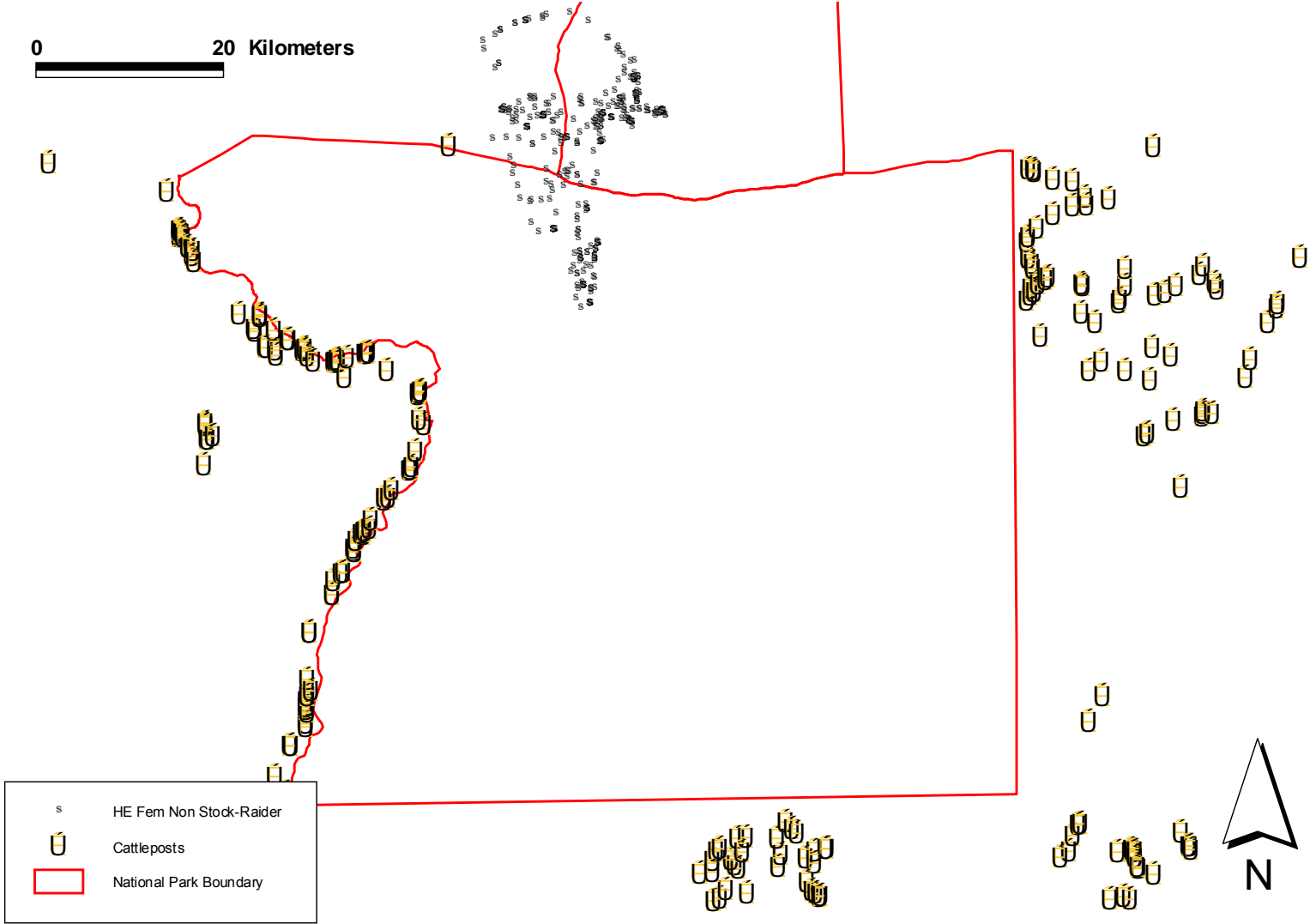
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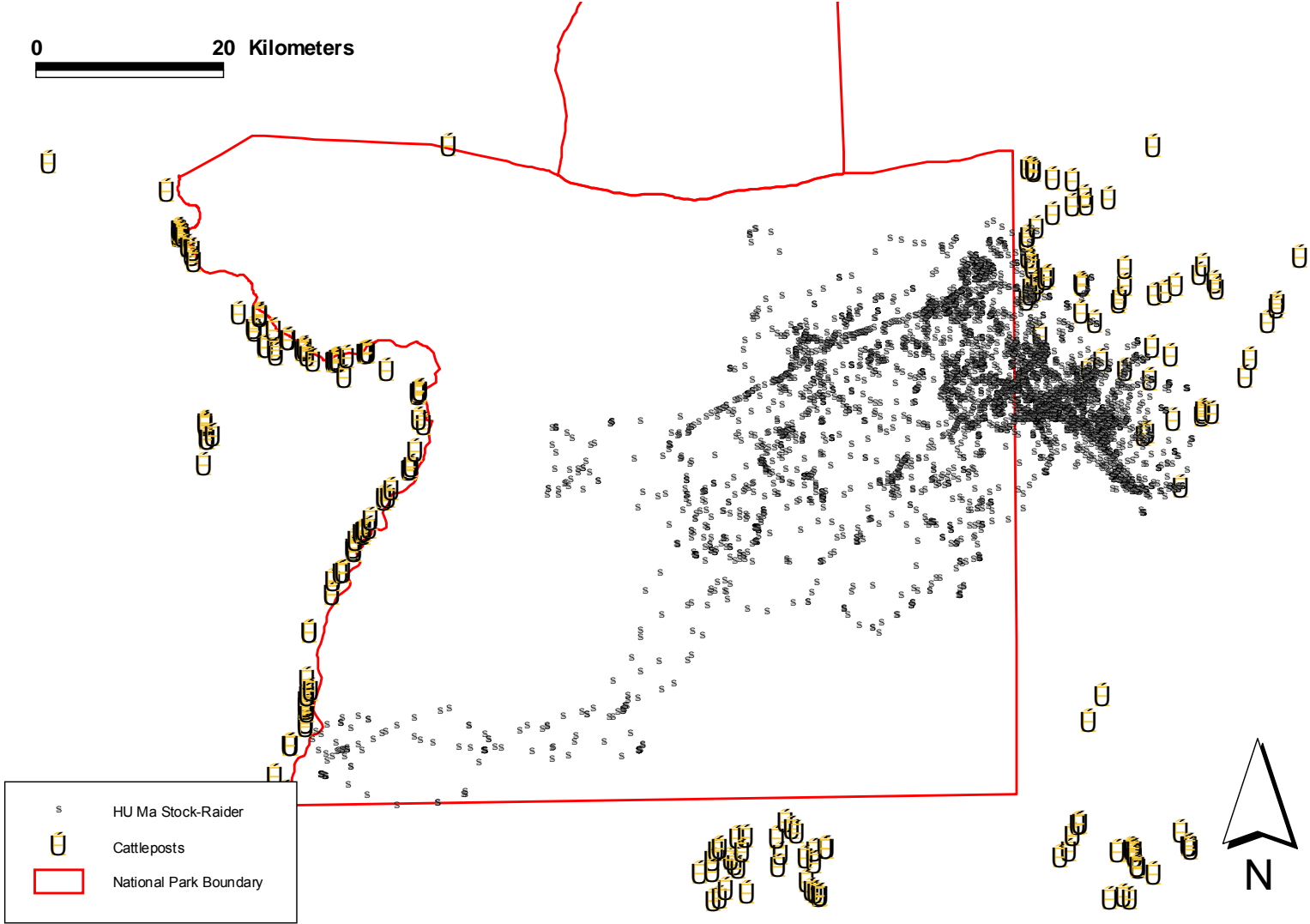
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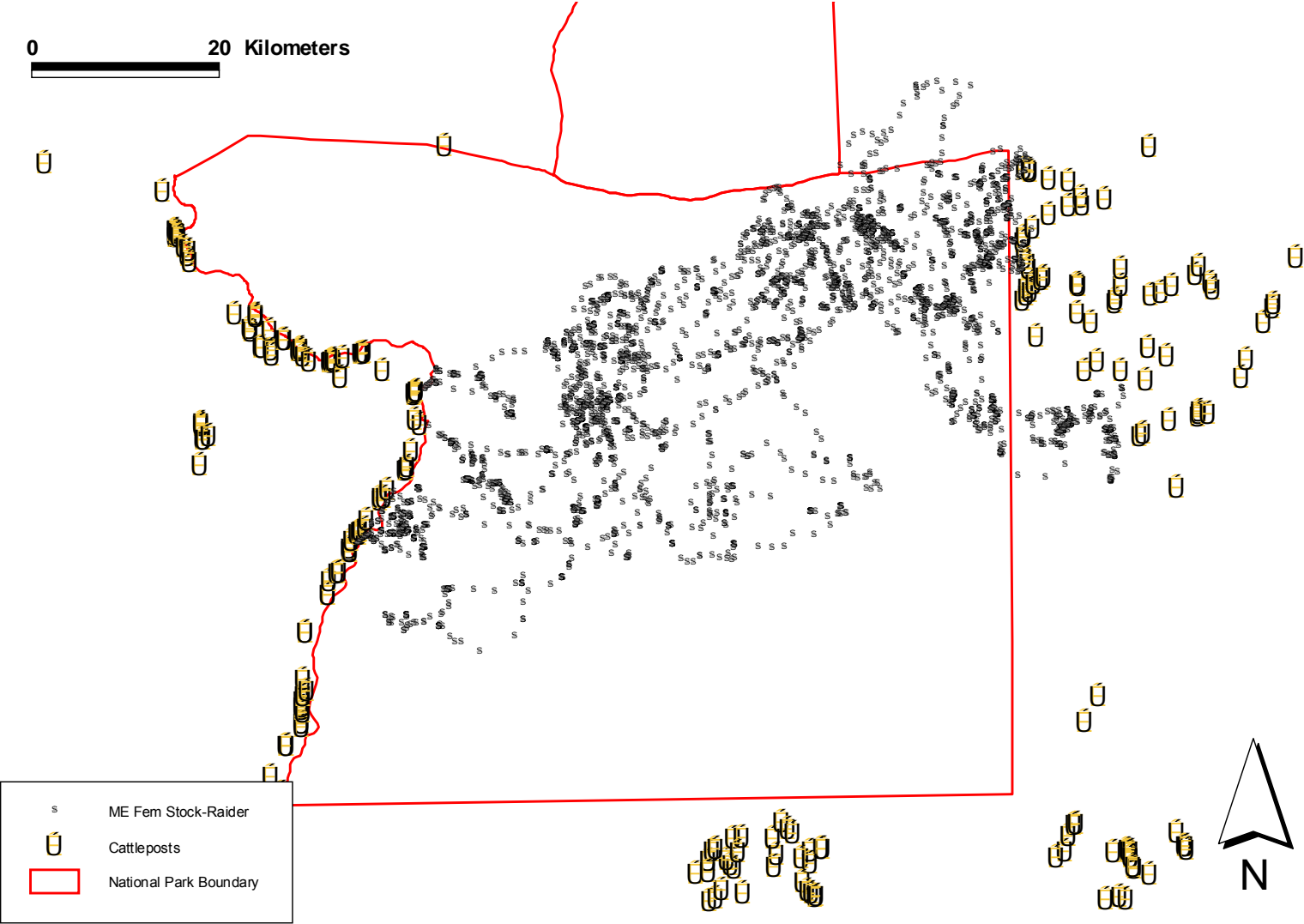
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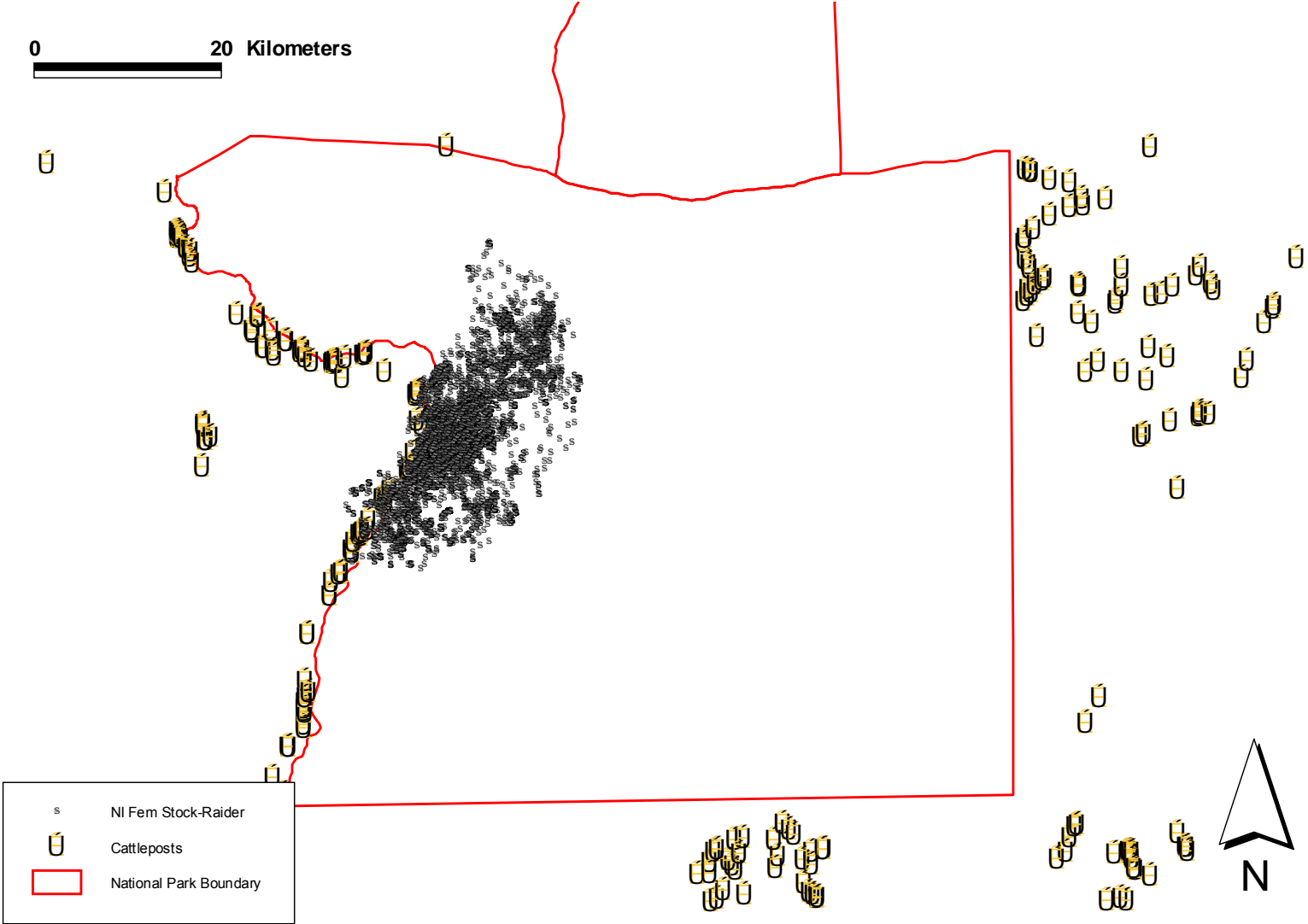
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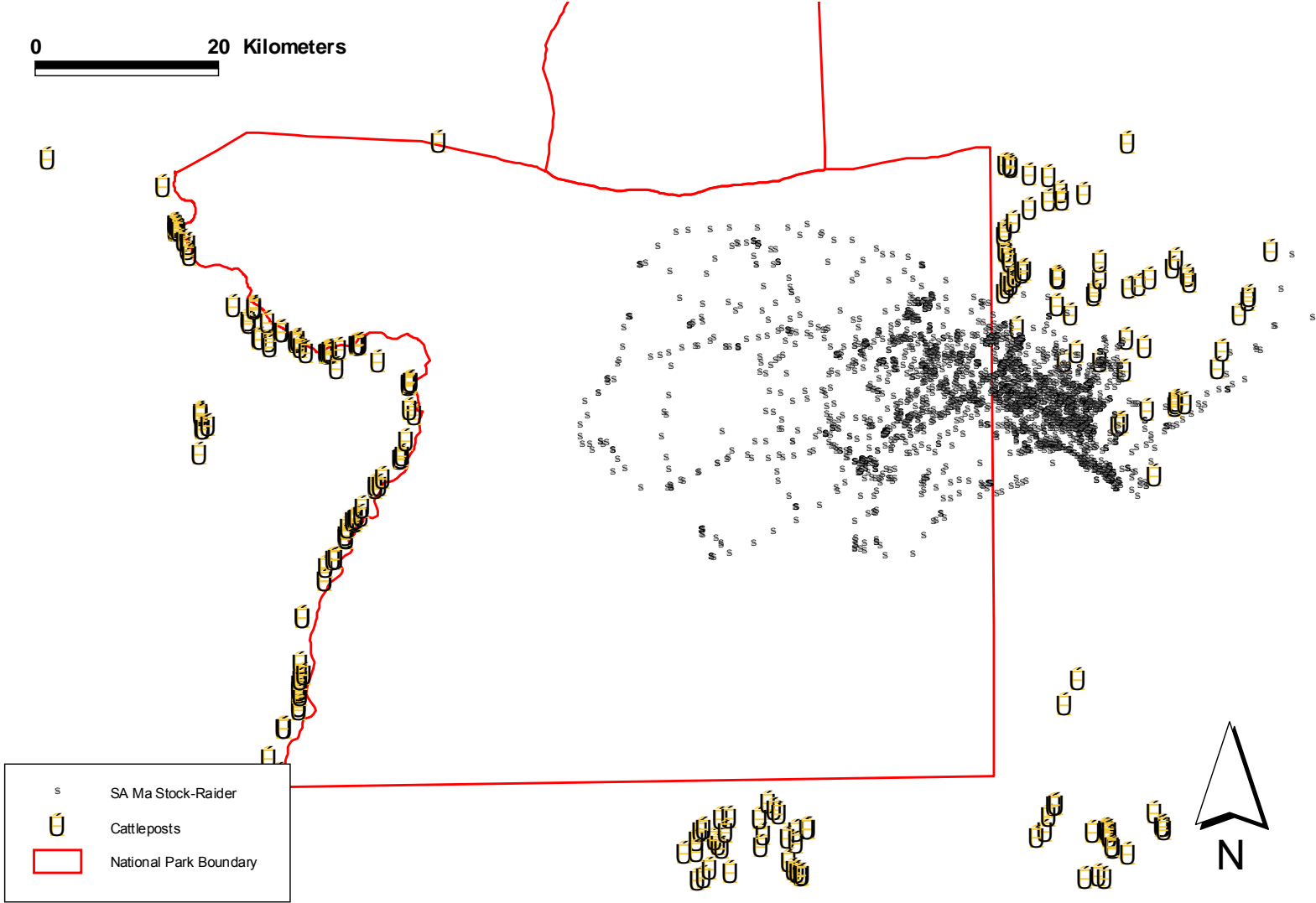


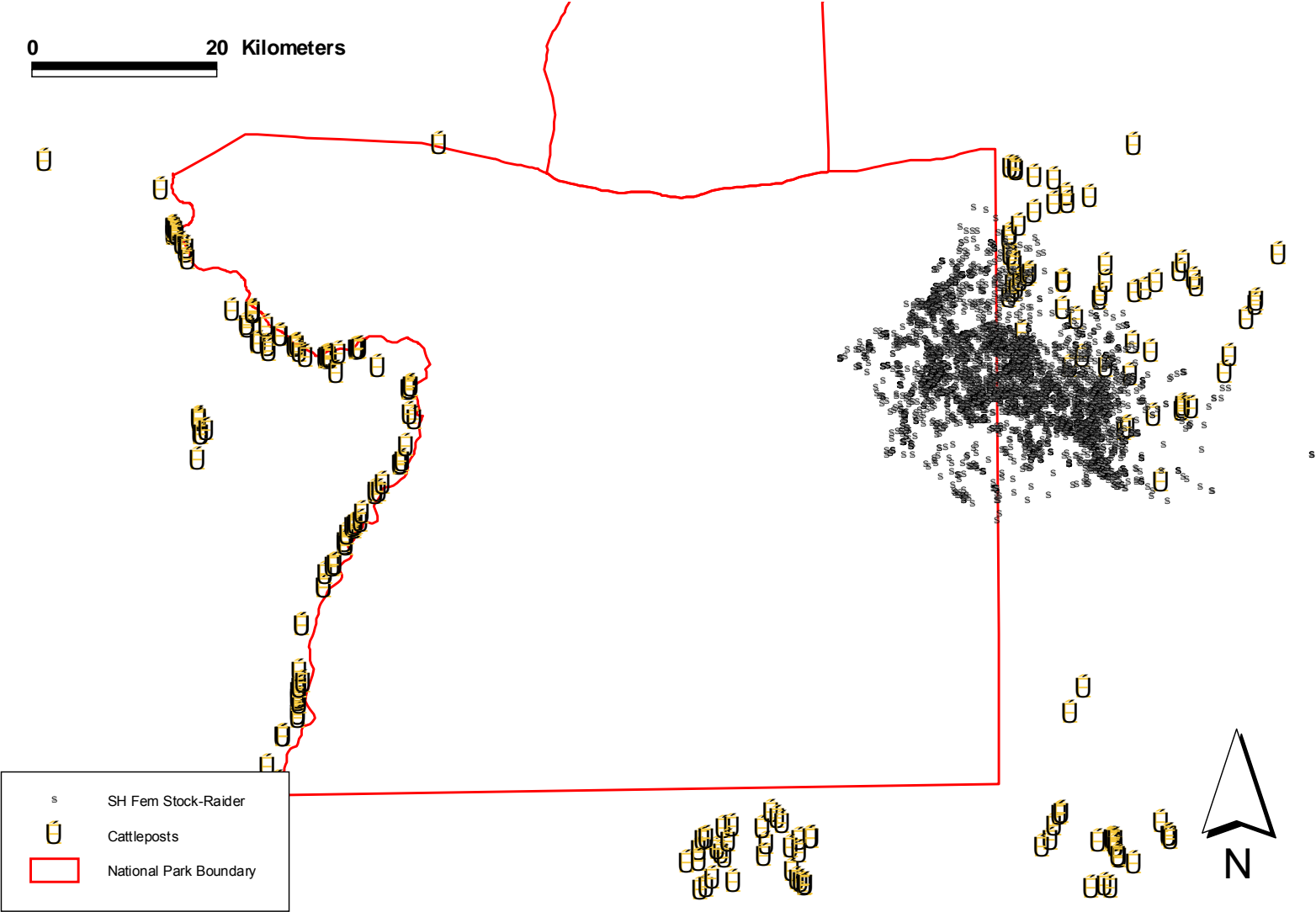


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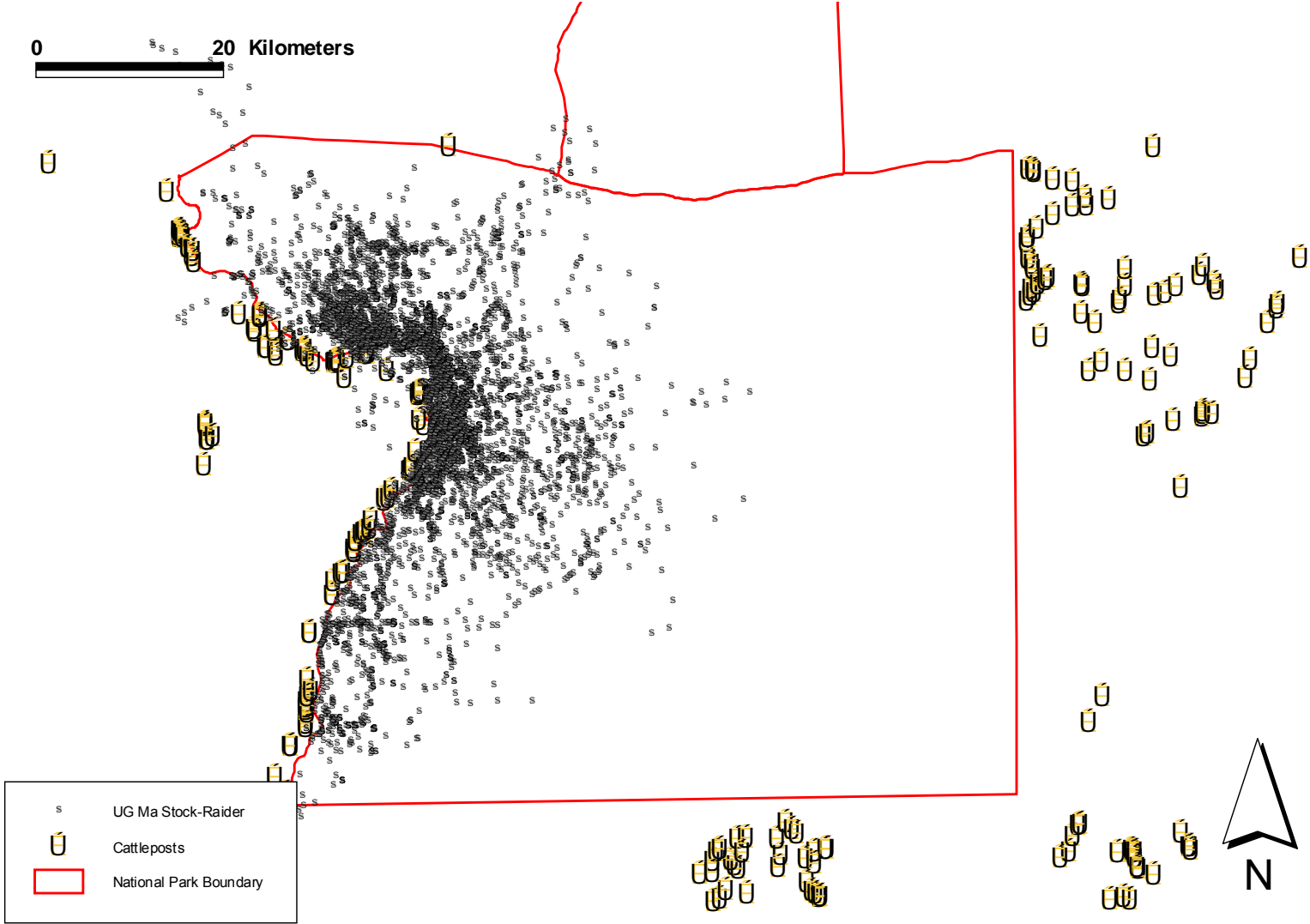


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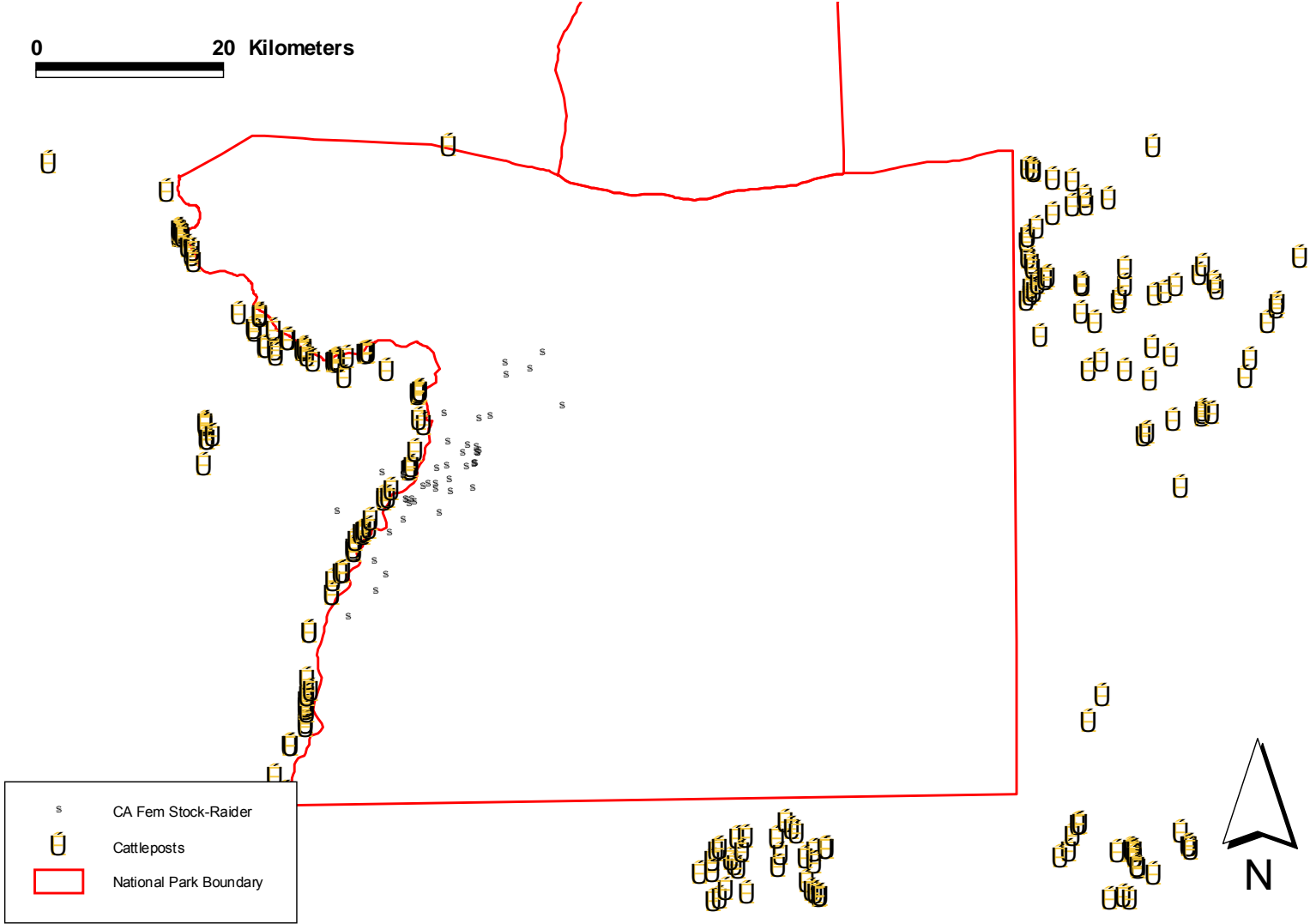


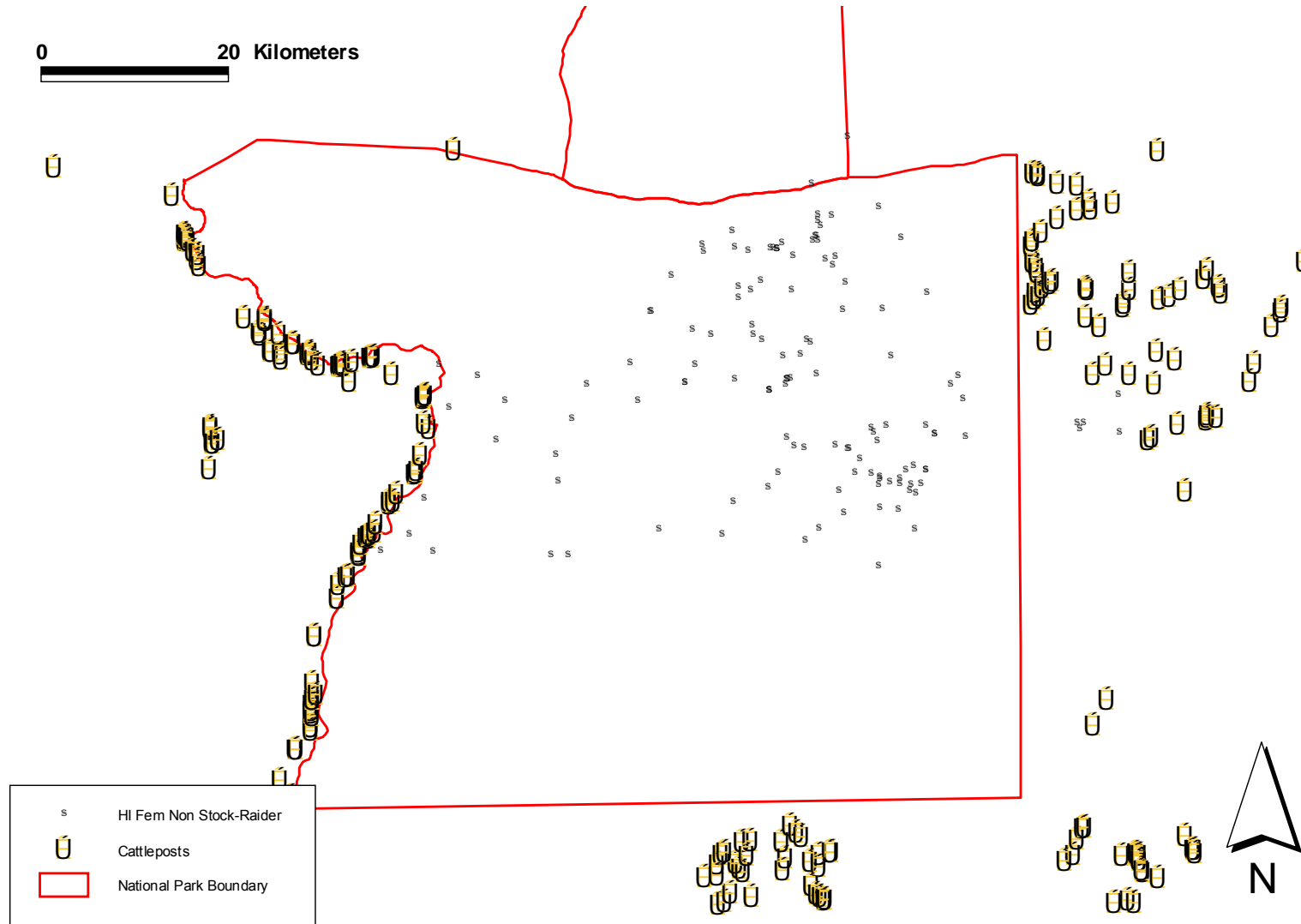


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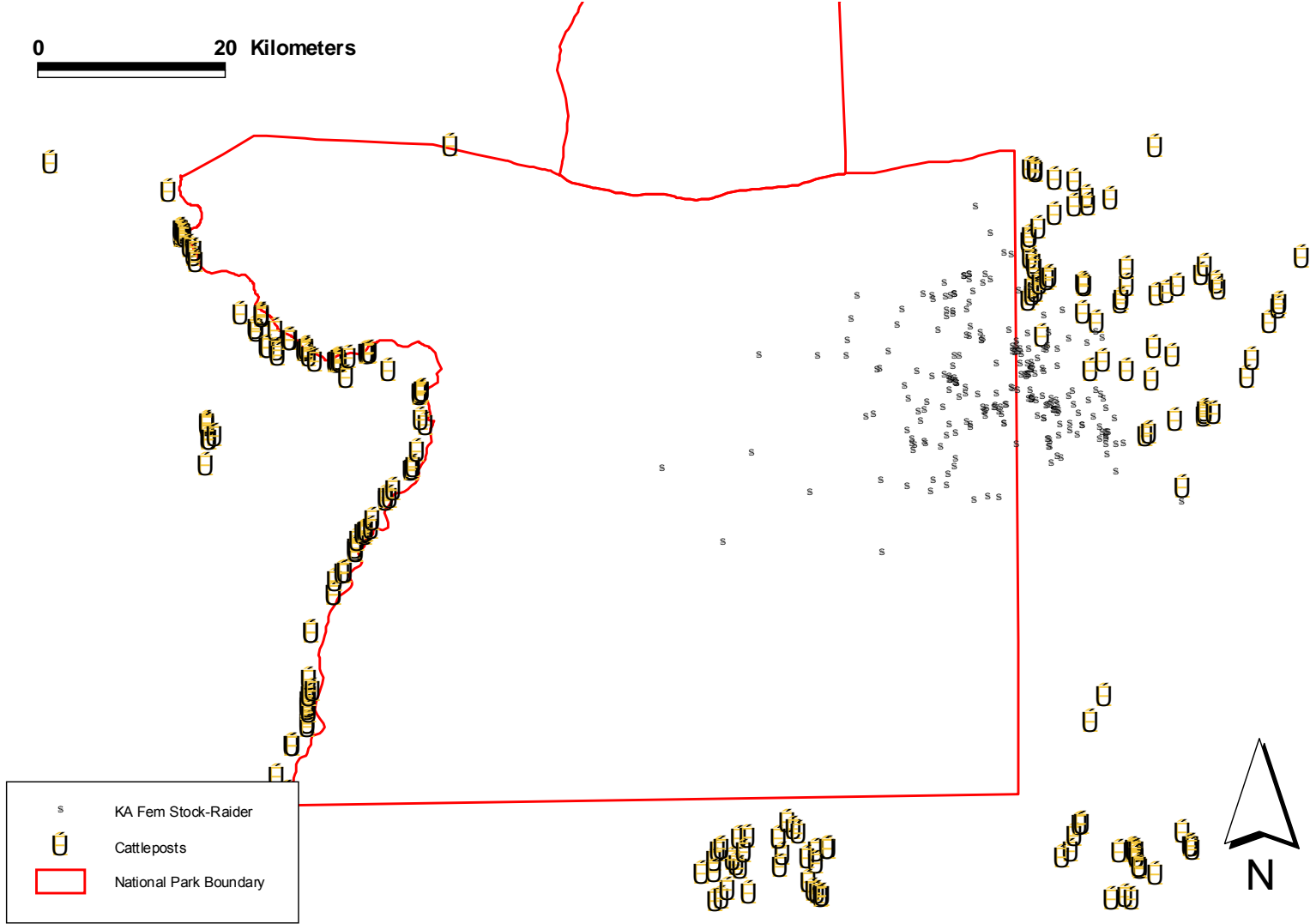


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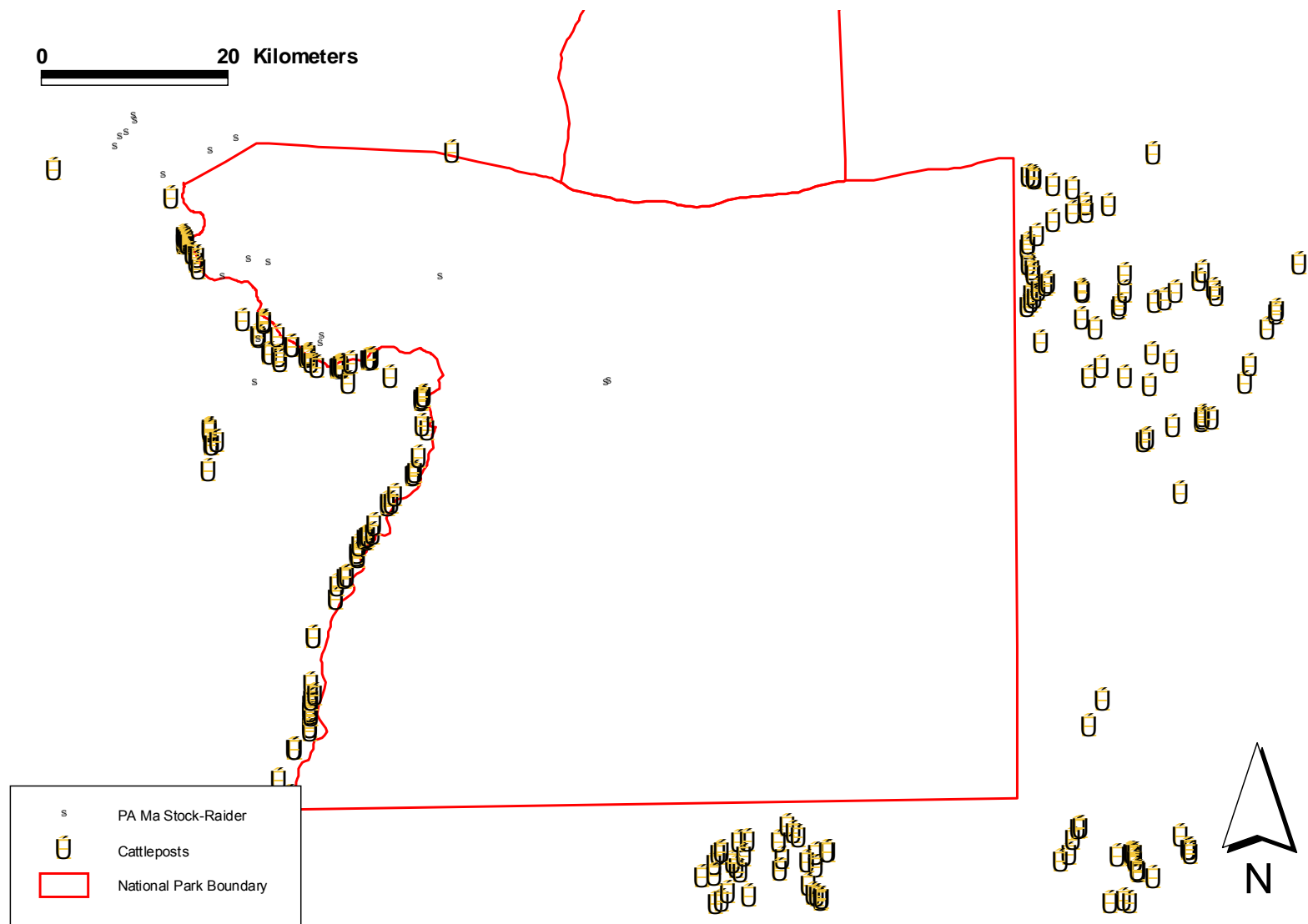




2m





$2n$ 

### **Appendix 3: The potential for using GPS collars on wild African lions (*Panthera leo*) some lessons from experience.**

Graham Hemson, WildCRU.

Global Positioning System (GPS) telemetry has been used extensively to investigate the movements of large- to medium-sized herbivores, such as moose (*Alces alces*), caribou (*Rangifer tarandus*), wild sheep (*Ovis aries*), white tailed deer (*Odocoileus virginianus*), red deer or elk (*Cervus elephas*), elephant (*Loxodonta cyclotis* and *L. africana*) and others (Moen *et al.*, 1996; Blanc & Brelurut, 1997; Lawson & Rodgers, 1997). However, tests and studies on large carnivores are less prevalent in the literature and are restricted to wolves (*Canis lupus*) and mountain lions (*Puma concolor*) (Merril *et al.*, 1998; Zimmermann *et al.*, 2001; Lyndzey *et al.*, 2001).

In May 2001, I placed the first of 10 GPS collars (Televilt Simplex Predator 2D) on lions in the Makgadikgadi Pans area of Northern Botswana. Performance of collars exceeded expectations; attaining 95% of GPS fixes attempted enabling us to monitor large movements of lions living in a semi-arid savannah. However, reliability was alarming with four collars failing completely; one through a faulty GPS connection, one through a bite and two presently undetermined. In this paper, I compare the cost and features of the Televilt system and other similar systems and discuss some of the potential and limitations of GPS telemetry for studies of African lions.

#### **The Systems**

There are five main manufacturers of GPS collars: Lotek, Televilt, Telonics, ATS and Vectronics. (Table 1).

Table 1. Comparison of GPS collars suitable for African lions.

<b>Manufacturer</b>	<b>System</b>	<b>Weight in grams</b>	<b>Predicted Number of Fixes (assumed GPS acquisition time)</b>	<b>Remote data acquisition</b>	<b>Remote rescheduling potential</b>	<b>Price of 5 collar system US \$</b>
Televilt	Simplex Predator 1D	1200	18000 (60)	Yes	No	25294
Televilt	Simplex Predator 2D	1000	12000 (60)	Yes	No	25670
Televilt	Simplex Predator 3D	1200	18000 (60)	Yes	No	26489
Televilt	Posrec 600	750	6900-3350 (60-120)	No	No	13280
Televilt	Posrec 900	1100	13900-6700 (60-120)	No	No	14837
Televilt	Posrec 1200	1250	20900-10100 (60-120)	No	No	?
Telonics	TGW-3500- GPS/SOB/D	810	3710-4200 (90)	No	No	18860- 16430
Telonics	TGW-3580- GPS/SOB/AR GOS/D	880	1928-2364 (90)	Yes	No	21875
Vectronic	GPS Plus 1C	280	1500-2000 (60-90)	On demand	Yes	15090
Vectronic	GPS Plus 1D	450	4000-5700 (60-90)	On demand	Yes	15090
Vectronic	GPS Plus 2D	630	8300-11800 (60-90)	On demand	Yes	15114
Vectronic	GPS Plus 3D	800	13000-18500 (60-90)	On demand	Yes	15570
Vectronic	GPS Plus 4D	950	18000-25000 (60-90)	On demand	Yes	15810
Vectronic	GPS Plus 5D	1150	22500-32000 (60-90)	On demand	Yes	16045
Lotek	GPS 2200L	950	9000 (not given)	No	No	
Lotek	GPS 4000	950	<2900 (not given)	On demand	Yes	
Advanced Telemetry Systems	GPS Drop off on demand collar	1100	3048*-370** (96)	No	No	15000

\*VHF beacon on constantly and one fix an hour

\*\*VHF beacon on constantly and one fix a day

Each manufacturer and system has additions and extensions to the basic collar technology including automatic collar drop off, user-controlled drop off, activity sensors, temperature sensors and different modes of data access. For the purposes of this paper, I consider only the technology specific to the basic operation of the GPS system in the field.

## **The Basics**

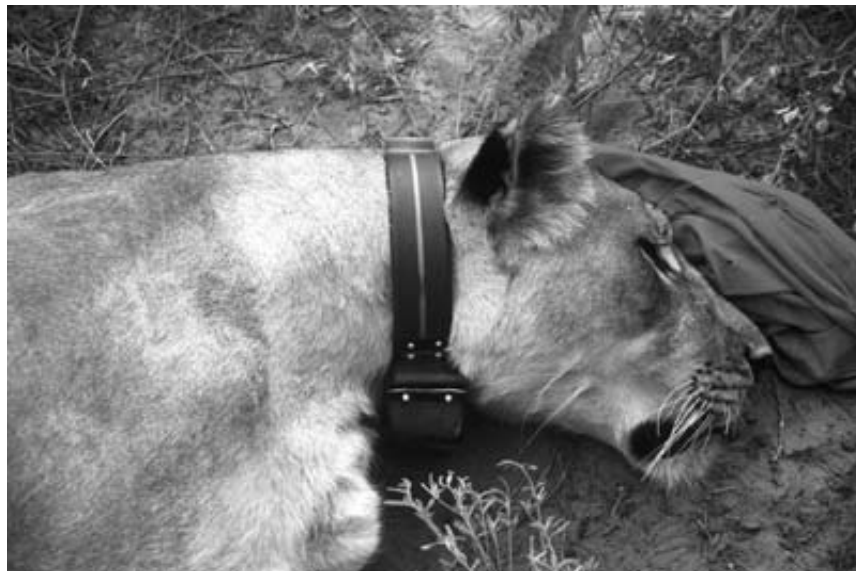
GPS is developed, funded and administered by the US Department of Defence (DOD). The terrestrial GPS unit receives coded signals from at least four of a network of 24 dedicated GPS satellites. The signals contain details of satellite position and local time, generated by four atomic clocks on board each one. By comparing time signals, the unit is able to calculate its own position. The more satellites and the more widely separated they are in the sky, the better the accuracy or, the lower the Dilution of Precision (DOP). In May 2001, the DOD removed Selective Availability (the system by which civilian GPS receivers could only calculate positional accuracies of 100m error) and GPS is currently accurate to within 10m with sufficient satellite visibility (Hulbert, 2001).

The basic components of all GPS collars are the GPS unit and a scheduling microprocessor. The microprocessor is accessed via a link from a PC and a user-defined schedule of GPS activity uploaded to the unit. Some collars are programmed by the company at the factory (e.g. TVP Posrec), others are capable of duplex communication via a UHF modem which enables rescheduling whilst on the animal (Lotek GPS 4000 and Vectronic GPS Plus systems) but more commonly users upload their schedule via a cable link from the PC before fitting. We were able to reschedule parameters on GPS Simplex collars on lions that were anaesthetised for battery replacement and data retrieval but this is not normally recommended as the programming stage and battery reattachment can be fickle and become significantly harder under pressure. Most collars also incorporate a VHF beacon for conventional radio tracking for observation or for recovery of the unit. In the TVP GPS Simplex system the VHF beacon is also the carrier signal for the GPS position data.

GPS units are typically lightweight (e.g. 44 grams, Advanced Telemetry Systems, *pers comm.*) but require significant power to locate satellite signals. Accordingly, the batteries comprise the bulk of the weight associated with GPS collars. Battery life is significantly affected by both number of GPS positions required and time taken to acquire each position. The environment, local satellite coverage and orientation of the collar to the sky (i.e., orientation of the animal) can have a dramatic effect on the latter (see below).

Considerable weight saving is possible if fewer GPS positions are required or the collars are to be deployed in an area in which position acquisition time is minimal and therefore battery requirement is minimised. However, all of the collars considered in Table 1 are less than 1% of a typical adult lioness' weight, 126kg (Schaller, 1972; Smithers, 1983).

Figure 2. A GPS Simplex 2D Predator Collar fitted to an adult female lioness.



## Data Delivery

Two main categories of data retrieval system are available, remote access and store-on-board (SOB). Remote access generally allows the user to monitor both collar

performance and download GPS position data from the animal without immobilisation. Most SOB collars now have VHF, UHF or GSM signals, which can indicate some form of collar efficacy or status, but generally, these signals contain minimal information such as battery status and do not always work (Johnson *et al.*, 2002).

The Telonics GPS/Argos system transmits data via the Argos satellite system; however, it is restricted to a maximum of seven positions a day.

The Televilt Simplex system employs a coded VHF signal broadcast at times predetermined by the researcher. The user must be 1-2km from animal at these times to complete data collection. Data transmissions can be scheduled to repeat up to 5 times if locating the animal is anticipated to be difficult. Data delivery takes approximately 2 seconds per fix which can add up to a significant time during which contact with the collar must be maintained, especially if you wish to download from the air.

Lotek and Vectronic employ UHF modems that transmit the data on receipt of a signal from the researcher. All collars store the data permanently in a non-volatile memory unit, which can be retrieved after collar removal. A Televilt Posrec unit was retrieved after being burnt in a bush fire and chewed by a jackal yet still produced the stored data on return to Televilt (J. McNutt, *pers comm.*). VHF and UHF systems both require the user to be present to retrieve data, whereas the Argos system sends data via the Internet.

New technologies are being developed to exploit cell phone/GSM network coverage to access data remotely via the web (OxLoc and Vectronic). These technologies may be less useful to current lion research, but some areas may have sufficient coverage in the future (e.g. Kruger National Park, South Africa) and GSM coverage is expanding rapidly throughout Africa. Vectronic have recently deployed a GSM collar on a wolf in Scandinavia and 3 red deer in Germany.

## ***Reliability***

Perhaps the most important factor in choosing GPS tags is reliability. Of ten collars (GPS Simplex Predator 2D) I fitted to lions, four stopped taking GPS fixes within 30-180 days: one due to a faulty GPS antenna connection; two for presently unknown reasons (although the GPS antenna housing was considerably damaged by a bite by another lion) and one in which a bite severed the GPS antenna connection. Televilt has now resolved the GPS antenna connection problem/fault and future collars should not suffer this problem. Only one battery went flat in 12 months on one unit with an unknown malfunction, which may have reduced battery life. I currently have ten operational collars in the field including two that have taken over 6,000 fixes and are still running after 13 months.

It is difficult to compare my detailed experiences with reviews available in the literature, as few people report reliability and a handful of subjective statements on the subject cannot make-up for the lack of objective estimates. Cross species comparisons are also difficult and reliability of five year old systems cannot realistically be compared with the contemporary technology. Furthermore it must be stressed that manufacturer estimates cannot fairly be compared with user reports and no objective long term reliability estimates are available.

Winterbach & Winterbach (appendix 3) report a deterioration of performance of a single GPS collar (Televilt Simplex 2D Predator) placed on a lioness in the Okavango Delta, Botswana. In 4 months, the collar had slipped from taking 97% of fixes attempted to less than 25% and was eventually removed and returned to Televilt for repair.

Frank (appendix 2) reports a 100% failure rate of three GPS/Argos collars on African lions within 46-117 days of deployment (see appendix 2). In contrast, Rumble (*pers. comm.*) is happy with Telonics collars on elk.

Lindzey *et al.* (2001) seem happy with their 17, generation-one SOB Telonics GPS collars and they also report success with ten Lotek GPS 2000 SOB collars used on

mountain lions. The latter stayed on the animals for only 1-6 months and it is hard to gauge from the report whether this was anticipated or whether malfunctions led to early removals.

Two Lotek GPS UHF download-type collars built in 1997 were tested on forest elephants (*Loxodonta cyclotis*) in Central Africa (Blake *et al*, 2001). Both collars failed within 45 despite exhaustive ground testing in the same area. Lotek suggested that these collars were experimental and were designed for moose, not for elephants and they have since improved their design. They stressed that the collars are intended for use on medium sized animals and elephants subject the collars to stresses beyond their design envelope. Dettki & Edenius (2001) infer that 15 Lotek collars that they deployed on moose in Sweden worked adequately.

However, Johnson *et al* (in press) report that only four of 22 Lotek GPS –1000 (precursor of the GPS 4000) collar deployments met or exceeded calculated expectations of battery life in the field on female caribou. They cite unexpected mortality mode start up, undetected collar failure (warning signal failed to start when collar ceased functioning as scheduled) and modem failure as the three principal causes of failure. They report similar failure rates on grizzly bears (*Ursus arctos horribilis*) (Heard *pers comm.*) and Rumble (*pers. comm.*) reported problems of moisture-induced failure from Lotek collars.

McNutt (*pers. comm.*) placed four lightweight Televilt POSREC collars on wild dogs (*Lycaon pictus*) in the Okavango Delta. These collars have an automated release mechanism that causes the collar to fall off on a set date or as the batteries run flat. Collars are then retrieved and sent back to Televilt for refurbishment and data retrieval. Three of the four collars fell off in fewer than 35 days (less than the 270 days anticipated) and were repaired by the researchers and replaced (without the remote drop off mechanism). On retrieval, it was found that the collars completed 50% of the GPS fixes attempted.

A project using six GPS Posrec collars on Burchell's zebra (*Equus burchelli*) had all collars fail before they were deployed and four failed again after return and repair. All collars are presently functioning and the problem was discovered to be with a faulty



battery voltage detector causing the collar to go into battery safe mode and stop taking positions. This problem was apparently related to the high temperature recorded in the Kalahari and this problem has now been resolved (Brooks, *pers. comm.*)

Advanced Telemetry System state that they have 85% reliability in the field i.e. 15% of collars will develop a malfunction, which may or may not cause the collar to stop functioning completely. Similarly, there are few independent data available on Vectronic collars but they have been used on European wild sheep, deer and reindeer and are being placed on wolves in Finland. One abstract suggests that the collars used on reindeer lasted from 22-227 days, but no mean is given (Kumpula *et al.*, 2001).

Common causes of collar failure cited are moisture penetrating water sensitive parts of the collar, faulty parts, physical trauma induced damage, premature battery expiry and poor workmanship but there do not seem to be trends in the reliability of different systems. Rather GPS collar reliability is still something of a lottery, albeit one in which the odds are being improved. Restrictively short battery life in the early systems restricts good estimates of reliability for longer-term applications possible with newer, low voltage long life GPS collars. There are no reviews of long-term use of GPS collar on predators available.

When collars malfunction, the manufacturers expect the user to accept responsibility for removing the collar from the animal and returning it to the vendor. On receipt, they will normally repair the defect, return, however it is likely that the physical abuse that lions inflict on collars may fall outside this warranty agreement, and I urge users to investigate these themselves. The time and effort that goes into removing and replacing collars cannot be underestimated and nor can the stress and physical harm inflicted on the animal(s). In my study, lions were often unapproachable before immobilization and were more so afterwards. In one case, two collar failures on one lioness required two collar changes and the use of a helicopter to immobilize her for the second time. The financial and opportunity costs of collar failures in situations like these can be extremely high.

## Performance

If GPS collars work, they can produce large quantities of accurate spatial data with minimal user intervention. In one year of VHF radio tracking, we could expect to gather 40-100 locations per animal if we had 10 animals collared. In one year of GPS deployment, we could expect 5,600 locations per animal with no physical constraint on the number of animals monitored. We obtain between 90-96% GPS fix success rate from functioning collars. However most researchers agree that habitat is an important predictor of both GPS acquisition time and acquisition success rate (Rempel *et al.*, 1995; Moen *et al.*, 1996; Blake *et al.*, 2001). My study area, the Makgadikgadi, has neither severe topography nor thick vegetation. Other recorded success rates are extremely variable ranging from 10-90% (Moen *et al.*, 1996; Blake *et al.*, 2001; Merrill *et al.*, 1999; Bowman *et al.*, 2000; McNutt *pers. comm.* & Biggs *et al.*, 2001) but there are too few reports and too many variables to detect any trends by manufacturer.

Orientation of the collared animal is also a key factor and collars on prone animals function considerably worse than on animals that are standing up (Bowman *et al.*, 2000; Rumble *et al.*, 2001). This may be of critical importance when scheduling a duty cycle for lions. Unlike many herbivores, lions are apt to spend considerable amounts of time lying on their side, in a position in which the GPS antenna will be oriented at 90 degrees to the sky resulting in longer acquisition times and lower success rates. However, low success rates during resting periods may also be exacerbated by selection of denser habitats during these times (Rumble *et al.*, 2001). An initial assessment of our lion data suggests that fixes attempted at times when lions are likely to be lying down take longer and some are not made at all.

## Cost

Lindzey *et al.* (2001) assessed the cost per fix of GPS against aerial VHF tracking in a mountainous region of the USA and reported costs of \$8 and \$65 respectively. In contrast, Frank (appendix 2) estimates relative costs of \$198 and \$12 per fix

respectively. Clearly, the cost per fix is sensitive to the reliability and performance of the collars employed.

In our experience with 10 GPS Simplex collars and the associated hardware and software (US\$ 44177 including taxes) we calculated a cost per fix of \$14 in one year and \$8 in the second year assuming the observed 40% per annum failure rate spread over the year and no retrieval and replacement. With no failure, one would expect \$12 per fix in the first year and \$6 in the second year from our system. However, this calculation does not include the money spent locating lions to download the collars. In comparison, aerial tracking costs us \$24 per fix (\$40 per fix (Marker., *pers comm.*) \$10 per fix with a microlight (Loveridge *pers comm.*)) and would restrict one to daytime fixes, and consume more researchers' time. For the purposes of this calculation, I have included only one GPS fix per collar per day to make the data comparable with those obtainable from an aircraft.

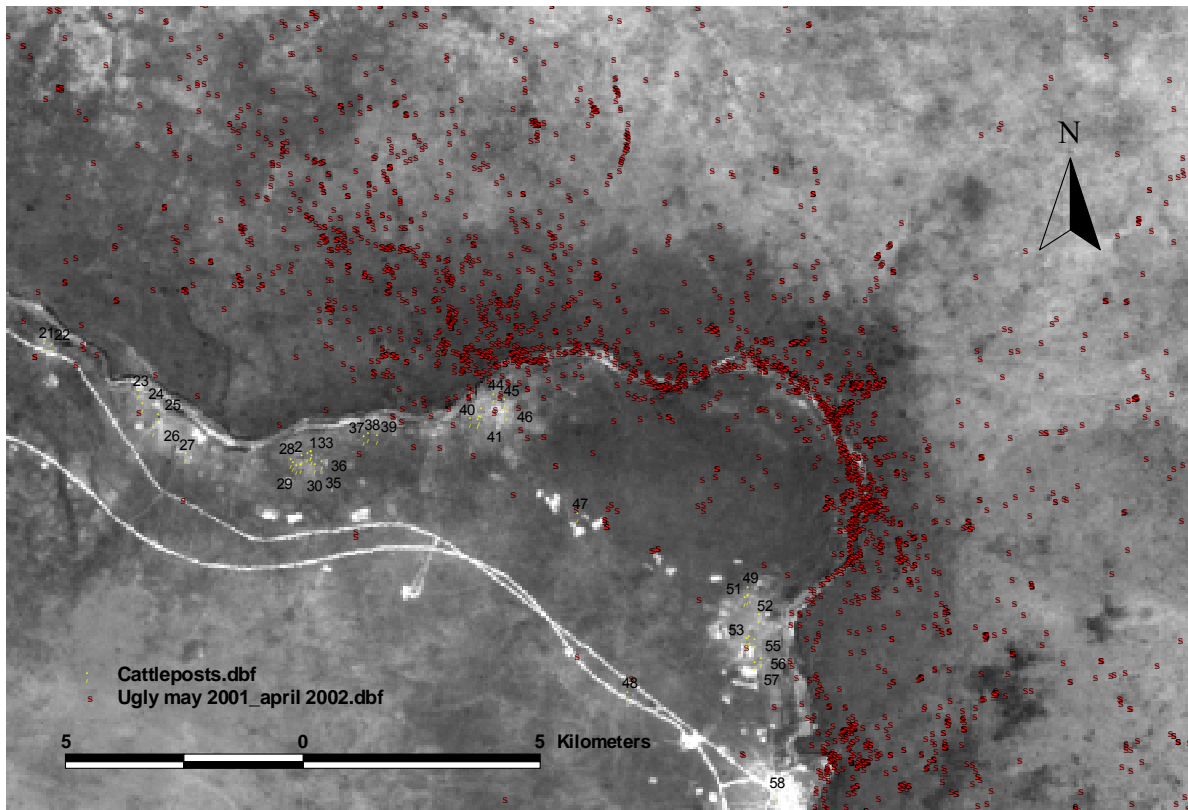
## **Data**

The data produced by our collars are impressive in detail, volume and accuracy (Figure 2). Currently, we have complete records of the movements of some lions for almost a year. Our schedule of 13 fixes hourly between 18:00 hrs and 06:00 hrs and one at 09:00 and one at 16:00 gives a detailed picture of the movements and range use of these animals.

Interesting movement patterns that would remain undetected in all but the most intense aerial tracking study are emerging from the data. Furthermore, these data offer the opportunity to model different VHF tracking strategies and their influence on predictors of home range calculations. We also have data on territory use during a pride takeover of one GPS-collared lion by a coalition including another GPS-tagged male. However, these data are corollaries to our main aims, to investigate the seasonal movement patterns and home range use fluctuations of lions affected by wild prey density changes in areas of livestock abundance. Although collar failures have restricted the efficacy of the system, I am optimistic that I have a unique and interesting contribution to make to our understanding the interaction between

carnivores and human/livestock systems due largely to the GPS data. One caveat is that other data for habitat and prey for example are rarely available in similar detail or volume, which can restrict the interpretation of the GPS data.

Figure 2. Detail from 11 months GPS data from an adult male lion.



## Conclusions

GPS tracking technology has been developed in the last decade. In 2000 only approximately 500 GPS tags were sold to wildlife biologists compared to an estimated 60,000 VHF tags sold per year (Hulbert, 2001). In the 13 months I have used GPS collars my original collars have become superseded by newer better collars, I have had three versions of the software and my receiver has had to have new hardware added. In comparison to VHF collars, which have changed relatively little over the past decade, GPS collars have undergone significant development and a 50% reduction in cost (Hulbert, 2001). Due to the speed of evolution and development of GPS collar systems; many of the traditional methods of literature comparison are not

realistic for comparative assessment. Due to this time lag my assessment has perhaps painted an over pessimistic perspective on the technology as reviewed systems are almost certainly obsolete. However, as one of the pioneers of the technology states “researchers must be prepared to accept the consequences of premature systems failure” (Rodgers, 2001).

A concern for all large-carnivore researchers are how collars will handle the inevitable violence they will be subjected to. While reliability on large herbivores seems good, large carnivores seem to inflict levels of physical stress on the components that ungulates do not; the subsequent failure rate is higher, and there is little encouragement in the literature suggesting that GPS collars function on large carnivores for more than 6 months. Collars will inevitably be bitten by other lions; they may be kicked by fleeing ungulates, battered by other lions and chewed on by cubs. One of my collars ceased functioning when a single bite severed the GPS antenna connection and another suffered GPS antenna housing damage from a bite to the back of the neck possibly through mating behaviour. The belting supplied with our collars seemed far tougher than that supplied with our VHF collars; however, the protected parts within were far more fragile resulting in failure. When communicating with collar manufacturers it is prudent to stress that lions are very big, quite social and are subjected to extremes of physical violence during their lives.

The failure rates of GPS collars on similar species should be monitored to maintain an ongoing assessment of reliability and performance in analogous situations. I recommend potential buyers request the contact details of people who have used GPS collars on similar species and encourage researchers to make sure they understand the manufacturer’s after-sales agreement clearly.

Any potential user of GPS technology must be clear on how much data is needed to address the relevant hypotheses and how much will alternatives cost to provide those data. Aerial tracking cannot provide detailed movement data or nocturnal location data, but it can provide regular daytime fixes to calculate basic diurnal home ranges and territories. In some parts of the world flying time is significantly more expensive than others (\$65-\$12) and in other areas, poor satellite coverage dense woodland and other environmental variables may limit the utility of GPS technology.

No GPS collars are likely to last undamaged on lions for more than two or three years. For detailed short-term work, they are ideal, with increases in reliability and battery life inevitable over the next few years, more long-term studies with large carnivores should be possible, and as prices come down and more units are deployed, our understanding of carnivore movements and range use may benefit significantly.

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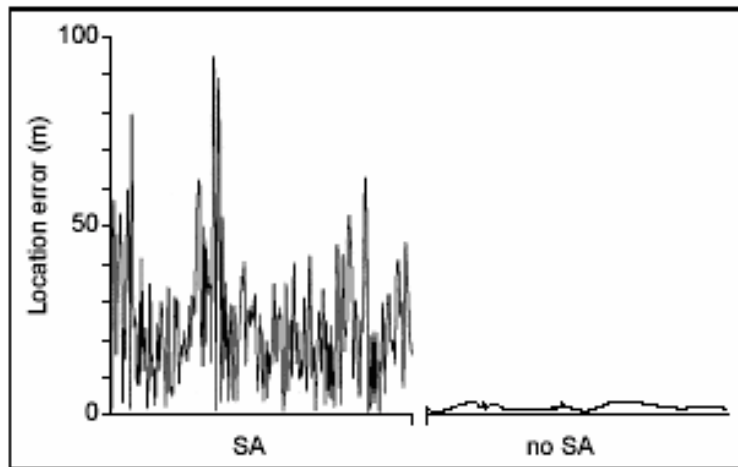
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**Appendix 1** Location error (m) for successive locations of a 12-channel GPS base station (from Trimble Inc.) in non-differential mode, one month before and one month after SA elimination (fix interval 5 sec.). From Janeau *et al*, 2001.





## Appendix 2

### A short report on Argos and GPS Argos collars on lions and spotted hyaenas (*Crocuta crocuta*) in Laikipia district Kenya.

Laurence Frank

The Laikipia Predator Project is studying large carnivore ecology and conservation in a 10,000 km<sup>2</sup> unprotected area of Kenya. Because of persecution, predators are nocturnal. Tracking from the ground is unrewarding because the landscape is heavily dissected and bush-covered, and road coverage is poor. Between 1998 and 2000, we purchased 4 ARGOS collars (model ST-14PTT/Mk4) and two GPS-ARGOS collars (ST-14/GPS/Mk6) from Telonics Inc., at costs of US\$3300 and US\$5200, respectively. One of each was subsequently recovered from animals, renovated cost-free by Telonics and refitted to new animals. A total of three male lions, three female lions, and two female hyenas were collared.

The ARGOS system calculates transmitter position from the Doppler shift in radio frequencies of consecutive transmissions detected in a single satellite pass. Transmitters were programmed to broadcast in the night (when the animals were likely to be active), during periods when several high azimuth satellite passes were scheduled. Because ARGOS satellites are in polar orbits, satellite coverage is poor at the equator. ARGOS supplies an estimate of the reliability of each fix, ranging from 0 (accurate to within 100m) to Z (no reliability estimate is possible). I considered only those reported to be within  $\pm 1$  km to be useable.

GPS-ARGOS transmitters contained a GPS unit, which could store up to five fixes. They were programmed to obtain one fix daily and broadcast stored data to a passing satellite every five days. GPS locations are significantly more accurate than straight Argos locations ( $\pm 100$  meters before Selective Availability was turned off by the US military).

<b>Type</b>	<b>Life (days)</b>	<b>Mean No. Fixes Obtained</b>	<b>Mean Cost per fix (US\$)</b>
<b>ARGOS</b>	0-206	28.4	159
<b>GPS- ARGOS</b>	46-117	29.7	198

### **Results and Costs**

For purposes of cost calculations, I have assumed that the renovated collars cost the same as new ones.

Neither type of transmitter performed satisfactorily. The ARGOS collars transmitted for 0-206 days, providing a mean of 28.4 good fixes, at a mean cost (collar purchase plus data acquisition from ARGOS) of about US\$159 per fix. One ARGOS collar did not provide a single useable fix. Another provided only 5 fixes; when Telonics renovated it, it was found to have a defective solder connection. The others provided many data points of unknowable reliability, which could not be included in the analyses. On one, the magnetic power switch had failed in the “on” position, so that it was transmitting (and consuming battery life) from the time it was delivered from the factory.

The three GPS-ARGOS collars lasted 46-117 days, providing a mean of 29.7 fixes at a mean cost of US\$198 per fix. Each GPS-ARGOS transmitter worked well initially, but each failed in a different way. One started transmitting the same data week after week. The other two started transmitting only partial data that could not be decompressed. Additionally, many transmissions were not detected by the satellite, so the data were permanently lost (the renovated GPS-ARGOS collar was programmed to retain data on board, but was never recovered from the animal after transmissions failed). The recovered GPS collar that provided 37 fixes over 117 days proved to contain a defective electronic component.

For comparison, ordinary VHF collars from Sirtrack, Inc. cost US\$170 each, last over three years and have been 100% reliable. At our cost of US\$150/hour to hire small plane, aerial tracking costs US\$10-12/per fix. Further, when we were using the

ARGOS and GPS-ARGOS collars early in the project, it often took weeks of effort to catch each lion. Although those personnel and equipment costs were the same when deploying VHF collars, the effort was essentially wasted when we put on satellite collars that yielded little or no data. Although it would be extremely useful to have the fine grain data theoretically obtainable from ARGOS and GPS-ARGOS technology, the benefits of this are currently outweighed by uncertain reliability.

### **Appendix 3**

Evaluation of a Televilt GPS collar on a lioness in the Okavango Delta.

#### **C.W. Winterbach and Hanlie Winterbach**

The Televilt GPS collars can be pre-programmed by the user to various data collecting schedules. The collar was pre-programmed to collect GPS positions daily at 9:00 and 16:00. For three days per week, positions are to be collected at either 2 hour or 4 hour intervals, alternating weekly. Reporting was programmed for transmission every second Monday at 11:00 and 17:00. The VHF frequency is transmitting between 7:00 and 17:00 each day to enable ordinary radio tracking of the individual.

During three downloads done between May and September only 3.8%, that is 10 of 260 of the recorded positions on the collar were not successfully captured with the remote download of the data.

Between 20 May and 10 September the collar recorded position data on every day, but from then on data recording was erratic with 17 to 28 days a month with no data collected (Fig. 1). This was reflected by the decrease in the total number of position points recorded per month from September onwards. The proportion of data expected data points collected decreased from 97% during June to 85% during August, and to less than 25% thereafter.

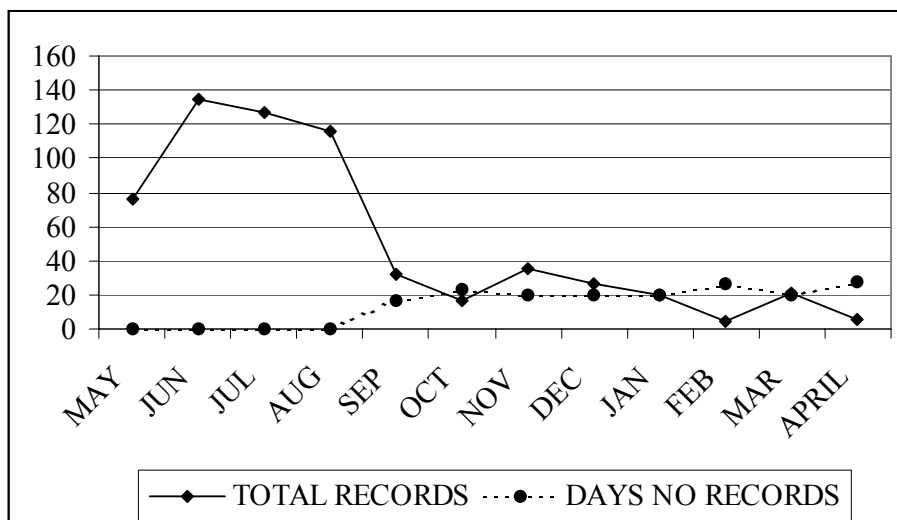


Figure. Number of position data points collected between May 2001 and April 2002 by a Televilt GPS collar fitted to a lioness.

Detailed movement data of the collared animal can be collected to calculate distances moved (Table 2). The remote download data for the 3-day intensive data collection sessions contained on average 83% of the position data, ranging between 47% and 100% for individual sessions (Table 1). Loss of data during the remote download is not the main source of missing positions, as only 3.8% of the recorded positions on the collar were not successfully captured with remote transmission. The test collar performed well during the first four months, but thereafter position data was collected erratically.

Table 1. The total distance moved a female of the Central pride, and the number of position plots collected by the GPS collar during the nine intensive position collection sessions (72 hours) during May to September 2001.

SESSION (72 hours)	DISTANCE MOVED (km)	PLOTS			
		TIME INTERVAL	EXPECTED (n)	RECORDED (n)	RECORDED (%)
<b>1</b>	10.6	4:00	15	7	47
<b>2</b>	14.6	2:00	33	30	91
<b>3</b>	15.3	4:00	15	12	80
<b>4</b>	15.9	2:00	33	26	79
<b>5</b>	12.7	4:00	15	15	100
<b>6</b>	8.8	2:00	33	27	82
<b>7</b>	7.2	4:00	15	11	73
<b>8</b>	18.6	2:00	33	32	97
<b>9</b>	10.1	4:00	15	12	80
<b>Grand Total</b>	113.9		207	172	83