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SOCIAL ORGANISATION AND POPULATION DEMOGRAPHICS OF LIONS (*PANTHERA LEO*) IN THE OKAVANGO DELTA

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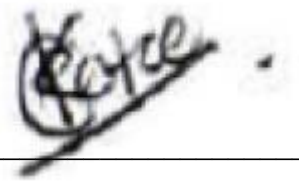
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A thesis submitted to the School of Animal, Plant and Environmental Sciences, Faculty of Science, University of the Witwatersrand, Johannesburg in fulfillment of the requirements for the degree of Masters in Science.

DECLARATION

I declare that this dissertation is my own, unaided, original work. It is being submitted for the Master of Science degree at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or any other examination at any other university.

Signed: 

15 August 2016

DISCLAIMER:

This dissertation consists of a series of chapters that have been prepared for submission to a range of scientific journals for publication. As a result the styles may vary between chapters in the dissertation and content overlap may occur between chapters.

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Abstract

The Okavango Delta in northern Botswana contains the largest, unfenced lion population in southern Africa, and is one of the most important population strongholds for the species on the continent. Despite its conservation importance, however, little information has been published on the drivers of lion ecology in this unique wetland ecosystem. In the Okavango Delta, the annual flood pulse causes dramatic seasonal contractions of available dry land, and consequently variable distribution and abundance of prey. Lions must therefore adapt to a dynamic environment not only on an annual basis, but also on a longer time-scale as inundation patterns cycle from periods of low to high floods. The main aim of the study was to determine which social and ecological factors were most important in determining lion population demographics and social organisation in the unique wetland environment of the Okavango Delta. Data were intensively collected on demographic rates and social organisation of five resident lion prides in the south-western Okavango Delta from 1997 to 2004, during which inundation patterns shifted from low to high floods. We investigated the effects of two ecological factors, namely prey availability and flood extent, and one social factor, namely intra-specific competition, on lion social organisation and population demographics. Lions occurred at high densities, and the population was regulated socially and not by resource limitation. Our results indicated that competition with neighbours exerted the most extensive influence on the lion population and significantly affected the survival of young cubs and reproductive rates. Competition reduced pride size, but contrary to our expectations, also negatively influenced sub-group size, indicating that territorial disputes do not drive sub-group patterns in the Okavango Delta. Prey availability did not appear to be an important limiting factor for the population, and group sizes were inversely related to prey availability, most likely due to habitat saturation resulting in higher levels of recruitment. Prey availability only influenced survival of young cubs, which are most vulnerable to nutritional stress. Higher levels of flooding led to smaller pride and sub-group sizes, indicating that higher flood levels for extended periods may lead to a decline in lion densities due to increased competition for available dry land. While flooding exerted no direct effect on demographic rates, we posit that habitat conversion during high flood cycles causes a decline in prey, resulting in a time-lagged effect on the lion population. Our results show that during low flood cycles when herbivore

abundance is high, lions occur at high densities and are largely self-regulated. However, as flood levels increase, prey availability declines and lions are placed under increasing pressure for space and resources, which could ultimately lead to population decline. From a conservation perspective, the south-western Okavango Delta population is thus most vulnerable during periods of high floods, when lion densities naturally decline, and lions may be pushed towards the veterinary fence where human-lion conflict is high. Future studies should focus on how anthropogenic threats around the Okavango Delta threaten the viability of the lion population in this conservation area, and seek to secure important corridors to neighbouring populations.

Keywords*: lion,* Panthera leo*, social organisation, pride size, population demographics, survival reproduction, Okavango Delta, flooding, competition, prey abundance*

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Chapter 1

Introduction

Context and study rationale

Across the African continent, lion (*Panthera leo*) populations are under considerable pressure. Lions now inhabit less than a quarter of their former range on the continent (Riggio et al. 2013), and face numerous threats including habitat loss and fragmentation (Björkland 2003), declining prey bases due to illegal bush-meat poaching, snaring (Becker et al. 2012, Midlane 2013), over-harvesting (Loveridge et al. 2007, Packer 2011, Becker et al. 2012) and conflict with local people (Woodroffe & Frank 2005, Van Bommel et al. 2007). The current lion population is estimated at around 20 000 individuals, and exists mostly in small pockets of national parks, protected areas, game reserves and wildlife management areas scattered throughout the continent (Riggio et al. 2013). A recent compilation of population surveys across the lion's remaining range revealed that the majority of surveyed lion populations are in decline (Bauer et al. 2015). In West Africa, the lion is critically endangered, and in central and east Africa, lions are classified as vulnerable (Henschel et al. 2014).

In contrast, many of the populations in southern Africa are stable or increasing, largely as a result of reintroduction efforts into small reserves and fenced populations which are intensively managed (Bauer et al. 2015). Among the southern African populations, the largest, unfenced population occurs in northern Botswana, in the Okavango Delta. Currently, this population is estimated at just over 1000 individuals, constituting a viable population that is likely to persist in the long-term (Treves et al. 2009, Riggio 2011, Bauer et al. 2015). Situated in the larger Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA), this population is therefore an important lion conservation unit (LCU – IUCN 2006) for the species in southern Africa, and is potentially an important source population for surrounding populations in Botswana and adjacent countries. However, a recent analysis of population trends indicates that this population is declining (Bauer et al. 2015).

Despite its importance as a lion population stronghold (Riggio 2011), little information has been published regarding the ecological or anthropogenic factors which drive the demographic processes

that lead to population change in the Okavango Delta. Due to the difficulties of collecting long-term demographic data for carnivores that are shy, long-lived, far-ranging and generally rare (Kelly et al. 1998, Riggio et al. 2013), relatively little is known about the factors which influence carnivore population dynamics (Fryxell et al. 1999, Watts & Holekamp 2009). Although the lion may be considered one of the most thoroughly studied carnivores, the majority of what we know today arises from the Serengeti Lion Project in Tanzania, which is the world's longest standing study on lion ecology, behaviour and population dynamics (Schaller 1972, Bertram 1975, Packer & Pusey 1983a, Packer & Pusey 1983b, Hanby et al. 1995, Packer et al. 2005). However, due to the behavioural flexibility and adaptability of carnivores in response to local ecological conditions, (Kruuk 1972, Macdonald 1979) studies from one ecosystem can not necessarily be extrapolated to another (Patterson 2007).

Furthermore, recent genetic analyses of lions from several populations in central, eastern and southern Africa have revealed that lions in the Okavango Delta are genetically distinct from all other savannah populations, and share similar mitochondrial and nuclear DNA haplotypes only with lions from Etosha National Park, Namibia - historically a large, seasonal wetland (Moore et al. 2015). This strict discrepancy in haplotypes between wetland and savannah habitats indicates habitat specialisation, and the shared haplotype amongst most savannah populations points to a possible genetic bottleneck in savannah lions believed to be linked to the Pleistocene (Antunes et al. 2008). Moore et al. (2015) therefore posit that lions in Africa were historically wetland specialists, and adapted to savannah habitats as grasslands expanded during the arid periods of the Pleistocene.

Given the evolutionary and conservation importance of the Okavango Delta lion population (IUCN 2006, Riggio 2011, Bauer et al. 2015, Moore et al. 2015), this thesis aims to identify and understand the fundamental ecological drivers of lion ecology in a wetland system, with a specific focus on population demographics and social organisation. Long-term data on demographic rates will not only help inform site-specific conservation management to ensure the future viability of the Okavango Delta lion population, but may also offer insight into processes driving lion demographics in other wetland systems (Kelly et al. 1998, Mills et al. 1999). Additionally, given the importance of lion social organisation in a population's response to ecological change (Packer et al. 2005), understanding

the drivers behind social behaviour will help us predict when lions are most vulnerable to population decline. Furthermore, as the current evidence suggests that lions were historically wetland specialists (Moore et al. 2015), investigating the ecological drivers behind social organisation in a dynamic wetland system may offer important insight into the development of sociality in the species. Lastly, understanding intraspecific variability in behaviour in lions which have adapted to different systems can contribute to the conservation of the species on a global scale by predicting how it may respond to altered environments or climates in the future (Patterson 2007).

Background

Social organisation and behaviour

Amongst felids, lions are the only social species, and live in matrilineal social units known as prides (Schaller 1972, Packer et al. 2001). Lionesses form the core of lion social organisation, and prides consist of between two and 21 adult females, their cubs, and the accompanying pride males (Schaller 1972, Bertram 1973, Bertram 1975, Packer et al. 1988). Lions are generally territorial, and work together to defend a territory against neighbouring prides (Bygott et al. 1979, Heinsohn 1997, Mosser & Packer 2009). While prides share the same territory, members often split off into smaller groups known as sub-groups or sub-prides (Van Orsdol et al. 1985). Lionesses are co-operative breeders, and generally all cubs which are born less than a year apart (often referred to as a cohort) are communally raised in a crèche (Schaller 1972, Pusey & Packer 1994, Packer et al. 2001). The mothers of the cubs tend to stay together during this period and co-operate to hunt, defend cubs against other predators and conspecifics and even allo-nurse (Pusey & Packer 1994). Once cubs reach sub-adulthood at around two years of age, sub-adult males are often evicted from the pride, and become nomadic until they reach sexual maturity and can take over a pride of their own (Hanby & Bygott 1987). During this transitory phase, young males may form coalitions, often with other members from the same cohort, who then co-operate to take over and defend a pride (Bygott et al. 1979). Sub-adult females are often recruited into the natal pride, unless the number of adult females in the pride becomes too large, in which case groups of females may break off to establish a new pride (Van Orsdol et al. 1985, Packer et al. 2005).

Factors affecting population demographics and social organisation

Prey availability

Predator population dynamics generally reflect the abundance of their natural prey resources (Bertram 1975, Laurenson 1995, Stander et al. 1997, Fuller & Sievert 2001, Hayward et al. 2007). In numerous carnivore species, short- and long-term changes in the abundance of prey, as well as its availability over time and space, are the major natural factors that affect population viability (reviewed in Fuller & Sievert 2001). This can have an influence on a number of demographic parameters, including age of first reproduction, reproductive success, litter size, inter-birth interval, group size and age-specific mortality; factors which ultimately determine population growth (Brand & Keith 1979, Mech 1995, Kelly et al. 1998, Goltsman et al. 2005). Indeed, the relationship between prey densities and various demographic parameters have been confirmed empirically by a number of studies on lions (Van Orsdol et al. 1985, Stander 1991, Hanby et al. 1995, Ogutu & Dublin 2002). During periods of low prey abundance, lions of all age groups may die from starvation (Schaller 1972, Van Orsdol 1985, Packer et al. 1988) and as a result, prides become smaller. Conversely, during periods of prey abundance, cub survival, adult survival, reproductive rate and ultimately, lion population density, is higher (Van Orsdol et al. 1985, Hanby & Bygott 1987, Pusey & Packer 1987).

Due to the fission-fusion nature of their social organisation, lions can adapt to fluctuating prey abundance by changing their grouping behaviour. For example, pride size has been linked to prey availability, and the abundance of prey can play a role in determining optimum group size in systems with varying prey abundance. In the Serengeti, Tanzania, the optimum pride size is higher in woodland habitats than on the plains, primarily due to higher year-round prey abundance in woodland habitats (Mosser & Packer 2009). Above this habitat-specific threshold pride size, young females are likely to disperse, particularly as aggression at feeding sites increases when per capita food intake is low (Van Orsdol et al. 1985, Mosser & Packer 2009). However, if the size of the expelled cohort is too small, difficulties in establishing and maintaining territories could lead to nomadism, in which case chances of successful reproduction and even survival are low (Schaller 1972, Pusey & Packer 1987, Fuller & Sievert 2001). During periods of prey abundance, however, increased recruitment

leads to larger pride sizes, and as this may be influential in both gaining and maintaining high quality habitat (Mosser & Packer 2009), this in turn can increase chances of survival and successful reproduction. When examining sub-group sizes, Packer et al. (1990) found that when prey numbers are low, either solitary hunters or large hunting groups which could take down large prey led to higher per capita food intake, while intermediate group sizes had lower food intake. However, during periods of prey abundance, hunting group size was of little consequence to individual food intake (Packer et al. 1990). Consequently, grouping behaviour is strongly influenced by prevailing prey availability, as well as the type of prey available (Caraco & Wolf 1975, Packer et al. 1990).

African predator-prey systems are complex (Erlinge et al. 1984, Mills & Shenk 1992, Owen-Smith 2015), and while prey abundance influences lion abundance and demographics, the inverse is also true. As apex predators, lions play an important role in limiting prey populations, either directly through consumption, or indirectly by intimidation (Preisser et al. 2005, Owen-Smith 2015). While mortalities from predation regulate prey abundance directly, indirect effects of predation on prey can cause changes in prey behaviour with cascading effects on the rest of the ecosystem (Lima & Dill 1990, Ripple & Beschta 2012). Increased vigilance, which may reduce feeding time, or habitat shifts and refuge seeking resulting in the selection of poorer habitats as a means of predator avoidance, suppress prey survival and reproduction, and in doing so may also promote biodiversity (Hamilton 1971, Lima 1987, Lima & Dill 1990, Creel et al. 2005, Preisser et al. 2005, Creel & Christianson 2008, Valeix et al. 2009). In Yellowstone National Park for example, the reintroduction of wolves reduced elk (*Cervus elaphus*) numbers and caused a shift in their habitat use, leading to the recovery of woody vegetation as well as beaver (*Caster canadensis*) and bison (*Bison bison*) populations, which depend on woody species (Ripple & Beschta 2012). In lions, the effects of predation on prey species in large, open systems are closely related to prevailing ecological conditions, and lions can opportunistically shift their prey selection according to prey vulnerability (Mills et al. 1995, Owen-Smith 2015). For example, in Kruger National Park, South Africa, lions show clear cyclical switches in prey selection; wildebeest (*Connochaetes taurinus*) are predated upon during wet cycles, while buffalo (*Syncerus caffer*), particularly calves, are preyed upon in dry cycles when they are nutritionally stressed (Mills et al. 1995, Funston & Mills 2006). The effects of lion predation on

herbivore populations are also influenced by the spatial and temporal distribution of these prey animals in response to ecological cues (Mills & Shenk 1992). For example, large migratory groups of herbivores such as those in the Serengeti are believed to be minimally impacted by lions, but predator effects are more pronounced in resident herbivore populations, such as the wildebeest in the Ngorongoro crater (Schaller 1972, Sinclair 1985, Fryxell et al. 1988). Lions therefore have an important and intricate role in the ecosystem as top predators.

Intraspecific competition

As lion populations approach carrying capacity in an ecosystem, density-dependent regulation becomes important in shaping lion population demographic parameters. Higher lion densities lead to increased competition for resources such as space and food, resulting in changes such as lower pregnancy rates, lower recruitment and/or lower survival rates (Kissui & Packer 2004, Sinclair 1995). At very high densities, intraspecific competition can be a major determinant of female reproductive success (Packer et al. 2001). Mosser and Packer (2009) showed that increasing numbers of neighbouring lions had a substantial negative influence on female survival and reproductive success. Similarly, high numbers of male neighbours was also related to increased female mortality and wounding, as well as lower cub survival due to infanticidal behaviour (Mosser & Packer 2009). As a result of this fierce territorial behaviour, solitary or paired females have little chance of maintaining stable territories, and experience high mortality rates at medium to high lion densities where competition is intense (Hanby et al. 1995).

An important aspect of lion social behaviour, and one which contributes to reproductive success, is the communal rearing of cubs. The survival of large cohorts of cubs is largely influenced by the number of adult females in a pride which synchronise births, as there are more females present co-operating to feed and defend cubs against potentially infanticidal males or strange conspecifics (Bertram 1975, Packer & Pusey 1983a, b, Mosser & Packer 2009). These females also tend to remain together to hunt, and since group hunts are often more successful, this reduces the risk of cub abandonment due to malnutrition, as well as the risk that cubs will starve (Bertram 1975). Litters which are born further apart, however (with an age gap of more than seven months), have lower

survival rates, presumably due to increased competition for food from older cubs once cubs are weaned (Bertram 1975). The occurrence of synchronous births, however, seems to be regulated by internal social mechanisms, rather than ecological influences (Bertram 1975). For example, synchronous oestrous often coincides with recent takeovers by new males (Packer & Pusey 1983a, b). Despite the mechanisms involved in producing this response, it nevertheless remains an important factor in cub survival, and simultaneously raising large cohorts of cubs can ultimately lead to an increase in lion population size (Packer et al. 2005).

Rising from the need to defend cubs against infanticide, and due to their territorial behaviour, competition from conspecifics may also influence pride size and sub-grouping behaviour. Recent studies using playback experiments in numerous systems have shown that larger prides are more likely to confront smaller ones, or recruit other pride members to increase the odds of winning a territorial encounter (McComb et al. 1994, Heinsohn 1997, Spong & Creel 2004). As a result, sub-group sizes tend to be larger when surrounded by more neighbours, presumably to avoid encounters with other groups where they could be potentially outnumbered (Mosser & Packer 2009). However, if pride sizes are too large, females may also struggle to reproduce due to intense competition for resources (Packer et al. 2005). Therefore, while having a large pride may grant territorial advantage, within-group competition for resources places a limit on group size (Packer et al. 2001). Pride size therefore has important ramifications for demographic rates, and ultimately population growth.

Abiotic processes

An investigation into abiotic processes which affect lion populations across a variety of ecosystems show that climatic factors (such as temperature and rainfall patterns), as well as landscape features, have a strong association with various aspects of lion ecology, including lion density and pride size (Celesia et al. 2009). While herbivore biomass, or prey availability, is important for lion survival, it is not singled out as a key influence in lion demography, probably because prey densities are fundamentally driven by the same abiotic processes (Celesia et al. 2009). Furthermore, abiotic features such as vegetation structure can influence lion social organisation by changing the relative advantages to be gained by different group sizes (Trinkel et al. 2007, Patterson 2007). In open habitat,

larger group sizes occur to increase the chance of hunting success, while in dense vegetation, prey are easier to ambush, allowing smaller group sizes and higher per capita food intake (Trinkel et al. 2007).

In the Okavango Delta, dry season flooding results in a dynamic and complex system (Ramberg et al. 2006). Flooding parameters such as frequency, duration and extent determine vegetation structure (Murray-Hudson 2009), which in turn determines herbivore biomass. The floods reach their maximum extent during the dry season between April and August, attracting migratory herbivores from surrounding areas, and allowing for year-round resident prey (Bartlam-Brooks et al. 2013). During the floods, available dry land becomes smaller and patchier, confining most prey species to small islands and island edges (Crawshaw & Quigley 1991). As flood patterns vary, lions in wetland systems must thus constantly adapt to changing prey abundance as well as distribution, on both a seasonal and annual basis.

On the same note, lions themselves experience significant range contractions as a result of the flood. Consequently, habitat necessary for hunting and raising offspring is reduced to a large extent, forcing lions into smaller areas during the dry season. This could potentially increase the chances of aggressive encounters with other prides, as well as exacerbate competition for resources. Wetlands such as the Okavango Delta therefore represent unique situations where density-dependent population responses are enhanced through a drastic reduction of space, rather than an increase in numbers. One way in which lions may adjust to these changes is through changes in group size. As prey becomes confined during the dry season, and island size becomes smaller, prides may splinter into smaller sub-groups to reduce within-pride competition. Alternatively, lion sub-groups may become larger to confer territorial advantage in potentially increased encounters with neighbouring prides (Mosser & Packer 2009).

One of the only other studies investigating the influence of flooding on big cat behaviour examines jaguar (*Panthera onca*) behaviour in the Pantanal, a large, seasonally flooded wetland in Brazil (Crawshaw & Quigley 1991). In this wetland system, similar conditions prevail where prey animals are more concentrated in the flood season when there is less available dry land, and jaguars adapt their home range use to prevailing flood conditions and prey distribution (Crawshaw & Quigley 1991). In

contrast, in nearby Belize, where flooding does not occur and where there is a more stable and higher density of prey year-round, home ranges are smaller and more stable (Crawshaw & Quigley 1991), indicating that flooding has a significant effect on both the jaguar and its prey in wetland systems. Changes in flooding and prey distribution may also influence social interactions; home ranges of adult female jaguars in the Pantanal overlap significantly in comparison to other areas, suggesting a 'degree of social tolerance', where segregation is maintained on a temporal scale (Crawshaw & Quigley 1991). However, jaguars are solitary felids, and the influence of a fluctuating environmental variable such as flooding on social felids such as lions, has never been investigated.

Aims

The main aim of this study is to determine which social and ecological parameters are most important in determining lion population demographics, particularly survival and reproduction, and social organisation, defined as the size, composition and spatio-temporal make-up of lion groups (Kappeler & van Schaik 2002), in a wetland environment, the Okavango Delta. I focus specifically on the effects of three main social and ecological factors, namely 1) prey availability, 2) competition (both within and between pride density-dependence) and 3) flood extent - an ecological factor unique to wetland environments - on lion social organisation (Chapter 2) and population demographics (Chapter 3). Finally, I summarise the findings and compare them to results from other studies which investigate the main drivers behind lion social organisation and population demographics (Chapter 4). I also suggest how this information can be used to benefit management of the Okavango Delta populations, and suggest future areas of research (Chapter 4).

References

Antunes, A., Troyer, J.L., Roelke, M.E., Pecon-Slattery, J., Packer, C., Winterbach, C., Winterbach, H., Hemson, G., Frank, L., Stander, P., Siefert, L., Driciru, M., Funston, P.J., Alexander, K.A., Prager, K.C., Mills, G., Wildt, D., Bush, M., O'Brien, S.J. & Johnson, W.E. 2008. The evolutionary dynamics of the lion *Panthera leo* revealed by host and viral population genomics. *PLoS Genetics,* 4, e1000251.

Bartlam-Brooks, H.L.A., Beck, P.S.A., Bohrer, G. & Harris, S. 2013. In search of greener pastures: using satellite images to predict the effects of environmental change on zebra migration. *Journal of Geophysical Research: Biogeosciences,* 118, 1427-1437.

Bauer, H., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L.T.B, Macdonald, D. & Packer, C. 2015. Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proceedings of the National Academy of Sciences,* 112, 14894-14899.

Becker, M.S., Watson, F.G.R., Dröge, E., Leigh.K., Carlson, R.S. & Carlson, A.A. 2012. Estimating past and future male loss in three Zambian lion populations. *Journal of Wildlife Management,* 77, 128-142.

Bertram, B.C.B. 1975. Social factors influencing reproduction in wild lions. *Journal of Zoology, London,* 177, 463–482.

Bertram, B.C.R. 1973. Lion population regulation. *East African Wildlife Journal,* 11, 215-225.

Björkland, M. 2003. The risk of inbreeding due to habitat loss in the lion (*Panthera leo*). *Conservation Genetics,* 4, 515-523.

Brand, C.J. & Keith, L.B. 1979. Lynx demography during a snowshoe hare decline in Alberta. *Journal of Wildlife Management,* 43, 27-48.

Bygott, J.D., Bertram, B.C.R. & Hanby, J.P. 1979. Male lions in large coalitions gain reproductive advantages. *Nature,* 26, 839-841.

Caraco, T. & Wolf, L.L. 1975. Ecological determinants of group sizes in foraging lions. *American Naturalist,* 109, 343-352.

Celesia, G.G., Peterson, A.T., Peterhans, J.C.K. & Gnoske, T.P. 2009. Climate and landscape correlates of African lion (*Panthera leo*) demography. *African Journal of Ecology,* 48, 58-71.

Crawshaw, P.G. Jnr & Quigley, H.B. 1991. Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. *Journal of Zoology, London*, 223, 357-370.

Creel, S. & Christianson, D. 2008. Relationship between direct predation and risk effects. *Trends in Ecology and Evolution*, 23, 177-236.

Creel, S., Winnie, J. A. J., Maxwell, B., Hamlin, K. & Creel, M. 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology*, 86, 3387-3397.

Erlinge, S., Göransson, G., Högstedt, G., Jansson, G., Lieberg, O., Loman, J., Nilsson, I.N., Von Schantz, T. & Sylvén, M. 1984. Can vertebrate predators regulate their prey? *American Naturalist*, 123, 125-133.

Fryxell, J.M., Falls, J.B., Falls, E.A., Brooks, R.J., Dix, L. & Strickland, M.A. 1999. Density dependence, prey dependence and population dynamics of martens in Ontario. *Ecology*, 80, 1311-1321.

Fryxell, J.M., Greever, J. & Sinclair, A.R.E. 1988. Why are migratory ungulates so abundant? *American Naturalist*, 131, 781-798.

Fuller, T.K. & Sievert, P.R. 2001. Carnivore demography and the consequences of changes in prey availability. In: *Carnivore Conservation*. (Ed by J.L. Gittleman, S.M. Funk, D.W.Macdonald and R.K. Wayne) pp. 163-178. Cambridge: Cambridge University Press and the Zoological Society of London.

Funston, P.J. & Mills, M.G.L. 2006. The influence of lion predation on the population dynamics of common large ungulates in the Kruger National Park. *South African Journal of Wildlife Research*, 36, 9-22.

Goltsman, M., Kruchenova, E.P., Sergeev, S., Johnson, P.J & Macdonald, D.W. 2005. Effects of food availability on dispersal and cub sex ratio in the Mednyi Arctic fox. *Behavioral Ecology and Sociobiology*, 59, 198-206.

Hamilton, W. D. 1971. Geometry of the selfish herd. *Journal of Theoretical Biology*, 31, 295-311.

Hanby, J. P., Byggot, J.D. & Packer, C. 1995. Ecology, demography, and behaviour of lions in two contrasting habitats: Ngorongoro Crater and the Serengeti plains. In: *Serengeti II: dynamics, management, and conservation of an ecosystem* (Ed by A.R.E. Sinclair and P. Arcese) pp. 315-331. Chicago: University of Chicago Press.

Hanby, J.P. & Bygott, J.D. 1987. Emigration of sub-adult lions. *Animal Behaviour*, 35, 161-169.

Hayward, M. W., O'Brien, J. & Kerley, G. I. H. 2007. Carrying capacity of large African predators: predictions and tests. *Biological Conservation*, 139, 219-229.

Heinsohn, R. 1997. Group territoriality in two populations of African lions. *Animal Behaviour*, 53, 1143-1147.

Henschel, P., Coad, L., Burton, C., Chatainger, B., Dunn, A., Macdonald, D., Saidu, Y. & Hunter, L.T.B. 2014. The lion in West Africa is critically endangered. *PLoS One,* 9, e83500. doi:10.1371/journal.pone.0083500

IUCN. 2006. Regional conservation strategy for the lion *Panthera leo* in eastern and southern Africa. IUCN SSC Cat Specialist Group, Yaounde, Cameroon.

Kappeler, P. M. & Van Schaik, C. P. 2002. Evolution of primate social systems. *International Journal of Primatology,* 23, 707-740.

Kelly, M.J., Laurenson, M.K., Fitzgibbon, C.D., Collins, D.A., Durant, S.M., Frame, G.W., Bertram, B.C.R. & Caro, T.M. 1998. Demography of the Serengeti cheetah (*Acinonyx jubatus*) population: the first 25 years. *Journal of Zoology, London,* 244, 473-488.

Kissui, B.M. & Packer, C. 2004. Top-down regulation of a top predator: lions in the Ngorongoro Crater. *Proceedings of the Royal Society of London, B. Biological Sciences,* 271, 1867-1874.

Kruuk, H. 1972. *The spotted hyena. A study of predation and social behaviour.* (Ed by G.B. Schaller) Chicago and London: The University of Chicago Press.

Laurenson, M.K. 1995. Cub growth and maternal care in cheetahs. *Behavioral Ecology* 6, 405–409.

Lima, S. L. & Dill, L. M. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, 68, 619-640.

Lima, S. L. 1987. Vigilance while feeding and its relation for the risk of predation. *Journal of Theoretical Biology,* 124, 303-316.

Loveridge, A.J., Searle, A.W., Murindagomo, F. & Macdonald, D.W. 2007. The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biological Conservation,* 134, 548-558.

Macdonald, D.W. 1979. The flexible social system of the golden jackal, *Canis aureus. Behavioral Ecology and Sociobiology,* 5, 17-38.

McComb, K., Packer, C. & Pusey, A. 1994. Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. *Animal Behaviour*, 47, 379-387.

Mech, L.D. 1995. A ten-year history of the demography and productivity of an Arctic wolf pack. *Arctic,* 48, 329-332.

Midlane, N. 2013. The conservation status and dynamics of a protected African lion *Panthera leo* population in Kafue National Park, Zambia. PhD Thesis. University of Cape Town.

Mills, L. S., Doak, D. F. & Wisdom, M. J. 1999. Reliability of conservation actions based on elasticity analysis of matrix models. *Conservation Biology,* 13, 815–829.

Mills, M.G.L. & Shenk, T.M. 1992. Predator-prey relationships: the impact of lion predation on wildebeest and zebra populations. *The Journal of Animal Ecology,* 61, 693-702.

Mills, M.G.L., Biggs, H.C. & Whyte, I.J. 1995. The relationship between lion predation, population trends in African herbivores and rainfall. *Wildlife Research,* 22, 75-88.

Moore, A.E., Cotterill, F.P.D., Winterbach, C.W., Winterbach, E.K., Antunes, A. & O'Brien, S.J. 2015. Savannah habitat specializations in different populations of lions. *Journal of Heredity,* esv097.

Mosser, A. & Packer, C. 2009. Group territoriality and the benefits of sociality in the African lion, *Panthera leo. Animal Behaviour,* 78, 359-370.

Murray-Hudson, M. 2009. Floodplain vegetation responses to flood regime in the seasonal Okavango Delta, Botswana. PhD Thesis. University of Florida.

Ogutu, J. O. & Dublin, H.T. 2002. Demography of lions in relation to prey and habitat in the Masai Mara National Reserve, Kenya. *African Journal of Ecology,* 40, 120-129.

Owen-Smith, N. 2015. Mechanisms of coexistence in diverse herbivore-carnivore assemblages: demographic, temporal and spatial heterogeneities affecting prey availability. *Oikos,* 124, 1417-1426.

Packer, C. & Pusey, A. E. 1983a. Adaptations of female lions to infanticide by incoming males. *The American Naturalist,* 121, 716-728.

Packer, C. & Pusey, A. E. 1983b. Male takeovers and female reproductive parameters: a simulation of oestrous synchrony in lions (*Panthera leo). Animal Behaviour,* 34, 334-340.

Packer, C., Brink, H., Kissui, B.M., Maliti, H., Kushnir, H. & Caro, T. 2011. Effects of trophy hunting on lion and leopard populations in Tanzania. *Conservation Biology,* 25, 142-153.

Packer, C., Herbst, L., Pusey, A.E., Bygott, J.D., Hanby, J.P., Cairns, S.J. & Borgehoff-Mulder, M. 1988. Reproductive success of lions. In: *Reproductive Success: Studies of Individual Variation*

in Contrasting Breeding Systems. (Ed. by T.H. Clutton-Brock) pp 363-383. Chicago: University of Chicago Press.

Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, J., Mduma, S. & Sinclair, A.R.E. 2005. Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science,* 436, 927-928.

Packer, C., Pusey, A.E. & Eberly, L. E. 2001. Egalitarianism in female African lions. *Science*, 293, 690-693.

Packer, C., Scheel, D. & Pusey, A.E. 1990. Why lions form groups: food is not enough. *American Naturalist*, 136, 1-19.

Patterson, B.D. 2007. On the nature and significance of variability in lions (*Panthera leo*). *Evolutionary Biology*, 34, 55-60.

Preisser, E. L., Bolnick, D. I. & Bernard, M. E. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology*, 86, 501-509.

Pusey, A.E. & Packer, C. 1987. The evolution of sex-biased dispersal in lions. *Behavior,* 101, 275-310.

Pusey, A.E. & Packer, C. 1994. Non-offspring nursing in social carnivores: minimizing the costs. *Behavioural Ecology,* 5, 362-374.

Ramberg, L., Hancock, P., Lindholm, M., Meyer, T., Ringrose, S., Silva, J., Van As, J. & Vanderpost, C. 2006. Species diversity in the Okavango Delta, Botswana. *Aquatic* Sciences, 68, 310-337.

Riggio J. 2011. The African lion (*Panthera leo*): a continent-wide species distribution study and population analysis. MSc Thesis, Duke University.

Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., Funston, P., Groom, R., Henschel, P., De Iongh, H., Lichtenfeld, L. & Pimm, S. 2013. The size of savannah Africa: a lion's (*Panthera leo*) point of view. *Biodiversity Conservation*, 22, 17-35.

Ripple, W.J. & Beschta, R.L. 2012. Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. *Biological Conservation,* 145, 205-213.

Schaller, G. B. 1972. *The Serengeti lion: a study of predator prey relations*. Chicago: University of Chicago Press.

Sinclair, A. 1995. Serengeti past and present. In: *Serengeti II Dynamics, Management and Conservation of an Ecosystem*. (Ed by A.R.E. Sinclair and P. Arcese) pp3-30. Chicago: University of Chicago Press.

Sinclair, A.R.E., Dublin, H., & Borner, M. 1985. Population regulation of Serengeti wildebeest: a test of the food hypothesis. *Oecologia,* 65, 266-268.

Spong, G. & Creel, S. 2004. Effects of kinship on territorial conflicts among groups of lions, *Panthera leo. Behavioural Ecology and Sociobiology,* 55, 325-331.

Stander, P.E. 1991. Demography of lions in the Etosha National Park, Namibia. *Madoqua,* 18, 1-9.

Stander, P.E., Haden, P.J., Kaqece & Ghau. 1997. The ecology of asociality in Namibian leopards. *Journal of Zoology (London),* 242, 343–364.

Treves, A., Plumptre, A.J., Hunter, L.T.B. & Ziwa, J. 2009. Identifying a potential lion Panthera leo stronghold in Queen Elizabeth National Park, Uganda, and Parc National ds Virunga, Democratic Republic of Congo. *Oryx,* 43, 60-66.

Trinkel, M., Van Niekerk, R.W., Fleischmann, P.H., Ferguson, N. & Slotow, R. 2007. The influence of vegetation on lion *Panthera leo* group sizes in the Hluhluwe-Umfolozi Park, South Africa. *Acta Zoologica Sinica,* 53, 15-21.

Valeix. M, Loveridge, A.J., Chamaillé-James, S., Davidson, Z., Murindagomo, F. Fritz, H. & Macdonald, D.W. 2009. Behavioural adjustments of African herbivores to predation risks by lions: spatiotemporal variations influence habitat use. *Ecology,* 9, 23-30.

Van Bommel, L., Bij De Vaate, M.D., De Boer, W.F. & De Iongh, H.H. 2007. Factors affecting livestock predation by lions in Cameroon. *African Journal of Ecology,* 45, 490-498.

Van Orsdol, K.G., Hanby, J.P. & Bygott, J.D. 1985. Ecological correlates of lion social organisation (*Panthera leo*). *Journal of Zoology (London),* 206, 97–112.

Watts, H.E. & Holekamp, K.E. 2009. Ecological determinants of survival and reproduction in the spotted hyena. *Journal of Mammalogy,* 90, 461-471.

Woodroffe, R. & Frank, L.G. 2005. Lethal control of African lions (*Panthera leo*): local and regional population impacts. *Animal Conservation,* 8, 91-98.

Chapter 2

Ecological and social factors determining social organisation of lions (*Panthera leo*) in the Okavango Delta

Abstract

Lions (*Panthera leo*) are the only social felids, and live in social groups called prides. Members of the pride co-operate to defend a territory, but are often fragmented into smaller sub-groups within the territory at any given time. Thus, lion social organisation is dynamic, and the composition and size of both prides and sub-groups can be altered according to prevailing social and ecological conditions in order to maximise individual fitness of pride members. The distribution and abundance of prey is often cited as the main determinant of lion group sizes, and advantages conferred by group hunting was originally believed to be the catalyst of lion social behaviour. However, other social factors, such as communal defence of cubs and territories against conspecifics, as well as abiotic factors, such as vegetation cover, can also influence lion group sizes. While recent genetic evidence suggests that lions ancestrally occurred in wetland ecosystems, most existing research investigates lion social organisation in arid and mesic savannah systems. This study therefore aims to assess lion social organisation in a wetland environment, the Okavango Delta (Botswana). The main aim of the study was to determine how prey availability, inter- and intra-pride competition, and flooding may influence lion social organisation at both a pride and sub-group level. Our results indicated that social factors were more important in determining grouping behaviour of adult females, but when sub-adults were included in the analysis (total pride and total sub-group size), ecological factors came to the fore. In a wetland environment, flooding negatively affected both total pride size and total sub-group sizes, suggesting that a decrease in available dry land increases competition both within and between prides. Competition from neighbouring prides, however, had the most over-arching influence on lion grouping behaviour. Competition negatively influenced total and adult female pride size, but contrary to expectations, also negatively influenced adult female sub-group sizes, suggesting that territorial behaviour was not as important in influencing sub-group behaviour in the Okavango Delta as in other savannah environments. Total pride size was inversely related to prey availability, most likely due to high levels of competition and thus lack of vacant territories, resulting in higher recruitment. On a sub-group level, lions formed larger sub-groups (sub-adults included) with declining prey, probably to increase hunting success rates and thus reduce variance in feeding frequency. Thus in the Okavango Delta, social factors and flooding are more important drivers of lion social organisation than prey abundance.

Keywords: *lions, pride size, social organisation, sub-groups, prey abundance, flooding, intra-specific competition, Okavango Delta.*

Introduction

Many social carnivores live in fission-fusion societies, where individuals who share a common territory may not be together all the time, and may be found either alone or in smaller sub-groups (Smith 2008). This fluid social organisation allows for considerable flexibility, where individuals can maximize individual fitness by choosing to remain with or leave a group based on concurrent environmental or social circumstances (Caraco & Wolf 1975, Gittleman 1989, Chapman 1990, Wrangham et al. 1993, Chapman et al. 1995, Smith 2008). Group sizes are influenced by social factors (van Orsdol et al. 1985, Higashi & Yamamura 1993, Smith 2008) as well as biotic and abiotic factors in the environment (Bowen 1981, Mills 1978, Feore & Montgomery 1999). As social systems can influence population response to ecological changes and influence the genetic make-up of populations (Spong et al. 2002, Packer et al. 2005), understanding how carnivores adapt their social organisation to local conditions can offer important insight into the degree to which populations can adapt to changing environmental and anthropogenic influences in the future (Patterson 2007).

Lions (*Panthera leo*) are the only social felids and live in fission-fusion societies known as prides (Schaller 1972). Prides consist of related and resident females, associating coalitions of males and their cubs (Schaller 1972). Although these individuals constitute a unified social unit, they may disband into smaller social units known as sub-groups or sub-prides, and use different areas of the pride's home range (Van Orsdol et al. 1985). These sub-groups may associate with one another regularly, or conversely, have very little contact with one another (Van Orsdol 1985). Adult females within a pride often give birth synchronously, and these mothers then co-operate to raise cubs and defend them, spending most of their time together until the cubs reach maturity (Packer & Pusey 1983, Van Orsdol et al. 1985, Packer et al. 2001). Young adult males generally disperse at an age of between two and four years old, primarily as a result of eviction by new pride males (Hanby & Bygott 1987). These evicted males then become nomadic until they find and take-over a pride of their own (Bygott et al. 1979). Females are philopatric and are often recruited into the pride, inheriting their natal territory (Van Orsdol et al. 1985). If pride sizes become too large and vacant territories are available, sub-groups may leave the natal area to form new prides, often in adjacent territories (Packer et al. 2005, Mosser & Packer 2009).

Initially, it was assumed that the explicit cause of lion sociality, and the main driver behind differences in group size, was the benefit gained through co-operative hunting (Schaller 1972, Macdonald 1983, Turner 1997). However, studies examining lion grouping behaviour have revealed that lion hunting group sizes are often larger than would be predicted based on maximizing individual food intake (Caraco & Wolf 1975). Theories put forward to explain this discrepancy include increased frequency of successful hunts due to larger group sizes, or more effective protection of carcasses against scavengers (Rodman 1981, Giraldeau & Gillis 1988). Indeed, in the Serengeti, Tanzania, sub-groups are generally larger when prey is scarce, and smaller during times of prey abundance (Packer et al. 1990). During periods of prey abundance, survival of young and sub-adults is enhanced, and recruitment into the pride is more likely (Hanby & Bygott 1979, Van Orsdol et al. 1985). Consequently, prey abundance has also been implicated as an important factor in determining overall pride size (Van Orsdol et al. 1985).

Social factors, such as the protection of cubs against unfamiliar males as well as territorial defence, have been indicated as important factors in sub-group size determination (Mosser & Packer 2009). Adult lionesses crèche cubs and co-operate to defend and raise litters that are of a similar age (Schaller 1972, Bertram 1975, Pusey & Packer 1994). In sub-groups where cubs are present, this is a primary and consistent determinant of grouping patterns within a pride (Pusey & Packer 1994). In sub-groups excluding cubs, however, factors such as competition with neighbours may influence grouping patterns, as larger groups have a numerical advantage in territorial disputes (Packer et al. 1990, Grinnell et al. 1995). Similarly, at the pride level, larger prides have clear territorial advantages over smaller neighbouring prides (Mosser & Packer 2009). Therefore, in habitats with high levels of intraspecific competition, the recruitment of sub-adult females increases the likelihood of gaining more favourable habitat (Mosser & Packer 2009).

Extrinsic, abiotic factors cannot be excluded as important influences in the grouping patterns of lions, but the extent to which these factors influence lion behaviour are not well understood (Celesia et al. 2009). Proximity to important landscape features such as river confluences or waterholes can strongly influence other aspects of lion ecology such as home range size and reproductive success (Van der Waal et al. 2009, Valeix et al. 2009), but few studies have focused on the influence of such abiotic

factors on lion group size. One study in Hluhluwe-Umfolozi Park, South Africa, however, showed that vegetation structure has a significant effect on the grouping behaviour of lions (Trinkel et al 2007). In this system, where prey is abundant and evenly distributed, group sizes are larger in open vegetation, while in the dense vegetation of the park, group sizes are much smaller (Trinkel et al. 2007). In open areas, lack of cover necessitates co-operative hunting and increased protection for cubs, while in thick vegetation hunting success is higher due to increased cover for ambush hunting, and cubs are easier to hide (Trinkel et al. 2007).

New genetic evidence indicates that ancestral lions may have been wetland specialists (Moore et al. 2015), suggesting that this type of environment may have played an important role in shaping the social behaviour of this large felid. The Okavango Delta in Botswana is a dynamic wetland ecosystem driven by annual flood pulses to which resident species must adapt over both long and short time-scales. In this ecosystem, during periods of high flood, lions experience significant range contractions, and must adapt to shifts in herbivore abundance and distribution brought on by shifting inundation patterns (Crawshaw & Quigley 1991). Similar conditions have been observed for jaguars (*Panthera onca*) in the Pantanal, a large seasonal wetland in Brazil (Crawshaw & Quigley 1991). This contraction of available dry land and seasonal shift in prey distribution may result in increased competition for both space and available prey, and in turn, affect lion grouping patterns. However, the importance of such a large landscape scale process in influencing lion social organisation has never been investigated.

The main aim of this study is therefore to investigate the extent to which flooding influences lion social organisation, while taking the more conventional social and ecological influences on lion group sizes into account. We use detailed information collected on lion group size and composition, spanning a period from low to high flood cycles in the Okavango Delta, to determine the effects of: 1) the maximum annual flood extent, 2) social factors and 3) prey abundance on lion pride sizes and sub-group sizes. We expected that 1) increasing flood levels would lead to increased competition for resources, resulting in smaller pride sizes and sub-group sizes; 2) competition would negatively affect pride size, but encourage larger sub-group sizes where cubs are absent; 3) communal rearing of cubs

would be an important influence on sub-groups of associating adult females; and 4) prey abundance would positively influence pride size, but be inversely related to sub-group size.

Methods

Study Area

The Okavango Delta, situated in north-western Botswana, is the biggest freshwater Delta in the world, covering approximately 14 000km^2 (McCarthy et al. 1998). Each year, seasonal rains which fall between October and April in the Angolan highlands flow down through the Caprivi Strip of Namibia and into Botswana, terminating in a unimodal, annual flood pulse (Ramberg et al. 2006, Murray-Hudson 2009). Besides the rainfall patterns in Angola, the extent and duration of the annual pulse is variable and is dependent on a number of other factors, including local seasonal rainfall and the attributes of the previous flood (Murray-Hudson 2009). Flood waters typically arrive from early April, and reach their full extent in late August or September (Gumbricht et al. 2004).

Small elevations in the Okavango Delta result in large differences in flood duration and frequency, leading to a patchwork of vegetation types (Ramberg et al. 2006). This complex pattern of vegetation types results from channel courses which can change from one flood to the next, and the formation of islands resulting from the accumulation of sediments or most commonly, from termite mounds (McCarthy et al. 1998). Inundated areas vary from permanent swamps dominated by *Papyrus* and *Cyperus* species, to seasonal swamps dominated by *Phragmites* and several water-tolerant grass species, which serve as an important dry season resource for herbivores (Meyer 1999, Ramberg et al. 2006, Gumbricht et al. 2004).

The edges of dry islands, which increase in size away from the main channels, are characterized by riparian woodlands communities of *Ficus sycamorus, F. natalensis, F. verruculosa, Diospyros mespilliformis, Syzigium cordatum* and *Garcinia livingstonei* (Ellery et al. 1993). Towards the island interior, these woodlands give way to *Senegalia nigrescens, Croton megalobotrys* and *Hyphenae ventricosa* (Ellery et al. 1993). Away from the main channels, the proportion of dry land in relation to inundated areas increases, forming large islands locally referred to as ‘sandveld tongues’, which are

dominated by *Colophospermum mopane* and *Lonchocarpus nelsii* communities (McCarthy et al. 1998).

The study area is situated in wildlife management concessions NG29 and NG30, between S 19° 33' and S 19° 53', and E 22° 48' and E 23° 06' (Figure 1). These concessions occur on the western side of the Delta, south-west of Chief's Island. This area is characterised by highly variable flooding patterns, with considerable fluctuations in flood levels with each pulse and large inter-annual variation in flood extent (Wolski & Murray-Hudson 2006a). From 1997, the Xudum channel, which flows through the centre of the study area, started receiving a sudden increase in inflow, proposed to be due to a tectonic event or permanent vegetation change (Wolski & Murray-Hudson 2006a). As a result of the re-directed flow, increases in water levels in the Xudum distributary were accompanied by a simultaneous decrease in flow in other nearby distributaries (Wolski & Murray-Hudson 2006a). Due to the increased inflow as well as higher overall flood levels post-2000, there was a considerable change in vegetation type from temporarily flooded grasslands to semi-permanent swamps dominated by *Cyperus* species (Christiaan Winterbach pers. comment).

Data collection

Lions

Detailed data on pride dynamics were collected for five prides in the study area between 1997 and 2004. This research was conducted with permission from the Office of the President (permit reference numbers: OP 46/1 LXVIII (133)) and the Minister of Environment, Wildlife and Tourism (MEWT, permit reference number EWT 3/3/8 XXIX (50)) in conjunction with the Department of Wildlife and National Parks (DWNP). During the study period, at least one lioness in each pride was fitted with a VHF (very-high frequency) radio collar to allow for easier and more consistent follow-up on prides, and an attempt was made to locate each pride once a week. Lions were also located opportunistically by following up on sightings reported by game view vehicles, or when lions were encountered during concession monitoring.

Prides were defined, according to Schaller's (1972) description, as "groups of resident lionesses with their cubs, as well as the attending males, which share a pride area and interact peacefully". Individuals in each pride were identified using whisker spot patterns (Pennycuick & Rudnai 1970), and assigned pride memberships based on Schaller's (1972) description. Sub-groups of prides were defined as the number of individuals of the same pride encountered together at any one time, separated by a distance of 200m or less. This distance of separation would assume that all pride members present would participate in group activities such as hunting or feeding and thus have some degree of direct social interaction. Data collected during observations included pride identity, Universal Transverse Mercator (UTM) location and group size and composition (sex and age of lions present). Ages of lions were estimated from body size to within two years - particularly for younger lions (Smuts 1982) - while the age of older lions was estimated using nose colour or tooth wear (Whitman & Packer 2007). Individuals were classified as cubs if younger than two years old, sub-adults if between two and four years old, and adults if older than four years (Smuts 1982). Only observations where all members of the sub-group were sexed and categorized into an age group were used in the analysis. Mean pride sizes are reported with 95% confidence intervals.

Prey abundance data

Transects were conducted along established roads in the wildlife management concessions NG27A, NG30 and NG29 (Figure 1). Transects were driven in the early mornings and late afternoons, when animals are most active. During transects, animals were counted on either side of the road for a perpendicular distance of up to 200m, and the species, herd size, UTM location, and time of day were recorded. Where possible, transects were repeated seasonally if flooding conditions did not inhibit data collection. Data collected during the dry season each year (August to November) was used for the analyses.

Data analysis

Group sizes

Pride sizes were estimated on an annual basis, in two different ways. The first included the number of adult females only, as adult females represent the most stable estimation of pride size (Bertram 1973). The second included both adult females and all sub-adults, as sub-adults are able to contribute to pride success by assisting with hunting, but also compete for resources within the pride. Sub-group sizes were also analysed in two ways: adult females only, and adult females plus sub-adults. While crécheing of cubs is the most important factor in determining sub-group size of adult females in the Serengeti (Pusey & Packer 1994), the tolerance of sub-adults may be more dependent on other variables, such as prey availability or carcass size or group territoriality (Trinkel et al. 2007, Van Orsdol et al. 1985). Therefore, for sub-group size including adult females only, number of dependent cubs was used as an additional predictor, and for sub-group analysis including adults and sub-adults, all observations including cubs were removed from the data to exclude the effect that cubs would have on the number of associating adults.

Covariates

We modelled the effects of two ecological and one social covariate on lion pride size and sub-group size. Per capita prey abundance, intraspecific competition and maximum annual flood extent were determined for each of the five study prides. Covariate data were analysed for each year from 1997-2002 and for 2004. The year 2003 was excluded as there was not enough dry season data to reliably estimate prey abundance for all five prides. To account for differences in covariates between prides, pride home ranges were calculated and the boundaries were used as cut-off points to divide herbivore transects between each pride, and to determine how much dry land was available to each pride at the maximum annual flood extent.

Home range calculations

Universal Transverse Mercator (UTM) data was used to determine home range boundaries for each lion pride, using the Animal Movements Extension in ArcView GIS 3.2 (ESRI, Redlands, CA). Due

to the limitations imposed by using VHF tracking to locate animals, location data was pooled from all of the years in the study period to construct long-term home ranges. Data collection by means of telemetry tracking and direct observation was restricted by the position and size of the flood, which hindered the ability to follow lions into areas which could not be traversed by vehicle. Additionally, differences in sampling intervals resulting from flood conditions may also result in an underestimation of range use due to missing clusters of locations used by prides (O' Kochanny et al. 2009). Annual home ranges tend to stay constant from year to year within prides, even if there are seasonal shifts within the home range due to the distribution of prey (Schaller 1972, Hanby et al. 1995). A long-term home range is therefore a more robust representation of area used per pride as it incorporates both seasonal and annual variation in range use.

Using pooled locations, fixed kernels were selected as the appropriate method of home range estimation. Utilisation distributions allow more accuracy in depicting home range use than minimum convex polygons, but provide sufficient detail necessary for our analysis, such as the location of the main nodes of home range use (Worton 1989). Furthermore, kernels are able to accurately estimate home range size at small sample sizes, which is the case in this study (Börger et al. 2006). The 90% isopleth was chosen as the representative of home range border (Borger et al. 2006). Börger et al. (2006) indicate that 50% and 90% isopleths serve as unbiased estimators of core home range and overall home range size respectively, and that isopleths below or above these values result in increased variance in home range estimation (also see Getz et al. 2007, Naidoo et al. 2012). Additionally, the 90% isopleth has also been used to represent lion home range size in several recent publications (Spong 2002, Funston et al. 2003, Loveridge et al. 2009, Midlane 2013). Due to the potential underestimation of home range size resulting from using VHF collars, a reference smoothing factor was used to smooth kernels (see Hemson et al. 2005). *Href* was chosen as the appropriate smoothing method because it is positively biased (Worton et al. 1995). *Href* would therefore likely overestimate home range size at small sample sizes, potentially including more areas in the home range missed due to unequal sampling intervals and accessibility issues (Worton 1995), but at larger sample sizes, accuracy in estimating true home rang size increases (Worton 1995, Kie 2013).

Per capita prey abundance

The kilometric abundance index (KAI - Vincent et al. 1991) was used to determine abundance of preferred lion prey per pride home range. For this study, this was defined as "number of observed animals/number of kilometres" of transect (Vincent et al. 1991). This index, if standardized, can reliably detect trends in animal abundance from one year to the next (Maillard et al. 2001, Vincent et al. 1991), and was used as an indication of the rate at which lions come across prey while travelling through the home range (Kiffner et al. 2009, Loveridge et al. 2009). Transects were apportioned to each study pride using the boundaries of lion home ranges as cut-off points. Data collected during the dry season (August to November) was used for KAI calculations.

Due to the strong relationship between preferred prey biomass and lion numbers (Hayward et al. 2007), data collected during the study period on successful and attempted hunts (n=129) were used to determine the prey preference of the study prides. Animals which made up only 1% or less of the diet were excluded as regular prey selection. The only other species, making up 7% of prey selection, excluded from the analysis were buffalo (*Syncerus caffer*). Buffalo herds were rarely encountered on transects, and due to the large biomass represented by large herds, were excluded from KAI calculations to prevent bias in the data from year to year. Buffalo in the Okavango Delta are largely migratory, and move large distances seasonally in search of suitable grazing (Burger et al. unpublished data). As such they do not represent a resident food source in the study area.

Kilometric abundance indices were calculated for each of the preferred prey species, and then converted to kilometric biomasses by multiplying the KAI for each species by average species weight for females (Loveridge et al. 2009). Each species' kilometric biomass was then multiplied by 0.75 to account for young and sub-adult animals in the population (Hayward et al. 2007, Schaller 1972, Midlane 2013). The kilometric biomasses for each species were then added to determine the total biomass of prey available to lions in their specific home ranges each year per kilometre, resulting in a total kilometric prey abundance. Lastly, as lions are social, the total kilometric prey abundances were divided by pride size (adult and sub-adults included) to reach a per capita prey abundance index. In group-living carnivores, individuals compete for both live prey and for their share of carcasses (Watts

& Holekamp 2009). A per capita prey abundance index is therefore a more accurate indication of prey abundance when dealing with groups of social carnivores (Watts and Holekamp 2009).

Competition

Competition was defined as the total number of adult female lions from other prides whose home ranges overlapped with the focal pride's home range (Mosser & Packer 2009). A caveat of this selection is that while large channels to the east and the north of the study area would reduce access from other prides, competition from the west and the south from neighbouring prides may be underestimated. However, given the significant overlap in home ranges observed in the study area, competition is taken to represent these observed overlaps. In Van der Waal et al. (2009), neighbours were considered as the number of prides whose core territories (50% kernel density isopleth) were within three kilometres of one another. This holds true for the five prides in the study area. For simplicity, only adult females were considered, as these are the members of the pride most likely to engage in territorial conflict, or take over kills (Heinsohn et al. 1996, Mosser & Packer 2009). As male coalitions often straddled more than one pride during the study period, they were excluded from the analysis.

Flooding

To determine the area of dry land available at maximum flood extent each year, satellite TM4 and TM+ imagery depicting maximum flood levels for the years 1997-2002 were obtained from the Okavango Research Institute (Wolski & Murray-Hudson. 2006b). Each image consists of 28m x 28m pixels, which were classified as either flooded or dry, the criteria for which are outlined in Wolski and Murray-Hudson (2006b). Home ranges of lions were superimposed on flooding maps using ArcMap 10.1 (ESRI, Redlands, California), and the area of dry land available for each year in each home range calculated. The time of maximum flood extent represents the time of the year where space is most limited by the water for both lions and their prey. For the year 2004, no satellite imagery was available, and consequently MODIS imagery depicting flooding extent was used as a substitute. While pixel size is much larger (250m x 250m), Murray-Hudson et al. (2014) have shown that MODIS imagery is just as accurate in determining flooding extent as satellite imagery, and can be

used as a reliable substitute where higher resolution data is missing. The amount of available dry land is taken to represent the effects of flooding, and this covariate is referred to as 'land availability' in all subsequent analyses.

Statistical analysis

Generalized linear models were used to determine the effects of per capita prey abundance, competition and amount of land available during maximum flood extent on lion pride sizes and sub-group sizes. For all group size response variables, a global model was constructed including competition, per capita prey availability and land availability as fixed effects. For both sub-group size analyses, overall pride size (adult females plus sub-adults) was included as an additional fixed effect, as was number of cubs for sub-group sizes where only the number of adult females was considered. In all models, both pride identity and year were included as random effects. These random effects take into account factors which may be at work within each pride and each year, which are not common to all prides and years, and would therefore introduce additional variation into the model (Bertram 1975, Bolker 2008). This extra variation is thus taken into account, without having to focus on the main effects of year and pride on the response variable (Bolker. 2008). Prior to linear modelling, variance inflation factors (VIF), which are commonly used as an indication of the degree of collinearity between independent variables in regression models (O'Brien 2007), were calculated for each covariate. All VIFs were <5, indicating no collinearity between covariates, and as a result, all covariates were retained in the global models. Due to differences in order of magnitude, and to make results directly comparable, covariates were standardized prior to modelling (Schielzeth 2010) using the *arm* package (Gelman et al. 2013) in R 3.1.0 (R Core Development Team 2014).

Generalized linear models were constructed using the *glmer()* function in the *lme4* (Bates et al. 2014) package in R 3.1.0 (R Core Development Team 2014). Global models (including all relevant predictor variables) were used as the starting model , and all possible nested models constructed using the dredge function of the *MuMIn* package (Barton 2013) to determine which model minimised Aikaike's Information Criterion for small sample sizes (Burnham and Anderson 2002). Models whose AIC value differed from the best model by <2 were included as equally parsimonious, and taken to

represent the best models to describe the data (Burnham and Anderson 2002). Inclusion of larger cut-off points e.g. Δ AICc<4 resulted in an inclusion of a large proportion of models in relation to total number of models, which is not recommended for model selection (Arnold 2010). To account for model uncertainty, models with Δ AICc<2 were averaged, and coefficients calculated using the zero method to identify factors which had the greatest effect on group sizes (Nakagawa & Freckleton 2010, Grueber et al. 2011).

Results

Over the study period, the mean pride size including only adult females was 6.14 ± 1.07 (range 2 – 14), and the mean pride size with sub-adults included was 8.51 ± 1.44 (range 4 -18). From year to year, the number of adult females in each pride remained relatively close to the mean (Figure 2), with the median group size varying between four and six adults. When sub-adults were included in pride size however, there was considerable inter-annual variation.

Sub-group sizes fluctuated from year to year, showing a general decrease in size towards 2000, and an increase in size once again after 2000. Median sub-group size for groups including adult females only varied between two and four individuals (Figure 3). For sub-group sizes including sub-adults, the median sub-group size was only slightly higher, and there was no considerable amount of increased variation (Figure 3).

There was a large degree of overlap between long-term home ranges of all five prides (Figure 4). There was also a general decrease in land availability for each pride between 1997 and 2004, coinciding with the redistribution of flow down the western side of the Okavango Delta and down the Xudum system (Figure 5, Wolski & Murray-Hudson 2006a). The average area of home range to remain dry during peak flood decreased from 80% in 1997, to only 25 % in 2004. During this time, there was also a general decline in prey availability, with a sharp decline observed after 1997 (Figure 5). The total number of lions in the study area, summed across five prides and including adults and sub-adults, also showed a subtle decline throughout the study period (Figure 5).

The best performing model using pride size of adult female lions as an outcome variable included both competition with neighbours and per capita prey availability as predictive factors, and explained 51.4% of the variation in the model (Table 1). Two other models had similar AICc weights, one of which included only competition with neighbours, and the other all three predictive variables. After model averaging, however, only competition emerged as an important factor in determining pride size including only adult females, and had a negative effect on pride size (Table 2).

The best model for overall pride size (both adult females and all sub-adults) was the global model and included all three covariates (Table 1). No other models were considered to be equally parsimonious, and the global model explained 57.4% of the variation in pride size. The next model AICc value did not fall within the selected cut-off range, and the cut-off was therefore extended to include models within $\Delta AICc<4$. This included an additional model which excluded competition. After model averaging was performed on these two models, all three covariates were still retained as influential. While competition had a 77% importance relative to per capita kilometric prey abundance and land availability, the effect size of competition was larger than both land availability and per capita kilometric prey abundance (Table2). Whereas competition and per capita prey abundance had a negative effect, land availability had a positive effect on overall pride size.

The best predictive model for sub-group sizes of adult females, including groups where cubs were present, included competition with neighbours, the number of cubs in the group as well as pride size (Table 1). This model accounted for 43.6 % of the variation in sub-group sizes of adult females. Three other models were considered to be equally parsimonious using a cut-off of $\Delta AICc<2$, and these included combinations of all five of our social and ecological variables. After model averaging was conducted on the top models, only competition with conspecifics and the number of cubs present were retained as covariates that influenced sub-group size of adult females (Table 2). Sub-group size had a positive relationship with the number of cubs in the group, but a negative relationship with the number of competing neighbours.

The best predictors for sub-group sizes where sub-groups with cubs were excluded, and considering both adult females and sub-adults, included both land availability and per capita prey availability

(Table 1). However, this model accounted for only 26% of the variation in sub-group size. One more model was considered to be equally parsimonious, which included pride size as an additional factor. After model averaging was conducted to account for uncertainty, per capita prey abundance and land availability emerged as important predictors in sub-group sizes where cubs were absent. While the availability of land had a positive effect on sub-group size, per capita prey availability had a negative effect on sub-group size (Table 2). While both effects were considered equally important, land availability had a larger effect size than prey availability.

Discussion

This is the first investigation of the influence of flooding patterns on lion social organisation, and our results revealed that flooding influences both pride size and sub-group size when sub-adults are included in the analyses. This confirms our hypothesis that group sizes decrease with increased flood levels, and we suggest that this may be related to inflated density-dependent effects, resulting from a decrease in area rather than an increase in population size. At the high lion density observed throughout the study period, competition for space would have increased dramatically with higher flood levels. This may have resulted in lower survival of cubs, and consequently lower recruitment. Additionally, inter-pride interactions resulting from prides sharing smaller areas could have led to increased wounding and mortality, as well as infanticide (Mosser & Packer 2009). Increased competition for space and resources may have also led to a lower tolerance of sub-adults, which could potentially disperse, and due to the high cost of emigration, lower sub-adult survival. Higher levels of flooding therefore regulate lion group sizes, and as a result may be an important driver of dispersal decisions for sub-adult lions in this environment. As group sizes get smaller with high floods, extended periods of high floods may therefore lead to a decline in the lion population, resulting from reduced reproductive success of smaller prides (Packer et al. 1988) or as a result of the difficulty in maintaining a territory as flood waters cover more land and prides become more fragmented.

A similar response to flooding was observed on the sub-group level, where higher floods also led to a decrease in sub-group size. During the flooding season, prey animals are confined to small islands and island edges, resulting in a more clustered distribution (Crawshaw & Quigley 1991). Furthermore, a

recent study on the relationship between flooding and herbivore distribution has shown that higher flood levels decrease the proportion of palatable grazing in floodplains, leading to increased competition for this dry season resource between grazing herbivores (Burger et al. unpublished data). Consequently, prey distribution would become even more clustered, increasing prey vulnerability to predation in the dry season and thus negating the necessity for larger sub-groups to increase hunting success (Owen-Smith 2015). Under such circumstances, sub-group sizes may decline to maximize individual food intake (Caraco & Wolf 1975).

Interestingly, prey availability was not a limiting factor for pride sizes in the Okavango Delta, and prey abundance was actually negatively related to overall pride sizes, in contrast with our hypotheses as well as other systems (Van Orsdol et al. 1985, Hanby & Bygott 1979). In Serengeti National Park and in Ngorongoro Crater, Tanzania, there is a positive relationship between lean season prey availability and pride size (Hanby & Bygott 1979, Bertram 1973, Van Orsdol 1985). Despite its proposed importance in limiting carnivore group sizes (Macdonald 1983), studies have shown that where prey is evenly distributed or plentiful, the resource dispersion hypothesis will not predict overall group size, and group sizes may be determined by other social or ecological factors (Messier 1994, Trinkel et al. 2007). In South Africa, for example, lions re-introduced into protected areas and game reserves often have an abundance of prey, and population size quickly increases until density-dependent factors come into play, and population growth is then limited by social rather than ecological factors (Hunter 1998, Trinkel et al. 2010, Kilian 2003). Alternatively, given the longevity of lions, the response of overall pride size through reduced survival or reproductive rates to declining prey may be time-lagged, and therefore not evident in the time frame of the study period (Fuller and Sievert 2001, Packer et al. 2005).

Prey availability did, however, influence the size of sub-groups of adults and sub-adults when cubs were removed from the equation, suggesting that advantages gained from co-operative hunting do influence lion sub-group sizes. As prey availability declined, lion sub-group sizes increased, which was consistent with our hypotheses that lower prey would lead to larger sub-group sizes (cf. Packer et al. 1990). While larger groups may lead to lower per capita intake of food, this drawback may be offset by the advantages of group hunting, particularly when prey is scarce (Caraco & Wolf 1975).

The probability of success in attempted hunts increases with increasing group size, particularly in open habitats such as the Okavango Delta (Schaller 1972, Van Orsdol 1981, Caraco & Wolf 1975, Wilson 1975, Stander 1991), and consequently, the variance in feeding frequency is reduced with increasing group size (Rodman 1981). Similar responses to declining prey have been observed in lynx (*Lynx canadensis*), which hunt in family groups during times of prey scarcity in order to increase hunting success (O'Donaghue et al. 1998). Furthermore, as prey availability declines, lions may also be forced to hunt larger, more challenging prey such as giraffe (*Giraffa camelopardis*), the difficulty of which may necessitate larger hunting parties (Packer 1986, Packer et al. 1990, Stander 1991). Given the observed high degree of overlap between home ranges, larger sub-group sizes during times of prey scarcity may have also allowed for better defence of kills (Rodman 1981), and reduced the chances of hyenas or competing groups of lions of taking over a carcass.

Our results strongly suggest that competition from conspecifics exerted the most influence on grouping behaviour of lions during the study period, at both the pride and sub-group level. Competition negatively influenced pride sizes, and was the single most important factor in determining the number of adult females in prides in the Okavango Delta, which form the core of lion social organisation (Bertram 1973). An increase in the number of neighbouring adults resulted in smaller pride sizes of adult females, suggesting that lion numbers in the study area were self-regulated. Similar responses have been observed in the Serengeti, where prides surrounded by a high number of neighbours experience suppressed reproduction and increased adult mortalities in their natal prides (Mosser & Packer 2009). This indicates that social factors relating to competing conspecifics were more important in determining adult female group size in the Okavango Delta than ecological factors. This provides empirical evidence for the social regulation, or 'social fence' hypothesis, which states that in the absence of limitation through food resources, social factors, and specifically a high number of competing neighbours, will regulate population growth (Hestbeck 1982). At high densities, emigration is prevented from natal groups due to high fitness costs of dispersal (Mosser & Packer 2009). Thus, while the likelihood of pride fission through sub-adult dispersal increases with increasing pride size, the probability of sub-adult female dispersal decreases with increasing neighbours and lack of vacant territories (Van der Waal et al. 2009, Packer et al.

2005). Pride sizes may therefore increase in size, even though prey numbers show a declining trend. Therefore, the large number of competing neighbours could explain the seemingly confounding negative relationship between overall pride size and per capita prey availability.

In sub-groups where cubs were present, the number of cubs played a large role in determining the number of adult females in sub-groups. Adult lionesses crèche cubs and co-operate to defend and raise litters that are of a similar age (Schaller 1972, Bertram 1975, Pusey & Packer 1994). This is consistent with other studies on lions in the Serengeti (Pusey & Packer 1994) as well as in the Kgalagadi Transfrontier Park (Funston & Hermann 2001), as increased reproductive success from communal rearing of cubs is an important benefit of sociality in lion society (Bertram 1975). The presence of cubs therefore remains the most consistent predictor of sub-grouping behaviour of adult females (Pusey & Packer 1994). Contrary to other studies, however, increased competition with neighbours also had a negative effect on sub-group size when only the number of adult females was considered. Even though larger sub-group sizes may have a competitive advantage when it comes to territorial disputes (Mosser & Packer 2009), the opposite effect of increased neighbours on sub-group size suggests that territorial disputes did not determine the number of adult lionesses which associated in sub-groups in lion prides in the Okavango Delta. We suggest that this may be related to flooding. Flooding may alter territorial boundaries by washing away scent, and by altering prey distribution seasonally and annually, the costs of maintaining exclusive territories may be too high, resulting in the large degree of home range sharing (McLoughlin et al. 2001). Consequently, as there was no territorial advantage to be gained by larger sub-groups, lions could have opted for smaller sub-groups when in areas of shared territory. This would have reduced conspicuousness, especially when cubs were present, in the presence of potentially infanticidal neighbours who share a large portion of the home range (Mosser & Packer 2009). Additionally, as competition for space increased, reproductive rates may have slowed down due to density-dependent effects, resulting in fewer mothers with cubs, and thus smaller sub-groups. This could be amplified by the fact that pride members without cubs may actively avoid crèches due to lower individual food intake (Packer 1986, Packer et al. 1990). However, this explanation would only account for groups where cubs were present, and does not account the lower number of adult females in sub-groups where cubs are absent.

Median pride size for adult females varied between four and six individuals, likely showing that this was the minimum size for a successful pride in the Okavango Delta system during the study period, given the constraints of competition, flooding and prey availability. The number of adult females in a pride is least susceptible to fluctuations and is thus the most stable representation of pride size (Bertram 1973). The pride sizes in the Okavango Delta are comparable to the range of pride sizes occurring in the Serengeti (mean=5.9, range 2-11, Schaller 1972), Kruger National Park (mean=4.2, range 2-9, Smuts 1976) and the nearby Kgalagadi Transfrontier Park (mean =4.0, range 2-8, Funston & Hermann 2001), but are smaller than prides in the Masai Mara system, Kenya (Ogutu & Dublin 2002, mean 9.2, range 2-18). These systems span a variety of vegetation biomes, rainfall patterns, and vastly different levels of prey density. This may suggest that pride sizes varying between four and six adult females are optimum to maintain individual fitness, protect a territory as well as successfully reproduce over a range of systems (Packer et al. 2001, Packer et al. 2005). Indeed, studies in the Serengeti show that prides which have two or less females have low reproductive success, as do prides with more than 10 adult females, due to high intra-pride competition (Packer et al. 1988, Packer et al. 2001, Packer et al. 2005). Median sub-group sizes ranged between two and four individuals for most of the study period, suggesting that individual fitness was maximised in groups of two to four individuals within the social and ecological constraints of the study area.

Conclusion

In the Okavango Delta, an area with high lion densities, the number of adult females in prides and sub-groups were primarily determined by social factors. When sub-adults were included in the analysis however, the emphasis shifted from social to ecological factors at both the pride and sub-group level. Although the social and ecological factors considered in this study explain a large amount of variation in models determining pride size, their influence on sub-group size is less clear. The lower explanatory power of sub-group models may have resulted from a number of factors. Firstly, predictors may have been diluted by the annual measurement of ecological variables. The drastic changes between seasons resulting from the flood levels, and the consequent changes in prey distribution, may lead to more pronounced seasonal differences in sub-group associations rather than annual differences. This could be clarified by collecting seasonal data more intensively and

investigating how sub-grouping patterns change seasonally in such a dynamic wetland environment. Alternatively, other social factors such as the degree of relatedness between associating individuals, may also play a vital role in determining whether an individual stays with or leaves a sub-group. Studies in Queen Elizabeth National Park, Uganda, for example, have shown that lion demographics and kinship largely influence grouping patterns, as individuals of the same sex and of similar age tend to associate more often (Van Orsdol 1981).

Flooding patterns exert considerable influence lion social organisation in the Okavango Delta, and this is the first study that we know of to examine the specific effects of flooding on lion social organisation. As recent genetic analyses have indicated that lions may historically be wetland specialists (Moore et al. 2015), this study may offer an important insight into the conditions which could have led to lions being social felids. As prey did not limit lion group sizes, the need to co-operate and defend cubs from a high density of conspecifics may have played a large role in the development of lion social behaviour. It would be beneficial to examine the social organisation of lions in other wetland environments to determine whether factors influencing grouping patterns are similar. For example, high prey densities occur in the wetland of Busanga Plains in Kafue National Park, as flood waters result in resident dry season prey that would have otherwise moved out of the area in search of suitable grazing and water (Midlane 2013). However, lion density in this area is largely suppressed by anthropogenic threats such as bush-meat poaching (Midlane 2013). Due to the abundance of resources and ecosystem services they provide, many of Africa's wetland areas are currently under increasing pressure from human populations (Silvius et al. 2000), and such comparisons may therefore be impossible at this stage. As lion densities in the Okavango Delta have appeared to decrease with increasing flooding patterns, continued long-term data collection on lion social behaviour may reveal whether lion densities will once again recover as flood levels decrease, and adapt their social organisation accordingly.

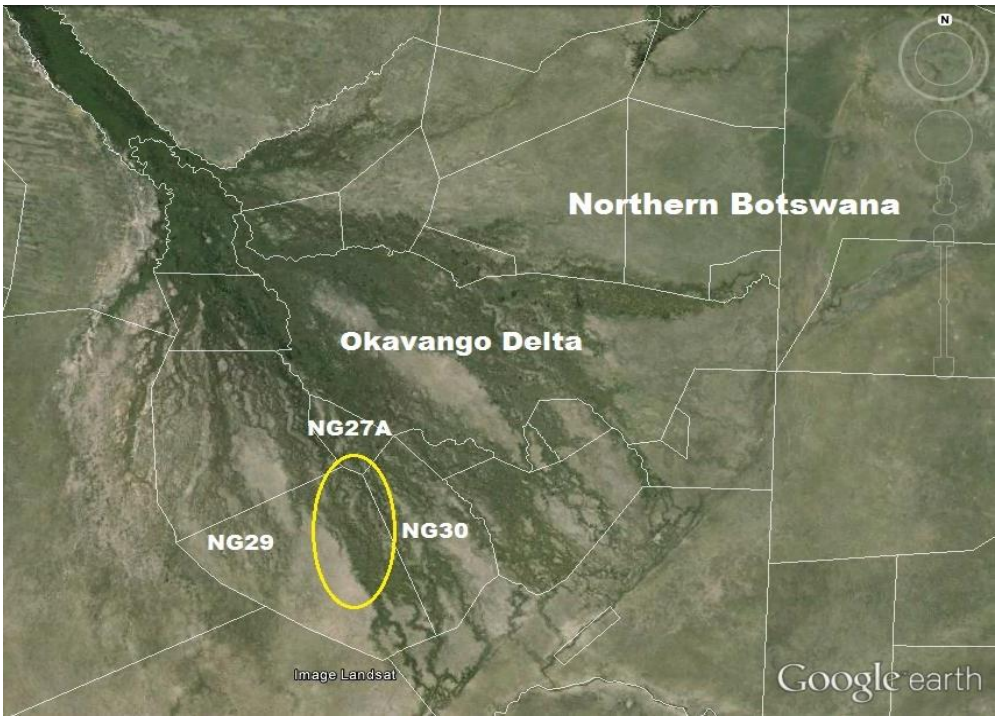


Figure 1. Study area in the south-western Okavango Delta, Botswana. The yellow ellipse indicates the intensive study area in which lion prides were located and collared for follow-up. The study area spanned three wildlife management concessions, namely NG29, NG30, and a small section of NG27A. This area is characterised by seasonal floodplain vegetation interspersed with small islands. *Source:* "Okavango Delta". S -19.340295° E 22.836576°. **Google Earth.** 1 January 2015. Accessed 15 July 2015.

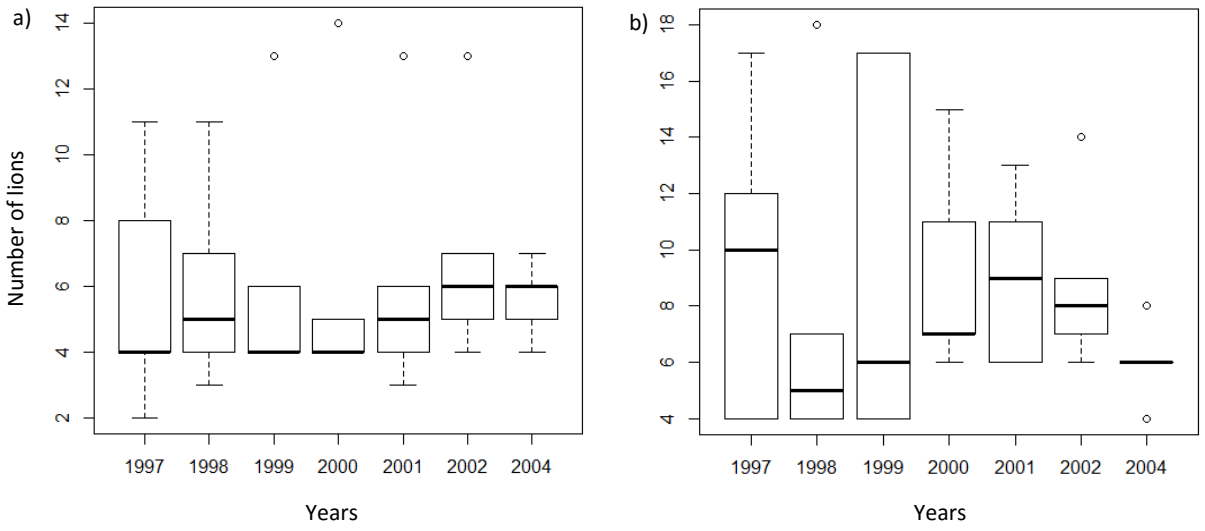


Figure 2. Distribution of pride sizes over five prides in the south-western Okavango Delta, Botswana, from 1997 to 2004. Prides were defined as all individuals that share a home range and interact peacefully. Pride sizes were investigated in two ways: a) including adult females only, and b) including both adult females and all sub-adults.

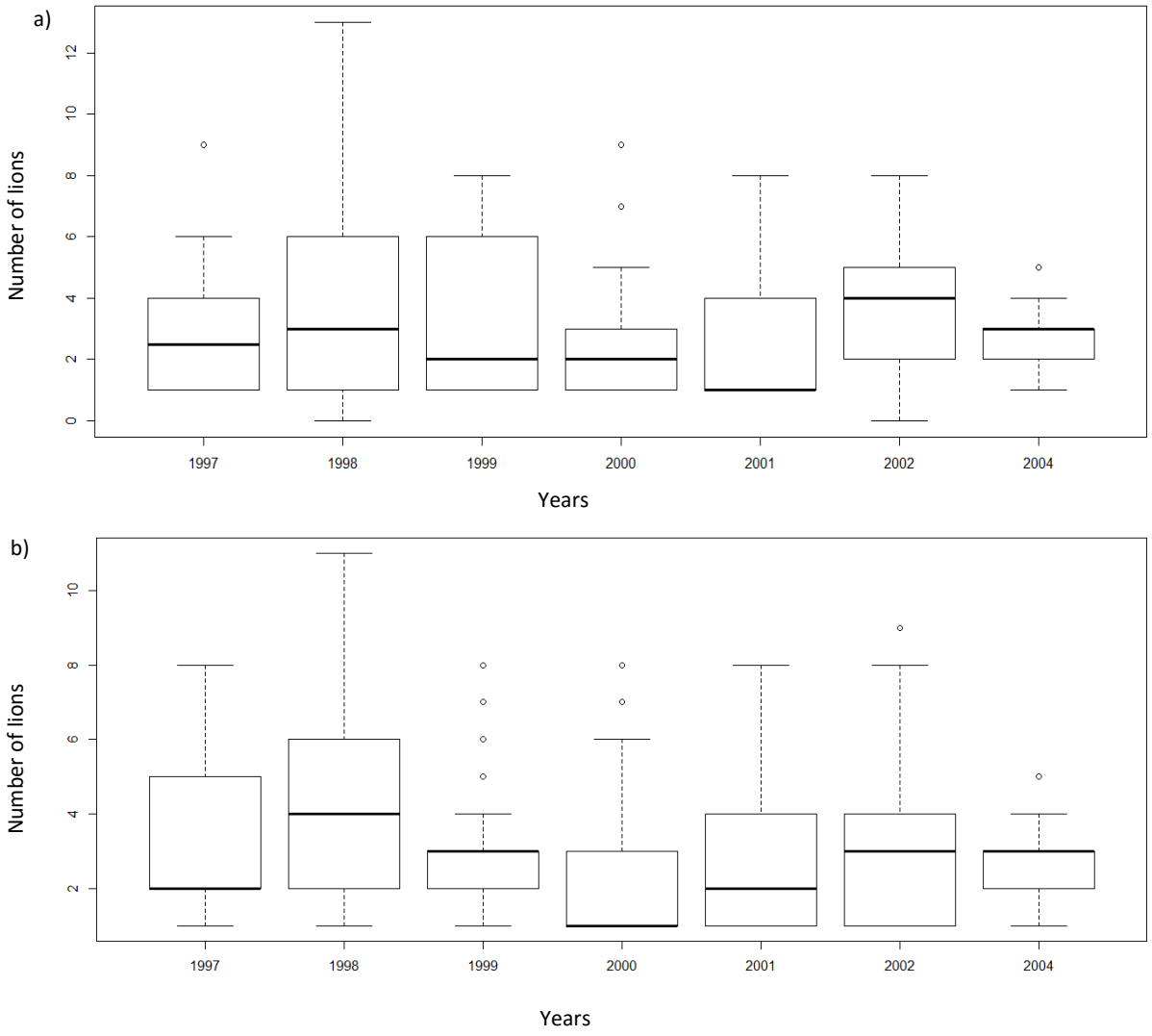


Figure 3. Distribution of sub-group sizes for five prides in the south-western Okavango Delta, Botswana, from 1997 to 2004. Sub-groups were analysed in two ways: a) number of adult females in sub-groups, including sub-groups where young cubs (0-2 years old) are present, and b) sub-group sizes where adult females and all sub-adults are included, excluding groups in which cubs are present.

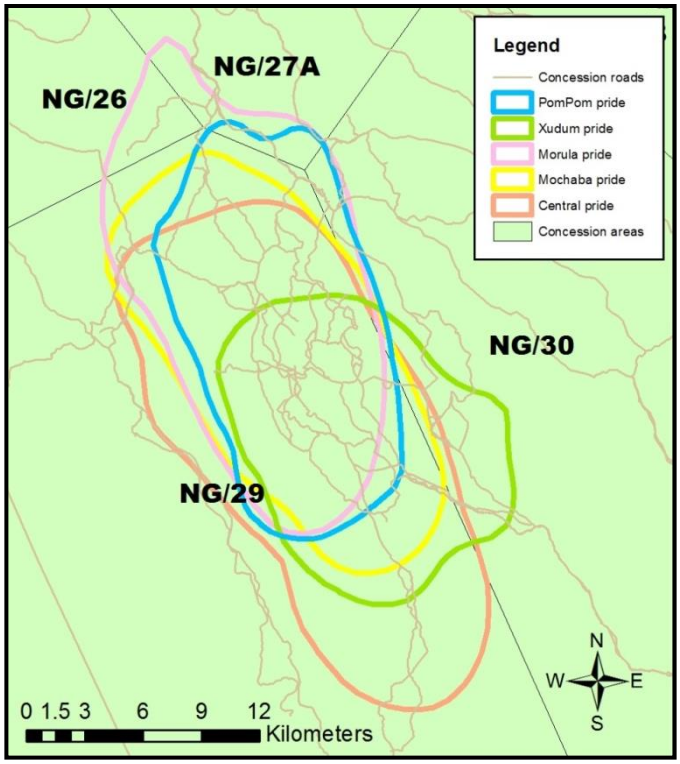


Figure 4. Home ranges for each of the five prides in the study area indicated by 90% kernel density isopleths. Locations used to form home range boundaries were collected by locating collared pride members using radio-telemetry, or when lions were sighted opportunistically. Locations were pooled across all of the study years to allow for adequate sample sizes for each pride, and home ranges therefore represent the long-term home ranges of each pride.

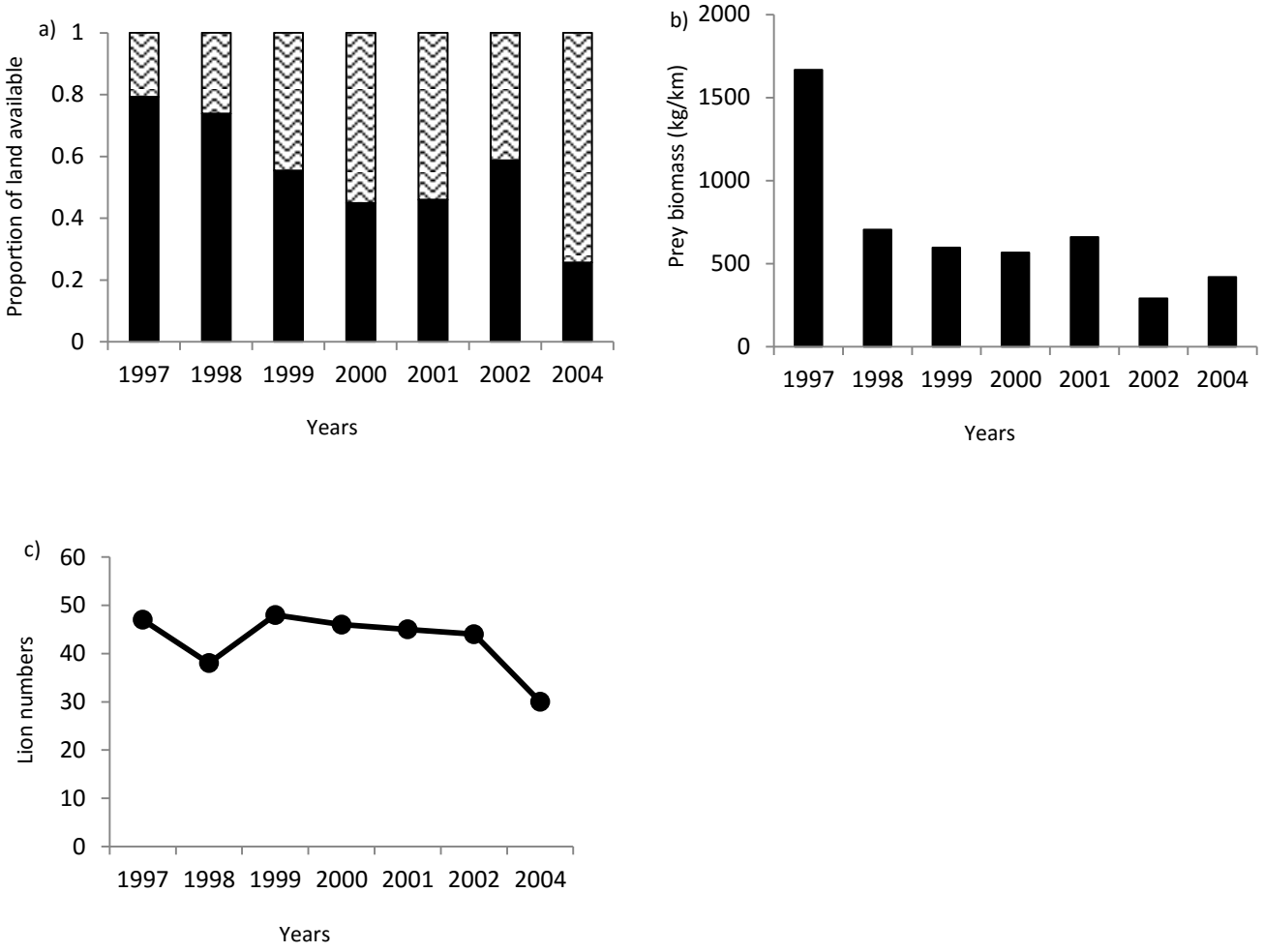


Figure 5. General trends in predictor variables for five prides in the south-western Okavango Delta, Botswana. a) Average proportion of dry land available (solid bars) in each pride home range during the period of maximum flood extent each year. b) Average biomass of prey available per kilometre within each pride's home range. c) Change in total lion numbers in the study area (n=5 prides).

Table 1. Generalized linear models depicting predictor variables present in the best models (ΔAICc<2) for pride sizes and sub-group sizes of lions in the south-western Okavango Delta, Botswana. Crosses indicate that the predictor variable is present in that model, and models in bold indicate the best models for each response variable. Predictor variables represent intraspecific competition, land availability during maximum flood extent and per capita prey availability. Additional variables added to models with sub-group sizes include pride size (adult females and sub-adults) and the number of cubs present in a sub-group. Response variables included a) pride size including adult females only, b) pride size including adult females and all sub-adults, c) all sub-groups, focusing on the number of adult females present and d) sub-groups where cubs are absent, including adult females and all sub-adults. AICc= Aikaike's information criterion for small sample sizes, ΔAICc=change in AICc between the current model and the best model, w=AICc weight.

	Competition	Land	Prey	Pride size	No. cubs	**AICc**	**ΔAICc**	**w**
Pride sizes								
a)Adult females								
	x		**x**			**147.2**	**0**	**0.404**
	x					147.9	0.64	0.294
	x	x	x			148.6	1.37	0.204
b) Adult females and sub-adults								
	x	**x**	**x**			**170**	**0**	**0.7**
Sub-group sizes								
c) Adult females								
	x			**x**	**x**	**2272**	**0**	**0.275**
	x	x		x	x	2272.9	0.91	0.175
	x				x	2273.2	1.29	0.145
	x		x	x	x	2273.6	1.66	0.12
d) Adult females and sub-adults								
		x	**x**			**1509.6**	**0**	**0.378**
		x	x	x		1511.6	1.98	0.141

Table 2. Model-averaged estimates for top models (Table 1) investigating the effects of social and ecological factors on pride size and sub-group sizes. Predictor variables were standardized for all of the models to make results directly comparable. All models within 2AICc units of the top model were used for model averaging using the zero method. The * indicates that model averaging was done with all models within 4AICc models of the best model, which included only one additional model for pride sizes including adults and sub-adults. Estimate represents the magnitude of the effect, and relative importance of each covariate is determined by the sum of Aikaike weights (w) for each model where the covariate is present, including only models used for averaging. Confidence intervals which did not cross zero are highlighted in bold and indicate variables that were considered influential in determining group sizes.

Variable	Estimate	Unconditional SE	Confidence interval	Relative importance
Pride sizes adult females only				
Intercept	1.72496	0.08172	(1.55813, 1.89179)	
Competition	-0.75421	0.15494	**(-1.06777 -0.44064)**	1
Per capita prey	-0.23168	0.21328	(-0.69160, 0.00460)	0.67
Land available	0.03737	0.09319	(-0.10376 0.43393)	0.23
Pride sizes adults and sub-adults*				
Intercept	2.05996	0.06619	(1.92465, 2.19528)	
Per capita prey	-0.22468	0.16155	**(-1.00992, -0.29693)**	1
Land available	0.42599	0.12491	**(0.17231, 0.67967)**	1
Competition	-0.65343	0.1751	**(-0.53687, -0.04596)**	0.77
Sub-group sizes adults including groups with cubs				
Intercept	0.98894	0.13362	(0.72656, 1.25132)	
Competition	-0.62542	0.15846	**(-0.93658, -0.31427)**	1
Number of cubs	0.39924	0.05063	**(0.29981, 0.49867)**	1
Pride Size	-0.1556	0.12715	(-0.41520, 0.02508)	0.8
Land available	0.05262	0.13391	(-0.16964, 0.59953)	0.24
Per capita prey	-0.01803	0.07966	(-0.43720, 0.22228)	0.17
Sub-group sizes adults and sub-adults (excluding cubs)				
Intercept	1.0825	0.08999	(0.90558, 1.25943)	
Land available	0.42163	0.14079	**(0.14484, 0.69842)**	1
Per capita prey	-0.25575	0.10888	**(-0.46980, -0.04169)**	1
Pride size	0.01146	0.07864	(-0.24608, 0.33067)	0.27

References

Arnold, T.W. 2010. Uninformative parameters and model selection using Aikaike's information criterion. *Journal of Wildlife Management*, 74, 1175-1178.

Barton, K. 2013. MuMIn: multi-model inference. R Package Version 1.12.1. CRAN R Project. Available from http://CRAN.R-project.org/package=MuMIn (accessed May 2015).

Bates D. M., Mächler M., Bolker B. M. & Walker S. C. 2014. lme4: Linear Mixed-Effects Models Using Eigen and S4. R Package Version 1.1-7. Available from: http://CRAN.R-project.org/package=lme4 (accessed May 2015).

Bertram, B.C.B. 1975. Social factors influencing reproduction in wild lions. *Journal of Zoology, London*, 177, 463–482.

Bertram, B.C.R. 1973. Lion population regulation. *East African Wildlife Journal*, 11, 215-225.

Bolker, B.M. 2008. *Ecological models and data in R*. Princeton: Princeton University Press.

Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S. & Colson, T. 2006. Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology*, 75, 1393-1405.

Bowen, W. D. 1981. Variation in coyote social organization: the influence of prey size. *Canadian Journal of Zoology*, 59, 639-652.

Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multimodal Inference: A Practical Information-Theoretic Approach, 2nd ed.* New York: Springer-Verlag.

Bygott, J.D., Bertram, B.C.R. & Hanby, J.P. 1979. Male lions in large coalitions gain reproductive advantages. *Nature*, 26, 839-841.

Caraco, T. & Wolf, L.L. 1975. Ecological determinants of group sizes in foraging lions. *American Naturalist*, 109, 343-352.

Celesia, G.G., Peterson, A.T., Peterhans, J.C.K. & Gnoske, T.P. 2009. Climate and landscape correlates of African lion (*Panthera leo*) demography. *African Journal of Ecology*, 48, 58-71.

Chapman, C.A. 1990. Association patterns of spider monkeys: the influence of ecology and sex on social organization. *Behavioural Ecology and Sociobiology*, 26, 409-414.

Chapman, C.A., Wrangham, R.W. & Chapman, L.J. 1995. Ecological constraints on group size: an analysis of spider monkey and chimpanzee sub-groups. *Behavioural Ecology and Sociobiology*, 36, 59-70.

Crawshaw, P.G. Jnr & Quigley, H.B. 1991. Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. *Journal of Zoology, London*, 223, 357-370.

Ellery, W.N., Ellery, K. & McCarthy, T.S. 1993. Plant distribution in islands of the Okavango Delta, Botswana: determinants and feedback interactions. *African Journal of Ecology,* 31, 118-134.

Feore, S. & Montgomery. W. I. 1999. Habitat effects on the spatial ecology of the European badger (*Meles meles*). *Journal of Zoology, London,* 247, 537-549.

Fuller, T.K. & Sievert, P.R. 2001. Carnivore demography and the consequences of changes in prey availability. In: *Carnivore Conservation*. (Ed by J.L. Gittleman, S.M. Funk, D.W.Macdonald and R.K. Wayne) pp. 163-178. Cambridge: Cambridge University Press and the Zoological Society of London.

Funston, P.J. & Hermann, E. 2001. Kalahari Transfrontier Lion Project. *Population ecology and demography of lions in the Kgalagadi Trasfrontier Park –adaptations and prospects of survival in a harsh environment.* Endangered Wildlife Trust, Upington, South Africa.

Funston, P.J., Mills, M.G.L., Richardson, P.R.K. & Van Jaarsveld, A.S. 2003. Reduced dispersal and opportunistic territory acquisition in male lions (*Panthera leo*). *Journal of Zoology, London,* 259, 131-142.

Gelman, A., Su, Y.S., Dorie, V. & Su, M.Y.S. 2013. Package 'arm'. Available from: http://CRAN.R-project.org/package=arm. (accessed May 2015).

Getz, W.M., Fortmann-Roe, S., Cross, P.C., Lyons, A.J., Ryan, S.J. & Wilmers, C.C. 2007. LoCoH: Non-parametric kernel methods for constructing home ranges and utilization distributions. *PLoS One*, 2, e207. doi: 10.1371/journal.pone.0000207.

Giraldeau, L.A. & Gillis, D. 1988. Do lions hunt in group sizes that maximize hunters' daily food returns? *Animal Behaviour,* 36, 611-613.

Gittleman, J.L. 1989. *Carnivore Behavior, Ecology and Evolution.* Cornell University Press, New York.

Grinnell, J., Packer, C. & Pusey, A.E. 1995. Cooperation in male lions: kinship, reciprocity or mutualism? *Animal Behaviour,* 49, 95-105.

Grueber, C.E., Nakagawa, S., Laws, R.J. & Jamieson, I.G. 2011. Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology,* 24, 699-711.

Gumbricht, T.P., Wolski, P.F. & McCarthy, T.S. 2004. Forecasting the spatial extent of the annual flood in the Okavango Delta, Botswana. *Journal of Hydrology,* 290, 178-191.

Hanby, J. P., Byggot, J.D. & Packer, C. 1995. Ecology, demography, and behaviour of lions in two contrasting habitats: Ngorongoro Crater and the Serengeti plains. In: *Serengeti II: dynamics, management, and conservation of an ecosystem* (Ed by A.R.E. Sinclair and P. Arcese) pp. 315-331. Chicago: University of Chicago Press.

Hanby, J.P. & Bygott, J.D. 1979. Population changes in lions and other predators. In: *Serengeti: Dynamics of an Ecosystem* (Ed by A.R.E. Sinclair and M. Norton-Griffiths) pp. 249-262. Chicago: Chicago University Press.

Hanby, J.P. & Bygott, J.D. 1987. Emigration of sub-adult lions. *Animal Behaviour*, 35, 161-169.

Hayward, M. W., O'Brien, J. & Kerley, G. I. H. 2007. Carrying capacity of large African predators: predictions and tests. *Biological Conservation*, 139, 219-229.

Heinsohn, R., Packer, C. & Pusey, A.E. 1996. Development of co-operative territoriality in juvenile lions. *Proceedings of the Royal Society of London, Series B*, 263, 475-479.

Hemson, G., Johnson, P., South, A., Kenward, R., Ripley, R. & Macdonald, D. 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross validation. *Journal of Animal Ecology*, 74, 455-463.

Hestbeck, J.B. 1982. Population regulation of cyclic mammals: the social fence hypothesis. *Oikos*, 39, 157-163.

Higashi, M. & Yamamura, N. 1993. What determines animal group size? Insider-outsider conflict and its resolution. *The American Naturalist*, 142, 553-563.

Hunter, L.T.B. 1998. Early post-release movements and behaviour of reintroduced cheetahs and lions, and technical considerations in large carnivore restoration. In: *Cheetahs as Game Ranch Animals* (Ed by B.L. Penzhorn). Onderstepoort, South Africa: Wildlife Group of the South African Veterinary Association.

Kie, J.G. 2013. A rule-based *ad hoc* method for selecting a bandwidth in kernel home-range analyses. *Animal Biotelemetry*, 2013, 1-13.

Kiffner, C., Meyer, B., Muhlenberg, M., & Waltert, M. 2009. Plenty of prey, few predators: what limits lions *Panthera leo* in Katavi National Park, western Tanzania. *Oryx*, 43, 52-59.

Kilian, P.J. 2003. The ecology of reintroduced lions on the Welgevonden Private Game Reserve, Waterberg. MSc Thesis. University of Pretoria.

Loveridge, A.J., Valeix, M., Davidson, Z., Murindagomo, F. Fritz, H. & Macdonald, D. 2009. Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savannah. *Ecography*, 32, 953-962.

Macdonald, D.W. 1983. The ecology of carnivore social behaviour. *Nature*, 301, 379-384.

Maillard, D., Calenge, C., Jacobs, T., Gaillard, J.M. & Merlot, M. 2001. The kilometric index as a monitoring tool for populations of large terrestrial animals: a feasibility test in Zakouma National Park, Chad. *African Journal of Ecology*, 39, 306-309.

McCarthy, T.S. & Ellery, W.N. 1998. The Okavango Delta. *Transactions of the Royal Society of South Africa,* 53, 157-182.

McLoughlin, P. D., Ferguson, S. H. & Messier, F. 2001. Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations. *Evolutionary Ecology*, 14, 39–60.

Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. *Ecology*, 75, 478-488.

Meyer, T. 1999. Ecological mappings in the research area of the Harry Oppenheimer Okavango Research Centre, Okavango Delta, Botswana. MSc Thesis. Hochschule Anhalt, Bern-burg, Germany.

Midlane, N. 2013. The conservation status and dynamics of a protected African lion *Panthera leo* population in Kafue National Park, Zambia. PhD Thesis. University of Cape Town.

Mills, M. G. L. 1978. The comparative socio-ecology of the Hyaenidae. *Carnivore,* 1, 1-7.

Moore, A.E., Cotterill, F.P.D., Winterbach, C.W., Winterbach, H.K., Antunes, A. & O'Brien, S.J. 2015. Savannah habitat specializations in different populations of lions. *Journal of Heredity,* esv097.

Mosser, A. & Packer, C. 2009. Group territoriality and the benefits of sociality in the African lion, *Panthera leo. Animal Behaviour,* 78, 359-370.

Murray-Hudson, M. 2009. Floodplain vegetation responses to flood regime in the seasonal Okavango Delta, Botswana. PhD Thesis. University of Florida.

Murray-Hudson, M.M, Wolski, P., Cassidy, L., Brown, M.T., Thito, K., Kashe, K. & Mosimanyana, E. 2014. Remote sensing-derived hyrdoperiod as a predictor of floodplain vegetation composition. *Wetlands Ecology and Management*, 23, 603-616.

Naidoo, R., Du Preez, P., Stuart-Hill, G., Weaver, L.C., Jago, M. & Wegmann, M. 2012. Factors affecting intraspecific variation in home range size of a large African herbivore. *Landscape Ecology,* 27, 1523-1534.

Nakagawa, S. & Freckleton, R.P. 2010. Model averaging, missing data and multiple imputation: a case study for behavioural ecology. *Behavioural Ecology and Sociobiology*, 65, 103–116.

O' Kochanny, C.O., Delgiudice, G.D. & Fieberg, J. 2009. Comparing global positioning system and very high frequency telemetry home ranges of white-tailed deer. *Journal of Wildlife Management*, 73, 779-787.

O'Brien, R.M. 2007. A caution regarding rules of thumb for variance inflation factors. *Quality and Quantity,* 41, 673-690.

O'Donaghue, M., Boutin, S., Krebs, C.J., Zuleta, G. Murray, D.L. & Hofer, E.J. 1998. Functional responses of coyotes and lynx to the snowshoe hare cycle. *Ecology,* 79, 1193-1208.

Ogutu, J. O. & Dublin, H.T. 2002. Demography of lions in relation to prey and habitat in the Masai Mara National Reserve, Kenya. *African Journal of Ecology,* 40, 120-129.

Owen-Smith, N. 2015. Mechanisms of coexistence in diverse herbivore-carnivore assemblages: demographic, temporal and spatial heterogeneities affecting prey availability. *Oikos,* 124, 1417-1426.

Packer, C. 1986. The ecology and sociality in felids. In: *Ecological Aspects of Social Evolution*. (Ed by D.I. Rubenstein and R.W. Wrangham), Princeton, Princeton University Press.

Packer, C. And Pusey, A. E. 1983. Adaptations of female lions to infanticide by incoming males. *The American Naturalist,* 121, 716-728.

Packer, C., Herbst, L., Pusey, A.E., Bygott, J.D., Hanby, J.P., Cairns, S.J. & Borgehoff-Mulder, M. 1988. Reproductive success of lions. In: *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems* (Ed by T.H. Clutton-Brock) pp 363-383. Chicago: University of Chicago Press.

Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, J., Mduma, S. & Sinclair, A.R.E. 2005. Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science,* 436, 927-928.

Packer, C., Pusey, A.E. & Eberly, L. E. 2001. Egalitarianism in female African lions. *Science,* 293, 690-693.

Packer, C., Scheel, D. & Pusey, A.E. 1990. Why lions form groups: food is not enough. *American Naturalist,* 136, 1-19.

Patterson, B.D. 2007. On the nature and significance of variability in lions (*Panthera leo*). *Evolutionary Biology,* 34, 55-60.

Pennycuick, C.J. & Rudnai, J. 1970. A method of identifying individual lions *Panther leo* with an analysis of the reliability of identification. *Journal of Zoology, London,* 160, 497-508.

Pusey, A.E. & Packer, C. 1994. Non-offspring nursing in social carnivores: minimizing the costs. *Behavioural Ecology,* 5, 362-374.

R Core Development Team. 2014. R: A language and environment for statistical computing. *R Foundation for Statistical Computing.* Vienna, Austria.

Ramberg, L., Hancock, P., Lindholm, M., Meyer, T., Ringrose, S., Silva, J., Van As, J. & Vanderpost, C. 2006. Species diversity in the Okavango Delta, Botswana. *Aquatic Sciences,* 68, 310-337.

Rodman, P.S. 1981. Inclusive fitness and group size with a reconsideration of group sizes in lions and wolves. *American Naturalist,* 118, 275-283.

Schaller, G. B. 1972. *The Serengeti lion: a study of predator prey relations*. Chicago: *Chicago* University Press.

Schielzeth, H. 2010. Simple means to improve interpretability of regression coefficients. *Methods in Ecology and Evolution,* 1, 103-113.

Silvius, M.J., Oneka, M. & Verhagen, A. 2000. Wetlands: lifeline for people at the edge. *Physics and Chemistry of the Earth, Part B: Hydrology, Oceans and Atmosphere,* 7, 645-652.

Smith, J.E., Kolowski, J.M., Graham, K.E., Dawes, S.E. & Holekamp, K.E. 2008. Social and ecological determinants of fission-fusion dynamics in the spotted hyena. *Animal Behaviour,* 76, 619-636.

Smuts, G.L. 1976. Population characteristics and recent history of lions in two parts of the Kruger National Park. *Koedoe,* 19, 153-164.

Smuts, G.L. 1982. *Lion.* Johannesburg: Macmillan.

Spong, G. 2002. Space use in lions, *Panthera leo,* in the Selous Game Reserve: social and ecological factors. *Behavioural Ecology and Sociobiology,* 52, 303-307.

Stander, P.E. 1991. Demography of lions in the Etosha National Park, Namibia. *Madoqua,* 18, 1-9.

Trinkel, M., Funston, P., Hofmeyr, M., Hofmeyr, D., Dell, S., Packer, C. & Slotow, R. 2010. Inbreeding and density-dependent population growth in a small, isolated lion population. *Animal Conservation,* 13, 374–382.

Trinkel, M., Van Niekerk, R.W., Fleischmann, P.H., Ferguson, N. & Slotow, R. 2007. The influence of vegetation on lion *Panthera leo* group sizes in the Hluhluwe-Umfolozi Park, South Africa. *Acta Zoologica Sinica,* 53, 15-21.

Turner, A. 1997. *The big cats and their fossil relatives.* New York: Columbia University Press.

Valeix. M, Loveridge, A.J., Chamaillé-James, S., Davidson, Z., Murindagomo, F. Fritz, H. & Macdonald, D.W. 2009. Behavioural adjustments of African herbivores to predation risks by lions: spatiotemporal variations influence habitat use. *Ecology,* 9, 23-30.

Van Der Waal, K.L., Mosser, A. & Packer, C. 2009. Optimal group size, dispersal decisions and post-dispersal relationships in female African lions. *Animal Behaviour,* 77, 949-954.

Van Orsdol, K.G. 1981. Lion predation in Rwenzori National Park, Uganda. PhD Thesis, University of Cambridge.

Van Orsdol, K.G., Hanby, J.P. &Bygott, J.D. 1985. Ecological correlates of lion social organisation (*Panthera leo*). *Journal of Zoology, London,* 206, 97–112.

Vincent, J.P., Gaillard, J.M. & Bideau, E. 1991. Kilometric index as biological indicator for monitoring forest roe deer populations. *Acta thereologica,* 36, 315-328.

Watts, H.E. & Holekamp, K.E. 2009. Ecological determinants of survival and reproduction in the spotted hyena. *Journal of Mammalogy,* 90, 461-471.

Whitman, K.L & Packer, C. 2007. *A hunter's guide to aging lions in eastern and southern Africa*. Huntington Beach, CA: Long Beach Press.

Wilson, E.O. 1975. *Sociobiology*. Cambridge: Harvard University Press.

Wolski, P. & Murray-Hudson, M.M. 2006a. Recent changes in flooding in the Xudum distributary of the Okavango Delta, and Lake Ngami, Botswana. *South African Journal of Science,* 102, 173-176.

Wolski, P. & Murray-Hudson, M.M. 2006b. Reconstruction of 1989-2005 inundation history in the Okavango Delta, Botswana, from archival Landsat imagery. In: *Globwetland Symposium*, ESA-ESRIN, Frascati, Italy.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, 70, 164-168.

Worton, B.J. 1995. Using Monte-Carlo simulation to evaluate kernel-based home range estimators. *Journal of Wildlife Management*, 59, 794-800.

Wrangham, R.W., Gittleman, J.L. & Chapman, C.A. 1993. Constraints on group size in primates and carnivores: population density and day-range as assays of exploitation competition. *Behavioural Ecology and Sociobiology*, 32, 199-210.

Chapter 3

Population demographics of lions (*Panthera leo*) in the south-western Okavango Delta

Abstract

Detailed studies on demographic rates of large carnivores are important for conservation and management planning. Investigating changes in demographic rates over time can help to identify which ecological and social drivers elicit population change, and may help identify potential conservation threats. In lions (*Panthera leo*), changes in population density and demographic rates such as survival and reproduction are often closely linked to prey abundance. However, this relationship can be confounded by a number of other factors. For example, once carnivores reach carrying capacity, demographic rates are regulated by intraspecific competition, territoriality and other social factors rather than resource limitation. Demographic rates may also be affected by abiotic factors such as climate or rainfall, which in turn affect prey abundance and so determine lion population growth. In the Okavango Delta, Botswana, seasonal flooding represents a large, landscape-scale process which can 1) alter prey abundance and distribution, and 2) increase intraspecific competition by reducing the amount of available dry land during high flood cycles. We therefore used long-term demographic data on lions in the south-western Okavango Delta to determine the effects of prey abundance, intraspecific competition and flooding extent on age-specific survival rates as well as reproductive rates, using mark-recapture analysis and generalized linear models. Survival and reproduction were primarily limited by social rather than ecological factors. While adult survival remained stable over the study period, cub survival was negatively affected by the number of competing neighbours, and decreased as prey abundance decreased. Sub-adult survival was inversely related to pride size, but because of the difficulties in distinguishing between survival and emigration in Cormack-Jolly-Seber survival models, we maintain that apparent low survival rates were more related to the dispersal of male cohorts than to mortality of sub-adults. Reproductive rates were also more dependent on social rather than ecological covariates: both competition with neighbours and pride size had a negative effect on reproductive rates. These results suggest social regulation of the lion population, and show that prides are limited by both inter- and intra-pride competition. While flooding did not have direct effects on reproduction and survival, the time-lagged effects of flooding on vegetation structure indirectly influences herbivore abundance, and we thus maintain that it is still important in influencing the lion population. Given the high density of people often bordering wetland systems, future studies should focus on how anthropogenic threats influence lion demographic rates in the Okavango Delta and other wetland environments.

Keywords: *lions,* Panthera leo, *demography, survival rates, reproductive rates, flooding, intraspecific competition, Okavango Delta, mark-recapture.*

Introduction

Long-term studies collecting baseline demographic data on animal populations are extremely useful for conservation management and planning (Kelly et al. 1998, Mills et al. 1999, Devenish-Nelson 2012). By examining changes in demographic rates over time, we can identify which ecological and anthropogenic factors are most important in eliciting population change (Gimenez et al. 2012). This knowledge can then be used to inform demographic models and management decisions so as to ensure the viability of a population in the future (Ruggiero et al. 1994, Kelly et al. 1998). However, due to the difficulties of collecting data on long-lived and large-ranging species such as carnivores, these studies are decidedly rare, or have large gaps of missing data which limit their analytical power (Kelly et al. 1998, Devenish-Nelson 2012). Furthermore, demographic rates between different populations of the same species may differ drastically in response to prevailing ecological conditions, making each ecosystem unique (Patterson 2007).

In lions (*Panthera leo*), the abundance of natural prey is often cited as the main driver of changes in demographic rates, and hence population growth (Bertram 1973, Van Orsdol 1984, Van Orsdol 1985). The availability of prey can influence numerous aspects of reproductive biology in lionesses, such as the timing of oestrus and the frequency of mating, resulting in birth peaks during periods of high prey abundance (Schaller 1972, Bertram 1973, Ogutu & Dublin 2002). In addition to increased reproductive success, survival in all age groups is higher when prey is abundant (Van Orsdol et al. 1985, Packer et al. 1988). When prey becomes scarce, lion mortality increases in adults and sub-adults due to starvation, and cub mortality increases as adults are forced to move further in search of suitable prey, leaving cubs vulnerable to starvation and other predators (Schaller 1972, Van Orsdol 1985, Ogutu & Dublin 2002).

At high prey densities, however, lions quickly reach carrying capacity (Trinkel et al. 2010). As lion numbers increase, density-dependent processes ensue, leading to adaptive responses such as reduced

reproductive rate, increased age at first reproduction and reduced litter sizes (Smuts et al. 1978, Packer et al. 1988, Trinkel et al. 2010). Survival is similarly negatively affected at high densities. In the Serengeti National Park, Tanzania, as the number of neighbouring conspecifics increases, rates of wounding, and consequently mortality, increases, either due to territorial disputes or in defence of cubs (Mosser & Packer 2009). Females in smaller prides with a higher number of neighbours therefore experience higher rates of adult mortality than females in larger prides and with fewer neighbours (Mosser & Packer 2009).

While the changes in lion demographic rates resulting from biotic (Van Orsdol et al. 1985, Hanby et al. 1995, Hayward et al. 2007) or anthropogenic (Creel & Creel 1997, Woodroffe & Ginsberg 1998, Woodroffe & Frank 2005) influences are well investigated in most ecosystems, the effects of abiotic factors on lion demography are only now becoming clear. Distance to surface water, rainfall, vegetation cover and landscape characteristics can all affect lion demographics either directly, or indirectly, by influencing prey abundance and distribution, and their vulnerability to predation (Ogutu & Dublin 2002, Valeix et al. 2009, de Boer et al. 2010, Owen-Smith 2015). A meta-analysis of climate and landscape variables affecting lion demography revealed that lion densities and changes in demographic rates are closely linked to climatic factors such as rainfall and temperature, and landscape features such as elevation, independent of herbivore biomass (Celesia et al. 2009). For example, in Serengeti National Park, reproductive success of females is closely linked to the proximity of river confluences (Mosser & Packer 2009). In arid systems such as the Kgalagadi National Park on the border of South Africa and Botswana, lion survival and reproduction are closely linked to rainfall patterns (Funston & Hermann 2001). During dry years in the Kgalagadi, survival and reproduction is much lower, but in years of good rainfall, conditions are more favourable, and higher reproductive and survival rates result in a significantly higher proportion of cubs and sub-adults in the population (Mills 1978, Funston & Hermann 2001).

Lions are not restricted to arid and mesic savannahs, however, and also occur in wetlands ecosystems throughout Africa. One of the most important wetland systems for lion conservation is the Okavango Delta in Botswana. The Okavango Delta has been classified as a vital lion conservation unit (LCU - IUCN 2006), holding one of the largest and most important lion populations remaining in Africa

(Riggio et al. 2013, Bauer et al. 2015). The Okavango Delta population, which is estimated at just over 1000 individuals (Bauer et al. 2015), meets the criteria for a viable free-roaming population (Riggio et al. 2013), and is an important source population not only for northern Botswana but for the greater Kavango-Zambezi Transfrontier Conservation area (KAZA). The Okavango Delta, however, is drastically different from mesic and arid savannahs, with the dominant landscape process being the annual pulse in flood waters. Flooding on this scale results in a constantly changing environment, and lions must adapt to extreme seasonal range contractions, and the resulting significant shifts in the distribution of their prey (Crawshaw & Quigley 1991).

The main aim of this study was to investigate which social and ecological factors were most important in determining survival and reproduction of lions in the south-western Okavango Delta. We used six years of intensively collected data on five lion prides in the study area to determine age-specific survival rates using mark-recapture analysis. We then tested the effects of three covariates, namely prey availability, intraspecific competition and the extent of flooding on age-specific survival rates, as well as reproductive rates. We hypothesized that 1) survival and reproductive rates would decline as prey abundance declined, 2) higher levels of intraspecific competition would negatively impact survival and reproductive rates due to density-dependence and 3) increasing flood levels may negatively affect cub survival, and result in lower reproductive rates due to increased competition for space.

Methods

Study Area

The Okavango Delta is the world's largest inland delta, and is situated in the north-western corner of Botswana (McCarthy et al. 1998). Each year, a unimodal flood pulse, resulting from seasonal rains in the Angolan highlands, travels down the Okavango river and terminates in an alluvial fan, covering an area of up to 14 000km^2 (McCarthy et al. 1998, Murray-Hudson 2009). This flood pulse occurs during the dry season, and takes three to four months (April to August) to move through the entire system, resulting in a mosaic of seasonally inundated floodplains and dry islands (Gumbricht et al. 2004). The seasonal floodplains in particular are highly productive, and receding floodwaters result in a green

flush of vegetation which attracts large numbers of ungulates, which in turn support a large predator guild (Ramberg et al. 2006, Lindholm et al. 2007). The annual flood pulse is thus the main driving force of all biotic processes within the ecosystem (Junk et al. 1989). Due to highly variable tropical rainfall, the extent of the flood pulse varies not only annually, but also on a multi-decadal time-scale, alternating between wet and dry periods lasting for 30 to 40 years (McCarthy et al. 2000, Mazvimavi & Wolski 2006, Murray-Hudson et al. 2014a). In addition to the temporal variation in flooding patterns, spatial variation in the distribution of water can result from shifts in tectonic plates, or sedimentation and vegetation build-up upstream (Wolski & Murray-Hudson 2006a). Consequently, the Okavango Delta is a highly dynamic environment to which resident biota must continually adapt.

The study area is located in the south-western Okavango Delta, between S 19° 33' and S 19° 53', and E 22° 48' and E 23° 06' (Figure 1). This area encompasses wildlife management areas NG29 and NG30, adjacent to Moremi Game Reserve, which were used for both hunting and photographic tourism throughout the study period. The study period extends from 1997 to 2004, as the Okavango Delta transitioned from one of the driest phases on record to a wetting phase in the multi-decadal cycle (Murray-Hudson et al. 2014a). This wetting phase also coincided with dramatic changes in the distribution of water down the western side of the Okavango Delta, which is characterised by large inter-annual variation in flood levels (Wolski & Murray-Hudson 2006a). Satellite images revealed that in 1997, the Xudum distributary, which is the main distributary in the study area, received increased inflow, while the adjacent Thaoge distributary further west showed a simultaneous decrease in inundation (Wolski & Murray-Hudson 2006a). The study area was thus increasingly inundated over the study period. This resulted in a shift in vegetation from seasonally flooded grasslands to sedge-dominated floodplains over a large portion of the study area, with potentially detrimental effects on resident ungulate populations (C. Winterbach pers. comment).

Data collection

Lion data

From 1997-2004, detailed demographic data and capture history data were collected on five lion prides in the south-western Okavango Delta. When lions were first encountered, identification cards

were created for each individual using whisker spot patterns (Pennycuick & Rudnai 1970). One lioness in each resident pride was fitted with a VHF collar to enable easier location for data collection. All five prides had at least one collared individual for the duration of the study period. Prides were located on a regular basis, either opportunistically or by telemetry, and for each encounter the Universal Transverse Mercator (UTM) position, age, sex and identity of individuals present was recorded. For new individuals, identification cards were created, and individuals re-encountered were recorded as present. To assess pride composition, all lions were aged according to Smuts (1982), where individuals under two years old are classified as cubs, those between two and four years as sub-adults, and those older than four years as adults. For cubs and sub-adults not followed from birth, age was determined by body size (or by mane development for sub-adult males), and adults were aged according to nose colour or tooth wear (Smuts 1982, Whitman & Packer 2007). Information was collected on litter size and composition when litters were encountered for the first time. Sex ratios and age ratios for the population in each year of the study, and on average, are presented in the results.

Covariates

Ecological and social covariates were used as predictors in generalised linear models to determine their effect on both age-specific survival and reproductive rate. To account for differences between prides, pride home ranges were used as borders to calculate maximum flood extent and prey availability for each pride.

Home Range Calculation

UTM data points for each pride were pooled over the entire study period to create estimates of long-term home ranges. Long-term home ranges are a more robust representation of home range, as they incorporate large seasonal variations in range use (Schaller et al. 1972, Hanby et al. 1995). Additionally, pooling location data helps to reduce annual variation that may result from the constraints of VHF sampling and unequal sampling periods, particularly during years of high flood (O' Kochanny et al. 2009). Home ranges were constructed using 90% kernel density isopleths, as 95% home ranges tend to overestimate home range size and have increased variance in relation to smaller density isopleths (Börger et al. 2006, Mosser 2008). The 90% kernel density isopleth has also been

used for the calculation of lion home range sizes in several recent publications (Spong 2002, Funston et al. 2003, Loveridge et al. 2009, Midlane 2013). Fixed kernels were selected as the appropriate home range measurement (Loveridge et al. 2009, Van der Waal et al. 2009), as we were interested in singular range boundaries and not multiple hulls of activity that would result from other methods of home range analysis such as LoCoH (Worton 1989, Getz et al. 2007). LoCoH tends to exclude hard boundaries created by barriers such as rivers or channels, and as data was collected by following up on VHF collars, LoCoH analysis would likely exclude large flooded areas of the home range (Getz et al. 2007). Kernels were smoothed using the *href* smoothing factor. As *href* is positively biased, it overestimates range size at small sample sizes, and thus accounts for underestimation of range size resulting from collecting location data by means of VHF, but also increases in accuracy with increasing sample size (Worton 1995, Kie 2013). Home range analyses were conducted in ArcView GIS 3.2 (ESRI, Redlands, CA) using the Animal Movements extension.

Prey

Prey availability was determined by conducting transects using the roads in the concession area, in the dry season from August to November. Roads were driven at 10-20km/h, three to four hours after sunrise and before sunset, and all animals within 200m of either side of the road were recorded. For each sighting, the species, group size, UTM position and time was recorded. Pride home ranges were overlaid on herbivore transects, and home range boundaries used as cut-off points to divide transects between home ranges using ArcMap 10.2 (ESRI, Redlands, CA). Prey availability for each pride was then determined by calculating a kilometric abundance index (total number of animals/total distance driven in kilometres - Vincent et al. 1991), which would serve as an indication of the average amount of prey encountered per kilometre when lions traverse their home range (Loveridge et al. 2009).

To determine the total amount of prey available per pride, the kilometric abundance index for each species was converted to kilometric biomass, calculated by multiplying the kilometric abundance of each species with the average female species weight (Loveridge et al. 2009). This total was then multiplied by 0.75 to account for the proportion of the population which are young or juvenile (Hayward et al 2007). The total kilometric biomass was then determined by adding together the

kilometric biomass of all prey species, representing the total biomass in prey species encountered per kilometre in each pride home range (Loveridge et al. 2009). Lastly, to account for within-pride competition for food, the total kilometric biomass was divided by the total number adult and sub-adult members of the pride (individuals over two years old) to produce a per capita prey index. In social carnivores, individuals compete for meat at carcasses once prey has been killed (Watts & Holekamp 2009). Particularly when food is scarce, group size has an important influence on individual food intake (Packer et al. 1990). A per capita prey index is therefore a more reliable indication of how prey availability would affect individual fitness of lions.

Flooding

The extent of flooding in the study area was determined using processed satellite TM4 and satellite TM+ imagery obtained from the Okavango Research Institute depicting wet and dry pixels (Wolski & Murray-Hudson 2006b). Images representing inundation at its maximum extent were used for analysis, as it is at this time of the year that both herbivores and carnivores are limited by the available dry land (Crawshaw & Quigley 1991). Home range boundaries for each of the five study prides were superimposed on flood images, and the amount of dry land available in each home range calculated by multiplying the number of dry pixels by the pixel area (28m x 28m). Satellite imagery were used for the years 1997 to 2002, and MODIS imagery for analysis of 2004 flood extent, as satellite imagery was not available for this year. Despite the difference in pixel size (250m x 250m in MODIS imagery), MODIS imagery is highly accurate in determining inundation extent in comparison to satellite imagery, and can therefore be used as reliable substitute of satellite images when calculating inundation extent (Murray-Hudson et al. 2014b). All calculations were done in ArcMap 10.2 (ESRI, Redlands, CA).

Inter- and intra-specific competition

Pride size was determined by adding the total number of adult females and sub-adults (both male and female) present in the pride. Competition was defined as the number of neighbouring adult females whose pride range overlapped with the current pride's home range (Van der Waal et al. 2009). While competition may arise from other lions outside the study area, the extent of overlap between the study

pride's home ranges was taken to represent direct competition for space and other resources. A caveat of this selection was that while large channels to the east and the north of the study area would reduce access from other prides, competition from the west and the south from neighbouring prides may be underestimated. Only neighbouring adult females were considered, as these are the members of the pride most likely to engage in territorial conflict, or take over kills (Mosser & Packer 2009). Sub-adults are only likely to respond to territorial behaviour as they become older, and even then their participation is largely dependent on the proportion of adult females to trespassers (Heinsohn et al. 1996). Adult males were excluded from the analysis, as coalitions often moved between prides and controlled more than one pride at a time.

Data analysis

Population demographics

Reproduction

Reproductive rate was defined as the number of cubs born in each pride each year. Using generalized linear mixed models, the effects of ecological predictors (per capita prey availability and land availability) and social predictors (pride size and competition) on reproductive rate were examined. Both year and pride were used as random effects, as this accounts for variation within prides and in each year that may not be common to all prides and years within the study period (Bolker 2008). Variance inflation factor (VIF) testing revealed no collinearity between predictor variables, and so all variables were included within the global model. All possible models nested within the global model were derived from the global model, and Aikaike's information criterion for small sample size (AICc) was used for model selection (recommended for models where $n/K<40$ – Burnham & Anderson 2002). To account for model uncertainty, model averaging was performed on all candidate models whose summed Aikaike weights exceeded 0.95 (Burnham & Anderson 2002). This produces a set of candidate models that fall within a 95% confidence interval, and represents models that most realistically estimate the best model (Symonds & Moussalli 2011, Burnham & Anderson 2002). Generalized linear models were constructed using the *lmer4* package (Bates et al. 2014), and nested

models derived from the global model using the *MuMIn* package (Barton 2013) in R 3.2.2 (R Core Development Team 2014).

Survival

General models

Mark-recapture data were condensed into annual intervals to represent each capture event, for the years 1997 to 2004 (Emmerson & Southwell 2011). Lions were considered 'captured' when they were encountered and whisker spots on both sides of the face recorded, and were considered 'recaptured' if they were spotted again in subsequent years. Capture history information was then analysed in RMark (Laake 2013) in R 3.2.2 (R Core Development Team 2014), using the Cormack-Jolly-Seber (CJS) model as the mark-recapture modelling framework (Lebreton et al. 1992). In CJS models, two "apparent" probabilities are estimated - the recapture probability (*p)* and the survival probability (*φ).* Recapture probability (*p),* represents the probability of re-encountering a lion, assuming it is alive and within the study area, and survival probability (*φ*), is the probability of the animal surviving and remaining within or returning to the study area (Emmerson & Southwell 2011). One of the caveats of the CJS model is that the survival probability cannot distinguish between mortality and emigration, and this probability should therefore be interpreted with caution (Lebreton et al. 1992). Recapture probabilities on the other hand represent the real probability of re-encountering an animal (Lebreton et al. 1992).

Goodness-of-fit testing is required to assess whether the data fits the assumptions of the CJS models, namely, 1) equal probability of being recaptured after initial capture at time *i*, and 2) equal probability of surviving from time *i* to *i+1* (Kéry et al. 2006). Failure to meet these assumptions may indicate the need to create age categories for individuals in the dataset, and re-assess the fit (Kéry et al. 2006, Emmerson & Southwell 2011). Using program RELEASE, the goodness-of-fit for the standard time-dependent CJS model *φ(t)p(t)* was tested. Systematic failure of cohorts across TEST 3, which tests the second assumption of the CJS model, indicated the need to include age structure in survival models. For recapture probabilities, examination of TEST 2 results, which tests the assumption of equal catchability, revealed no capture heterogeneity between individuals. Despite their territorial nature

which might affect random movement of individuals throughout the study area (Ogutu et al. 2006), the collaring of one or two individuals in each pride, and the social structure of prides, allowed for homogeneity in observability throughout the study period.

In general, there are marked differences in survival rates amongst various age groups of lions (Schaller 1972, Bertram 1975, Ogutu & Dublin 2002). Cubs under the age of twelve months generally have higher mortality rates than other age groups, mainly due to their vulnerability to predation by other large carnivores, the risk of infanticide, as well as increased vulnerability to nutritional stress or abandonment during periods of prey scarcity (Schaller 1972, Van Orsdol et al. 1985). However, mortality rates considerably improve after the first year, and survival at different life stages may be governed by different factors (Van Orsdol et al. 1985, Ogutu & Dublin 2002). Taking this into account, we categorised age groups in two different ways to determine which age group structure best represented the differences in observed survival between age groups in the population. The first was a four tier age group structure φ(4a), divided into young cubs (cub1: 0-1 years of age), older cubs (cub2: 1-2 years of age), sub-adults (sa: 2-4 years of age) and adults (ad: >4 years), and the second was a three tier age structure φ(3a), where older cubs and sub-adults were collapsed into a single group (csa: 1-4 years of age).

In order to select a model with the best age structure for survival, and best recapture probability, four different models were constructed. These models were a combination of full-time dependent survival models for each age group structure φ4a(t) and φ3a(t), and the two most simple models for recapture probabilities, namely time-dependent p(t) and constant p(.). To account for differences in survival between prides, pride was included as an additive effect in the model structure for survival. As one member of each pride was fitted with a radio-collar, and to maintain simplicity in recapture probabilities, pride differences in capture probabilities were not considered. For model selection, models with ΔAICc <2 were considered parsimonious and were considered the best models describing the data (Burnham & Anderson 2002). The model with the highest AICc weight to fall within this category was selected as the best age structure model to estimate apparent survival and recapture rates for the population (Burnham & Anderson 2002). The goodness-of-fit for the best age group structure was then assessed by importing the data into MARK v 6.1 (White & Burnham 1999)

and using the median ĉ approach, with a lower bound of 1, an upper bound of 5 and with 100 replicates. A ĉ value of more than three would indicate a general lack of fit of the model (Lebreton et al. 1992). All other models, which would be nested within this model, were then adjusted for over-dispersion according to the median ĉ value, resulting in quasi-likelihood AICc values adjusted for small sample size.

Covariate models

To select the model which best described temporal variation in survival for each age group, additional survival models were structured, each constraining one of the age classes to have a constant survival probability (Dybala et al. 2013). As each of these models was nested within the general model, each model was adjusted for over-dispersion (ĉ=1.5). The best model to describe temporal variation in survival included constant adult survival, and this model was then used to determine the general trends in survival across the population, and as the baseline time-varying model for covariate analysis. New models constraining the survival of the remaining age groups to constant were derived from this model.

To examine the effects of environmental and social covariates, the covariates were added to constant models for each age group. Effectively, by substituting time in the model, QAICc can be used to determine whether covariate models perform better than constant and time-varying models, and thus best describe temporal variation in survival for each age group (Kéry et al. 2006, Grosbois 2008, Emmerson & Southwell 2011, Dybala et al. 2013). All covariates were standardized by centring and dividing by one standard deviation in order to make the results directly comparable (Schielzeth 2010, Dybala et al. 2013). To reduce model parameterization and maintain model simplicity, each covariate was considered individually, and covariate models were then compared to baseline time-varying and constant models using the information-theoretic approach (Emmerson & Southwell 2011, Burnham & Anderson 2002, Grosbois et al. 2008). Following Grosbois et al. 2008, covariates were considered to be statistically supported when covariate (co) models performed better than constant models (cst), but were as well or better supported than the time-variant models (t) (Anderson & Burnham 2002,

Guthery et al. 2005). Consequently, if ΔQAICc(co)-ΔQAICc(cst) < -2 and ΔQAICc(co)-ΔQAICc(t) ≤ 2 the effect of the covariate is considered statistically significant (Grosbois et al .2008).

To quantify the magnitude of the effect of each covariate, the analysis of deviance approach was applied to covariate and baseline constant and time-variant models (Skalski 1996, Grosbois et al. 2008). This approach determines the fraction of annual variation in survival explained by the covariate for each age group (R^2 *dev*), and is similar to a "coefficient of determination" (Emmerson & Southwell 2011, Dybala et al. 2013). R^2 dev is therefore calculated as $\frac{Dev(cst)-Dev(cov)}{Dev(cst)-Dev(t)}$, where Dev(cst) is the deviance for the constant model, Dev(cov) the deviance for the covariate model, and Dev(t) the deviance for the time-varying model (Skalski 1996, Grosbois et al. 2008, Emmerson & Southwell 2011). Covariates with an R^2dev value of higher than 0.2 are considered potentially influential, as these covariates explain more than 20% of the annual variation in survival (Grosbois et al. 2008).

Results

Population structure

For the entire eight-year study period, sex ratios of lions indicated an overall sex ratio biased towards females for adult and sub-adult age groups combined, with one male to every three females (Table 1). Especially in the adult age-groups, sex ratios were often over four females to every male in the population - pride males and nomadic males included (Table 1). Sex ratios in sub-adult age groups varied, but were generally in favour of females, with the exception of 1999 (1:0.75), and 2004, where only one sub-adult male was recorded (Table 1). Overall, female sub-adults out-numbered males almost two to one (Table 1). Sex ratios of cubs whose entire litters (or litters where only one cub could not be sexed) were sexed, indicated a general sex ratio over the study period closer to parity than in the sub-adult and adult age groups, although still in favour of females (1:1.5) (Table 2).

An examination of the age structure of the lion population revealed that the number of adults in the population remained relatively stable over the eight-year study period (Figure2). Adults consistently represented about two-thirds of the lion population, with the exception of 1997, when there were large

cohorts of cubs, and 2004, when there were very few sub-adults and cubs present. Sub-adults represented around one-fifth of the lion population until 2001 (with the exception of 1998), and then declined sharply from 2002 to 2004. The proportion of cubs in the population showed the most noticeable change, declining from 35.7% of the population in 1997 to 5.1% of the population in 2004 (Figure 2).

Reproduction

The largest cohorts of cubs were produced in 1997 and 1998, after which reproductive rates slowed down (Figure 3). The top candidate models representing a 95% confidence interval included all four social and ecological predictors (Table 3). Competition occurred in all of the selected models, with per capita prey availability, pride size and land availability having summed Aikaike weights of 0.743, 0.591 and 0.198 respectively (Table 3). Model-averaging results confirmed that competition was an influential factor in influencing reproductive rates amongst all the predictor variables considered (Table 4). Although per capita prey availability was present in more candidate models, pride size was the only other variable considered influential in determining reproductive rate (Table 4). Both competition and pride size had a negative relationship with reproductive rate (Table 4).

Survival

General models

While testing for age-structure, the three-tier age group model (φa3(t)) was selected as the most parsimonious model for survival, with a model weight of 0.994 (Table 5). This model also indicated p(t) as the most parsimonious model for recapture probabilities. Goodness-of-fit testing revealed a $\hat{c}$ value of 1.5, and all subsequent models were adjusted according to this value. The time-varying three tier-age group model was then used as the baseline model for construction of subsequent models restricting each of the age groups to constant survival (Table 6). These models revealed that a model structure with constant adult survival (φ(t/t/.)) (where / separates age groups from youngest to oldest, t=time-varying survival and .=constant survival) best described the temporal variation in survival in the dataset (Table 6). This model then became the time-varying reference model (Ref_t), and models

constraining cub (Ref_C) and sub-adult (Ref_{SA}) survival to be constant were constructed from the new reference model (Table 6).

General survival rates indicated that cub survival and sub-adult survival followed a similar time trend (Figure 4). Apparent cub survival over the study period averaged at 0.34 (± 0.27 SD), while sub-adult survival for lions between two and four years of age average at 0.75 (± 0.18 SD). Adult survival was estimated at a constant 0.84 (± 03 SE). Recapture probabilities were relatively high over the study period, and were lowest in the year 2000, probably as a result of high floods (Figure 4 & 5).

Covariate models

Covariates were added to the baseline models Ref_C and Ref_{SA}, to determine the effects of covariates on cub and sub-adult survival (see Figure 4 and 5 to compare survival and covariate trends). For cub survival, only two covariates substantially increased the fit compared to the constant model, namely per capita prey availability and intraspecific competition. These covariates explained 41.85 % and 41.31% of the variation in cub survival annually respectively, and while cub survival was positively related to prey availability, it had a negative relationship with competition (Table 7). Both flooding and pride size were considered equally parsimonious with the constant model, and were therefore not considered as important factors describing temporal variation in cub survival. For sub-adult survival, only one covariate, pride size, performed better than the constant model (Table 7). Pride size described a significant proportion in sub-adult survival at 58.33%, and was inversely related to sub-adult survival. All other environmental and social factors combined explained less than 5% of temporal variation in survival, and were therefore not significant in predicting sub-adult survival.

Discussion

Survival and reproduction in the lion population of the western Okavango Delta is largely subject to density-dependent effects. Competition from conspecifics proved to be an important factor in reducing reproductive rates as well as the survival of young cubs, whose survival is vital to population growth (Packer et al. 2005). This high degree of competition may be responsible for the sex skew towards females in the population, as prides would gain most from raising and recruiting females that

would enhance pride size, resulting in increased reproductive success (successfully raising cubs to adulthood) and maintaining access to high quality habitat despite high inter-pride competition (Mosser & Packer 2009). However, survival of sub-adults and reproduction was also negatively influenced by increasing pride size, an indication that competition within prides is also a limiting factor for the lion population (Packer et al. 2005). The only environmental variable which came to the fore in significantly affecting demographic rates was per capita prey availability, where lower prey abundance led to lower cub survival. This is consistent with studies in other protected areas (Bertram 1973, Van Orsdol 1985). Although flooding did not directly affect survival or reproduction, it is an important driver of vegetation composition and available grazing for herbivores in the Okavango Delta, and can exert considerable influence on their abundance and distribution (Burger et al. unpublished data). Consequently, changes in flooding patterns directly affect prey, and cannot be excluded as a factor influencing lion demographic patterns.

The average sex ratio of one male to four females for adults was relatively high in comparison to other protected areas such as the Serengeti , Tanzania (1:2, Schaller 1972), the Masai Mara, Kenya (1:1.3 to 1:2, Ogutu & Dublin 2002), Kgalagadi Transfrontier Park (1:3.2, Funston & Hermann 2001; 1:3.3, Van Vuuren et al. 2005), Etosha National Park, Namibia (1:1.6, Stander 1991) and Kruger National Park (1:1.7 to 1:2.4, Smuts 1976). These calculated sex ratios included nomadic males who remained in the pride natal area in the absence of attending pride males, without which adult ratios would be even more skewed in favour of females. The scarcity of adult males within the ecosystem may be related to hunting, which continued in the area until it was banned in 2001. Similar male-female sex ratios of 1:4.5 and of up to 1:6.5 were reported in South Luangwa and Lower Zambezi National park, where populations were believed to be male-depleted as a result of hunting (Becker et al. 2012). It is also possible that dispersing males experienced higher levels of mortality – if forced south towards the veterinary fence, they may have resorted to cattle depredation, resulting in retaliatory killing by local farmers. However, while hunted or persecuted populations often respond by producing litters with sex ratios skewed towards males (Funston & Hermann 2001, Loveridge et al. 2007), this population's sex ratio was skewed in favour of females for both cub and sub-adult groups,

suggesting a response to natural environmental or social circumstances and not anthropogenic pressure.

While the skew towards females in sub-adulthood may reflect differential mortality in sub-adulthood, where young males are less likely to survive after dispersal (Funston & Hermann 2001), we posit that the female skewed sex ratio in cubs is related to high densities. With a large number of conspecifics and a large portion of shared home range, recruitment of females into prides resulting in larger pride sizes may confer territorial advantages, and result in lower wounding and mortality of adults from territorial disputes (Mosser & Packer 2009). Furthermore, if prides were to split, larger cohorts of females would potentially exceed the minimal viable pride size necessary to establish a successful pride in such a high density area (Van der Waal et al. 2009). This is consistent with the theory that sex ratios can be skewed towards the sex that will benefit the rest of the group by securing local resources through co-operation (Clark 1978, Emlen et al. 1986, Pusey & Packer 1987). The sex ratio amongst cubs would then be amplified into sub-adulthood and ultimately result in an adult population consisting of a large number of females.

Age ratios indicate a healthy population with adults forming around two thirds of the population. This is however, slightly larger than other populations, where adults generally constitute half of the population (Kruger National Park - Smuts 1976, Masai Mara - Ogutu & Dublin 2002, Etosha National Park - Stander 1991). This ratio became even higher towards the end of the study period, as reproductive rates slowed down, although, it is important to note that data may be slightly biased due to the difficulty of finding new-born litters. Nevertheless, high proportions of sub-adults in the population between 1999 and 2000, resulting from the large cohorts of cubs in 1997 and 1998, translated into an increase in the size of the adult population, which would explain why competition from competing female adult neighbours increased over the study period, even though the overall number of lions (including sub-adults) decreased.. Most of the variation in age composition occurred in cub and sub-adult age groups, which are age groups whose survival is more dependent on prevailing ecological or social conditions (Funston & Hermann 2001), as indicated in our survival analyses.

Survival rates of cubs younger than twelve months were the lowest of all demographic groups throughout the study period, and were influenced to a large extent by prey availability. This is consistent with our hypothesis and with other demographic studies on lions where survival rates of cubs are lowest in the birth year (Schaller 1972, Bertram 1975, Hanby & Bygott 1979, Van Orsdol et al. 1985, Ogutu & Dublin 2002), and where there is a consistent relationship between cub survival and prey availability (Bertram 1973, Van Orsdol et al. 1985). Due to their small size and the demands of the growing period, cubs have higher energetic demands, and are therefore more vulnerable to nutritional stress (Van Orsdol et al. 1985). Young cubs may be susceptible to nutritional stress, and even mortality, as a result of feeding competition at carcasses from other members of the pride, particularly older cubs (Bertram 1975, Van Orsdol et al. 1985, Packer et al. 2001). This may be a reason for the apparent low cub survival in 1999, as large cohorts of cubs were born in 1997 and 1998. Additionally, during periods of food scarcity, cubs may be abandoned as adults move further from dens in search of food (Packer et al. 1990, Schaller et al. 1972, Orford et al. 1988).

As predicted, competition with neighbours had a negative influence on two aspects of reproductive success in this study – the survival of young cubs up to the age of one year, as well as reproductive rate. Reproductive rates in lions are density-dependent, and decrease with increasing density of conspecifics (Trinkel et al. 2010, Smuts et al. 1978, Packer et al. 1988). In the Serengeti, female reproductive success, which was defined as the number of cubs per adult female surviving to twelve months, declined as the number of neighbours increased (Mosser & Packer 2009). The decline in reproductive rates with increasing density has been well-documented in South Africa, where lions have been reintroduced onto small reserves (Trinkel et al. 2010, Miller & Funston 2014). As lions reach their carrying capacity, numerous changes in reproductive cycles occur, among which are reduced reproductive rates (Trinkel et al. 2010, Miller & Funston 2014). Given the extensive overlap in home range use amongst prides in the study area, young cubs left unprotected may have been more vulnerable to infanticide by both males and females from neighbouring prides. The effect of competition on lion reproduction during the study period indicates that density-dependence exerted a strong negative influence on lion population growth, and that the lion population was likely near carrying-capacity. Similar patterns of self-regulation have also been observed in other carnivores (see

Wallach et al. 2015). For example, in brown bears (*Ursus arctos*), neighbouring females with cubs caused reproductive suppression of nearby females (Ordiz et al. 2008), and in protected populations of gray wolves (*Canis lupus*), densities are higher and reproductive rates lower than in hunted populations (Haber 1996).

Pride size proved to be the most important factor in influencing survival of sub-adults and older cubs between one and four years old. Lions in the Okavango Delta are therefore limited not only by competition, but by within group density-dependence (Van der Waal et al. 2009). However, it is important to note that the mark-recapture analysis does not distinguish between survival and emigration, and that the results are therefore a mixture of both demographic processes (Lebreton 1992). Young male lions disperse between the age of two and four years (Bygott et al. 1979, Pusey & Packer 1987), and as such may never be recaptured, resulting in lower apparent survival rates. For example, in 1999, sub-adult survival was shown to be low at only 50%, but we posit that this is in fact due to emigration of a large cohort of sub-adult males who were born in 1997. Thus, apparent low survival rates for 1999 are largely as a result of emigrating young males. While it appeared that most sub-adult females were recruited into natal prides during the study period, it is possible that high within-group competition may have resulted in dispersal, and perhaps mortality, of sub-adult females as well. The threshold between recruitment and dispersal of females is dependent on the relationship between natal pride size, prey availability and the level of intra-pride competition (Van der Waal et al. 2009). In systems with sufficient prey, high inter-pride competition may reduce dispersal of females, who may gain more benefits by staying with the natal pride than trying to establish a territory on their own in saturated habitats (Van der Waal et al. 2009). However, if the optimal pride size specific to that system is reached, a size above which reproductive success and individual fitness decreases, females may be forced to disperse regardless (Packer et al. 2005, Van der Waal et al. 2009). Aggression between young sub-adults and other members of the pride also increases when prey numbers are low or at small carcasses, a mechanism which could also lead to dispersal (Schaller 1972, Van Orsdol et al. 1985).Unless dispersing cohorts are of the minimum viable pride size, such sub-adults are subject to mortality from starvation, or from conflict with unfamiliar lions (Hanby & Bygott 1987, Mosser & Packer 2009). While mortalities are likely, we posit that the negative relationship

between pride size and sub-adult survival could be largely explained by sub-adult emigration and not mortality.

Pride size also had a negative effect on reproductive rate, suggesting that intra-pride competition can influence demographic rates. This is concurrent with similar data on lion prides in the Serengeti, Tanzania (Packer et al. 1988, Packer et al. 2001, Packer et al. 2005, Van Der Waal et al. 2009). Depending on factors such as vegetation type and local prey abundance, each system has a pride size threshold, or optimum pride size, above which reproductive rates decline (Trinkel et al. 2007, Van der Waal et al. 2009). For example, in Tanzania, prides living in woodland habitat and prides living on the plains both showed declines in reproductive success as the number of adult females in the pride exceeded 11 and six respectively (Van der Waal et al. 2009). This would also explain why at higher pride sizes, apparent survival rates, which we attribute to dispersal, are lower, as sub-adult dispersal is also more likely once prides reach the area-specific size-threshold (Hanby & Bygott 1987, Van der Waal et al. 2009). As both within pride and between pride competition influences reproductive rate, this is further evidence that at high densities, and without resource limitation, lions are self-regulated by social factors.

Contrary to our hypotheses, flooding did not have a direct negative effect on cub survival. However, we maintain that it is an important factor in the survival of young cubs due to its direct effect on herbivore populations. Studies on climate and landscape correlates with lion demography indicated that prey biomass in a variety of ecosystems is in fact secondary to environmental factors (Celesia et al. 2009). In the Okavango Delta, Murray-Hudson (2009) discovered that vegetation composition is largely dependent on flood duration in months, averaged over the past three years. Therefore, while there was no collinearity between flood and prey availability within the same year, there is evidence, based on data from the same area and over the same time frame, that flooding can exert a significant, but time-lagged effect on prey abundance as a result of changes in vegetation composition (Burger et al. unpublished data). Indeed, a recent aerial survey of the Okavango Delta revealed a considerable decline in medium-sized grazers such as tsessebe (*Damascus lunatus*) and wildebeest (*Connochaetus taurinus*), prey which fall within the lion's preferred weight range (Hanby & Bygott 1991, Hayward & Kerley 2005, Chase & Landen 2011). Therefore, while the proximate cause of reduced cub survival

during the study period was declining prey availability, the ultimate cause may indeed be the increase in flooding patterns. In other wetland environments, such as the Busanga floodplains in Kafue National Park, Zambia, high periods of inundation seemingly lead to low cub survival (Midlane 2013). Over a period of two years, resident prides were successful in raising a mere 14. 7% of cubs past the age of one year (Midlane 2013), which is half of the average cub survival rate over this study period in the Okavango Delta. Whether the flooding was the ultimate cause of this low survival rate was undetermined, but both Midlane's (2013) data and this study's data suggests that flooding patterns have a key role to play in the survival of cubs in wetland habitats.

Despite the fluctuations in social and ecological factors, survival in adult age-group remained constant and high throughout the study period. In demographic studies across numerous species, adult survival rates are indeed most resistant to environmental stochasticity or density-dependence (Gaillard et al. 1998, Forcada et al. 2008, Portier et al. 1998, Altwegg et al. 2005, Dybala et al. 2013). By buffering adult survival against temporal variability, variation in population growth is limited, allowing time for populations to adapt to changing circumstances, particularly in long-lived species (Forcada et al. 2008). Indeed, in the Kgalagadi Transfrontier Park, sensitivity analyses conducted to determine the effects of persecution of lion along park borders showed that female adult survival was the single most important factor in ensuring the viability of the park's population (Van Vuuren et al. 2005). Constant adult survival in lions is therefore an important life-history strategy in guarding against population crashes during times with fluctuating resource availability or high levels of competition (Forcada et al. 2008, Gaillard et al. 1998, Dybala et al. 2013). Adults would therefore only be vulnerable to extreme ecological events such as disease outbreaks (Roelke-Parker 1996), or other dramatic ecological changes such as a large decline in prey availability or vegetation changes which could affect hunting success (Packer et al. 2005). This pattern, or saltatory equilibrium, is evident in the Serengeti and Ngorongoro crater, where diseases caused a large die-off in adults, after which survival rates stabilised again until the next stochastic event (Roelke-Parker 1996, Packer et al. 2005). Such stability in adult survival is important in a dynamic system such as the Okavango Delta, which can experience large fluctuations in the flooding regime which would have knock-on effects for the entire food chain. Alternatively, as lions are long-lived animals, the study period may not have been

long enough to detect significant temporal patterns in adult mortality. This mortality may have mostly been as a result of senescing lions, or alternatively wounding caused by fights with conspecifics or hyenas (Mosser & Packer 2009). It may be useful to compare whether mortality rates during periods of lower lion densities are lower than during periods of intense inter-pride competition.

Conclusion

Social factors, as a result of inter- and intra-pride competition, were more important than ecological factors in determining demographic rates of lions in the western Okavango Delta. This density-dependence is as result of a large pride sizes, as well as large numbers of competing conspecifics which share a relatively small area, with extensive home range overlap. While flooding did not show a direct effect on lion population demographics, the effects of flooding on a landscape level cannot be ignored as an important ultimate driver of lion population change. We posit that increasing levels of inundation on the western side of the Okavango Delta was not only responsible for exacerbating intra-specific competition by decreasing land availability, but also for the decline in prey availability observed over the study period (Burger et al. in press). This ultimately led to reduced reproductive rates, as well as lower survival rates for young cubs.

As lion numbers are increasingly under threat in Africa, particularly in unfenced ecosystems (Bauer et al. 2015), understanding how lion demographic rates are affected by local ecological conditions is important for their conservation. If lions are below the carrying capacity predicted by baseline demographic rates in relation to current ecological conditions in a particular system, this could potentially indicate the negative influence of anthropogenic effects such as human-lion conflict or over-hunting (Woodroffe & Frank 2005, Kiffner et al. 2009). Similarly, it may also indicate natural threats, such as increased mortality from disease, or reduced reproductive rates and survival due to inbreeding (Roelke-Parker et al. 1996, Fuller & Sievert 2001, Björkland 2003). Timeously identifying and addressing such conservation issues is particularly important in maintaining healthy and viable lion populations, particularly in important regional source populations such as those in the Okavango Delta.

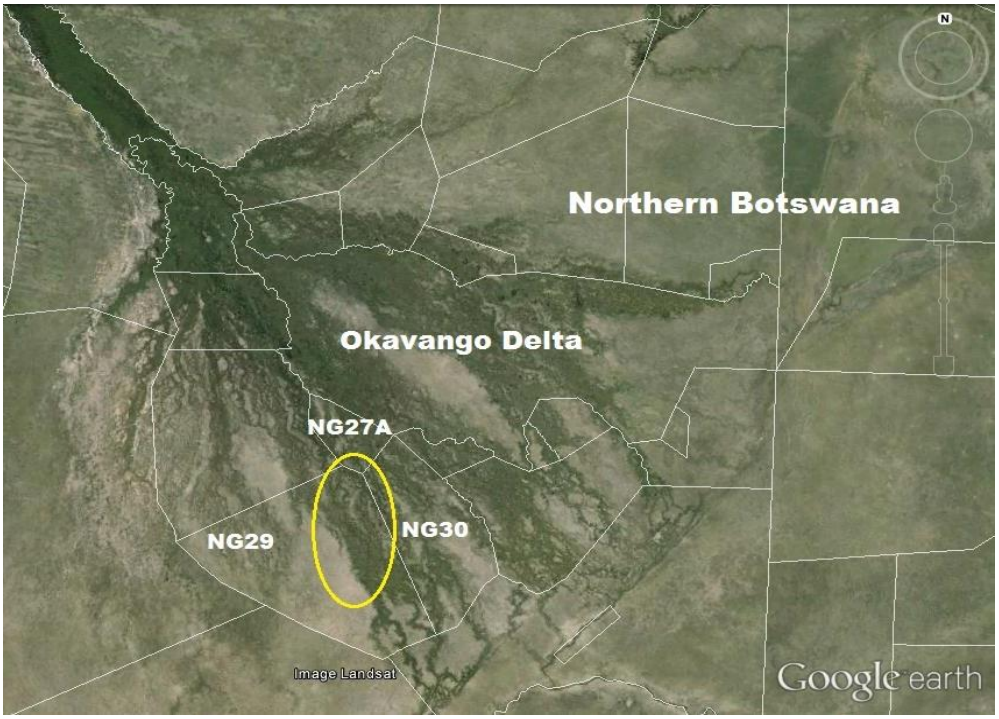


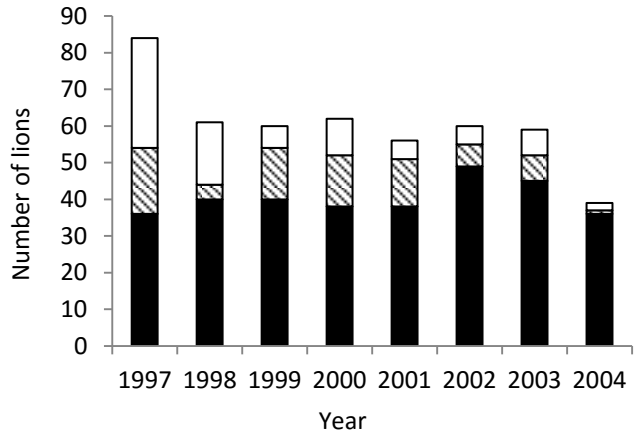
Figure 1. Study area in the south-western Okavango Delta, Botswana. The yellow ellipse indicates the intensive study area in which lion prides were located and collared for follow-up. The study area spanned three wildlife management concessions, namely NG29, NG30, and a small section of NG27A. This area is characterised by seasonal floodplain vegetation interspersed with small islands. *Source:* "Okavango Delta". S -19.340295° E 22.836576°. **Google Earth.** 1 January 2015. Accessed 15 July 2015.

Table 1. Sex-ratios (indicated in bold) of male to female adults and sub-adults each year, and averaged over the entire study period. Numbers in brackets indicate actual numbers of individual lions, as does the total column.

Year	Adult (M:F)	Sub-adult (M:F)	Combined	Total
1997	**1:4** (7:29)	**1:1.25** (8:10)	**1:2.6** (15:39)	n=54
1998	**1:3** (10:30)	**0:1** (0:4)	**1:3.4** (10:34)	n=44
1999	**1:3.4** (9:31)	**1:0.75** (8:6)	**1:2.1** (17:37)	n=54
2000	**1:4.4** (7:31)	**1:1.8** (5:9)	**1:3.3** (12:40)	n=52
2001	**1:4.4** (7:31)	**1:2.25** (4:9)	**1:3.6** (11:40)	n=51
2002	**1:2.5** (14:35)	**1:5** (1:5)	**1:2.7** (15:40)	n=55
2003	**1:4.6** (8:37)	**1:2.5** (2:5)	**1:4.2** (10:42)	n=52
2004	**1:3.5** (8:28)	**1:0** (1:0)	**1:3.1** (9:28)	n=37
Average	**1:3.6**	**1:1.7**	**1:3**	

Table 2. Sex ratio of cubs in litters where all cubs were sexed before the age of twelve months. Numbers in brackets in the Cubs column indicate that an extra cub was present for which the sex was unknown.

Year	Pride	Litters	Cubs	M	F	Ratio (M:F)
1997	Central	1	4	2	2	
	Morula	1	2	1	1	
	Total	**(n=2)**	**6**	**3**	**3**	**1:1**
1998	Mochaba	1	2	0	2	
	Mochaba(2)	2	5 (1)	2	3	
	Total	**(n=3)**	**7**	**2**	**5**	**1:2.5**
1999	Morula	1	3	0	3	
	Total	**(n=1)**	**3**	**0**	**3**	**0:1**
2000	Central	1	3	2	1	
	PomPom	1	2(1)	1	1	
	Mochaba	1	2	1	1	
	Total	**(n=3)**	**7**	**4**	**3**	**1:0.75**
	TOTAL		**27**	**9**	**14**	**1:1.5**



Year	Adults	Sub-adults	Cubs
1997	42.9%	21.4%	35.7%
1998	65.6%	6.6%	27.9%
1999	66.7%	23.3%	10.0%
2000	61.3%	22.6%	16.1%
2001	67.9%	23.2%	8.9%
2002	81.7%	10.0%	8.3%
2003	76.3%	11.9%	11.9%
2004	92.3%	2.6%	5.1%

Figure 2. Age structure of the lion population in the south-western Okavango Delta, summed over all five of the study prides. The graph represents the actual number of adults (solid), sub-adults (pattern) and cubs (clear) in the population in each year, and the accompanying table the proportion of the population represented by each age group. Adults = > 4years, sub-adults = 2-4 years and cubs = 0-2 years.

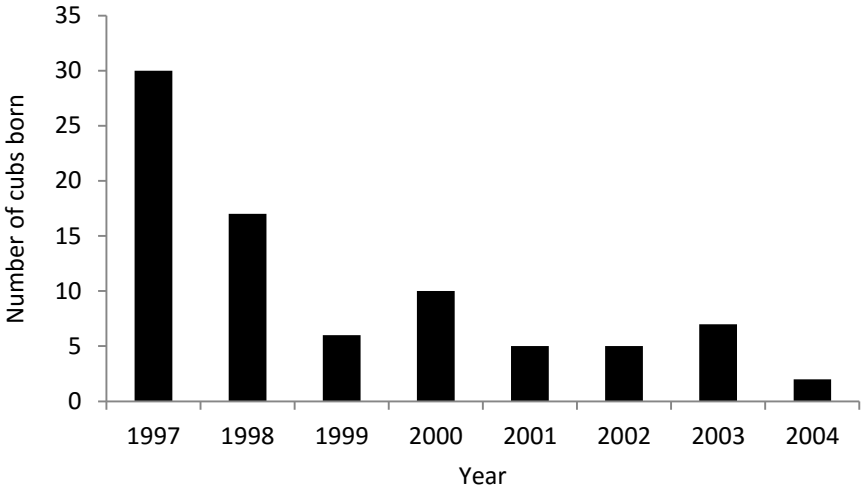


Figure 3. Reproductive rate, defined as the number of cubs born in each pride annually, summed over all of the study prides (n=5) for each year in the study period.

Table 3. Generalized linear model results for reproductive rate of lions in the south-western Okavango Delta. Models represent the top candidate models whose summed Aikaike weights exceed 0.95, and which were used for model averaging in subsequent analysis. Crosses indicate which social and ecological predictors are present in the candidate models. df=degrees of freedom, AICc=Aikaike's information criterion for small sample size, ΔAICc=change in AICc between top model and subsequent models, w=Aikaike's weight for each model.

Competition	Land	Per capita prey	Pride size	df	AICc	ΔAICc	*w*
x		x	x	6	156.2	0	0.485
x				4	158.6	2.4	0.146
x		x		5	159.1	2.86	0.116
x	x	x	x	7	159.3	3.05	0.106
x	x			5	160.5	4.32	0.056
x	x	x		6	161.4	5.21	0.036

Table 4. Social and ecological variables affecting reproductive rate of lions (n=5 prides) in the south-western Okavango Delta. Parameter estimates represent full model-averaged results. The top models representing a 95% confidence interval (summed Aikaike weights <=0.95) were used for model averaging. Relative importance represents the summed Aikaike weights (AICc) for models used in model averaging. Figures in bold indicate variables whose confidence intervals do not cross zero, and are therefore considered significant.

Variable	Estimate	Unconditional SE	Confidence Interval	Relative importance
(Intercept)	0.35073	0.46384	(-0.60182, 1.30329)	
Competition	-1.42407	0.44064	**(-2.31913, -0.52900)**	1
Per capita prey	-1.49182	1.15621	(-3.85026, 0.05439)	0.79
Pride Size	-1.03238	0.98306	**(-3.13825, -0.16524)**	0.63
Land availability	0.09916	0.48716	(-1.46842, 2.41830)	0.21

Table 5. Model selection to determine the age group structure for survival probabilities and the general structure for recapture probabilities. Two age group structures were tested, including three and four age groups respectively. The four age group structure consisted of young cubs (0-1 years), older cubs (1-2 years), sub-adults (2-4 years) and adults (4 years). The three age group structure pooled older cubs and sub-adults into one age group (1-4 years). To maintain model simplicity, only time-varying and constant recapture probabilities were tested. k=parameter index, AICc=Aikaike's information criterion for small sample size, ΔAICc = change in AICc and w=model weights.

Survival (φ)	**Recapture (p)**	**k**	**AICc**	**ΔAICc**	**w**
Three age-groups (t/t/t)	Time (t)	23	509.99	0.00	0.9939
Three age-groups (t/t/t)	Constant (.)	18	520.22	10.23	0.0060
Four age-groups (t/t/t/t)	Time (t)	11	527.25	17.26	0.0002
Four age-groups (t/t/t/t)	Constant (.)	6	543.52	33.53	0.0000

Table 6. Model selection to select a baseline model that best described temporal variation in the dataset, using three age groups. The model showing constant adult survival and time-varying cub and sub-adult survival was then selected as the baseline model for further analysis. k=number of parameters, AICc=Aikaike's Information Criterion for small sample sizes, ΔAICc=change in AICc, w=model weight, ĉ=median c-hat value for the most general model.

Survival (*φ*)	**Recapture (p)**	**k**	**AICc**	**ΔAICc**	**w**	**ĉ**
Adult constant (t/t/.)	Time (t)	24	359.02	0.00	0.7430	1.5
Sub-adult constant (t/./t)	Time (t)	24	361.40	2.38	0.2258	1.5
Cub constant (./t/t)	Time (t)	24	365.65	6.63	0.0270	1.5
All time-varying (t/t/t)	Time (t)	29	369.37	10.35	0.0042	1.5

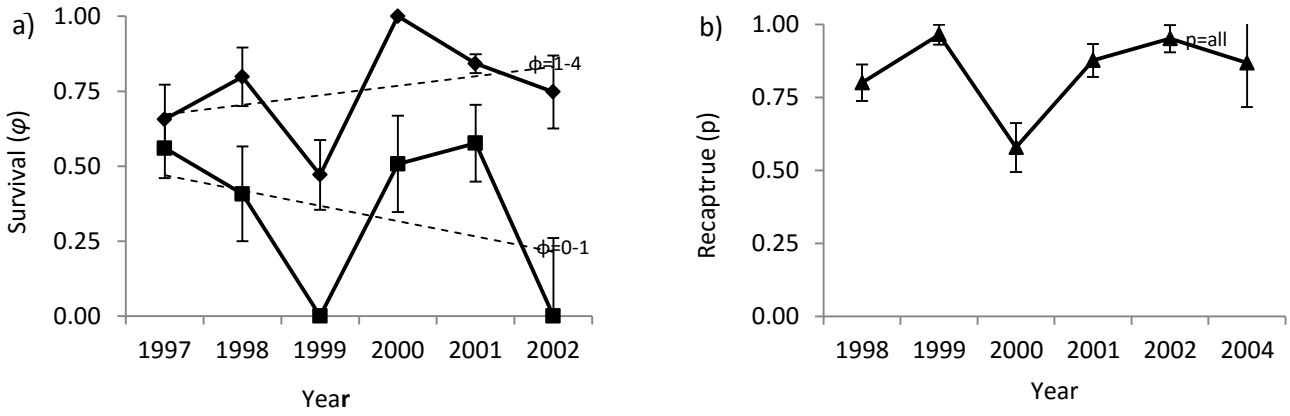


Figure 4. Apparent survival (a) for cubs (0-1 years old) and pooled older cubs and sub-adults (1-4 years old) and b) recapture rates for lions in the south-western Okavango Delta. Dotted lines indicate trend lines for survival of each age group over the study period. Error bars indicate standard errors as estimated in RMark. Standard errors for survival for the pooled sub-adult age class in 2000 and for survival of cubs in 1999 were estimated at boundaries.

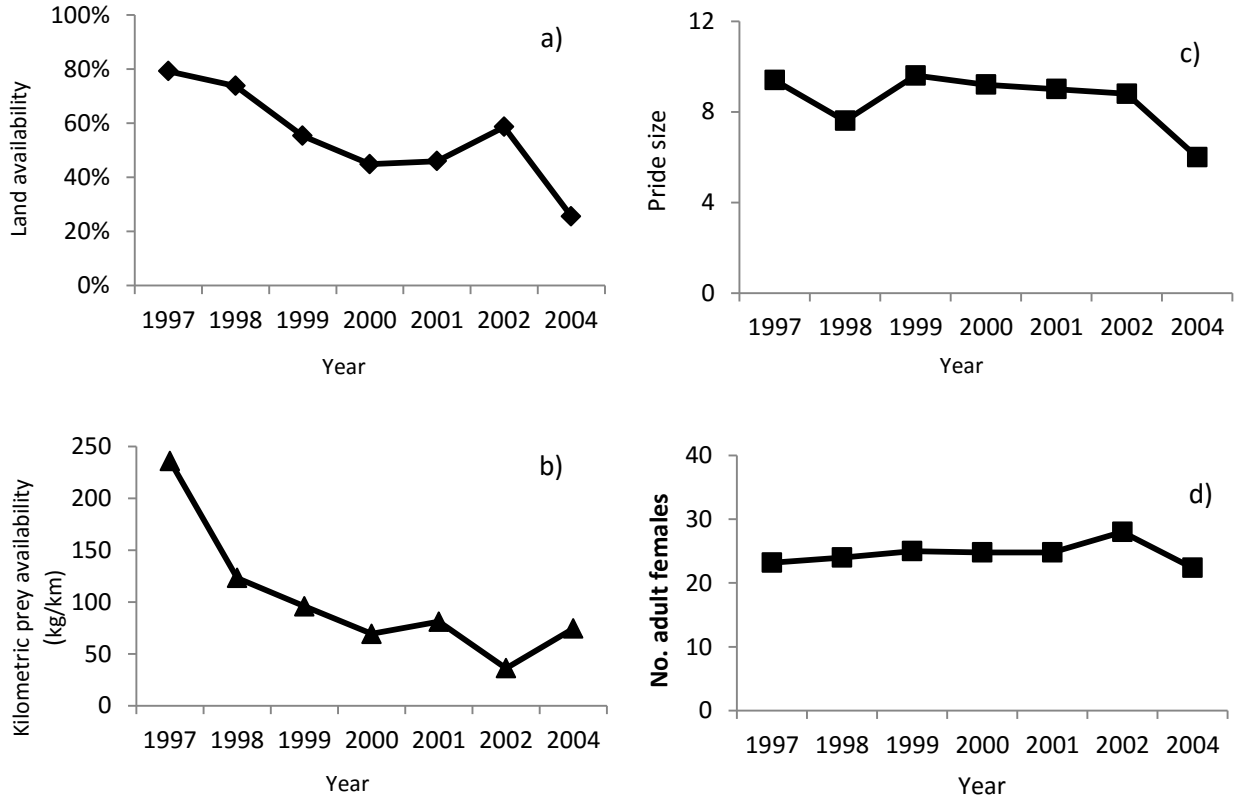


Figure 5. General temporal trends in covariate factors over the study period. a) Average percentage of land available in each home range during the annual flood peak, b) average prey availability, measured in kilograms of biomass per kilometre, in each pride's home range, c) average pride size (adults and sub-adults included) in the study population and d) the average number of competing adult female lions in the study area.

Table 7. Baseline models and covariate models examining temporal variation in survival for cub and sub-adult lions. Subscripts for covariates indicate whether the covariates are classified as social ($_S$) or environmental ($_E$). QAICc = quasi-likelihood model ranking for small sample size, K=number of parameters in each model, Dev=model deviance, Δ(t-cov)=difference in QAICc for time-varying and covariate model for each age group, Δ(cov-t)=difference in QAICc between covariate and time-varying reference model, Δ(cov-cst)=difference in QAICc between constant and covariate models. Numbers in bold indicate covariates that are considered statistically significant and account for more than 20% of the variation in survival.

Cub and sub-adult survival	**QAICc**	**k**	**Dev**	**ĉ**	**Δ(cov-t)**	**Δ(cov-cst)**	**%Dev**
Baseline models							
Constant sub-adult (φ(t/./.)p(t))	351.77	19	466.60	1.5			
Constant cub (φ(./t/.)p(t))	355.73	19	472.54	1.5			
Time-varying (φ(t/t/.)p(t))	359.02	24	460.01	1.5			
Covariates for cub age-group							
Prey availability$_E$	352.24	19	467.30	1.5	-6.78	**-3.50**	**41.85**
Competition$_S$	352.28	19	467.36	1.5	-6.74	**-3.45**	**41.31**
Flood$_E$	355.31	19	471.91	1.5	-3.71	-0.42	5.05
Pride size$_S$	355.46	19	472.13	1.5	-3.56	-0.27	3.29
Covariates for sub-adult age-group							
Pride size$_S$	349.21	19	462.75	1.5	-9.81	**-2.56**	**58.33**
Flood$_E$	351.66	19	466.43	1.5	-7.36	-0.11	2.46
Prey availability$_E$	351.71	19	466.50	1.5	-7.31	-0.06	1.39
Competition$_S$	351.73	19	466.54	1.5	-7.29	-0.04	0.84

References

Altwegg, R., Dummermuth, S., Anholt, B.R. & Flatt, T.L. 2005. Winter weather affects asp viper *Vipera aspis* population dynamics through susceptible juveniles. *Oikos*, 110, 55-66.

Anderson, D.R. & Burnham, K.P. 2002. Avoiding pitfalls when using information-theoretic methods. *Journal of Wildlife Management*, 66, 912-918.

Barton, K. 2013. *MuMIn: multi-model inference*. R Package Version 1.12.1. CRAN R Project. Available from http://CRAN.R-project.org/package=MuMIn (accessed May 2015).

Bates D. M., Mächler M., Bolker B. M., Walker S. C. 2014. *lme4: Linear Mixed-Effects Models Using Eigen and S4*. R Package Version 1.1-7. Available from: http://CRAN.R-project.org/package=lme4 (accessed May 2015).

Bauer, H., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L.T.B, Macdonald, D. & Packer, C. 2015. Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proceedings of the National Academy of Sciences*, 112, 14894-14899.

Becker, M.S., Watson, F.G.R., Dröge, E., Leigh, K., Carlson, R.S. & Carlson, A.A. 2012. Estimating past and future male loss in three Zambian lion populations. *Journal of Wildlife*, 77, 128-142.

Bertram, B.C.B. 1975. Social factors influencing reproduction in wild lions. *Journal of Zoology, London*, 177, 463–482.

Bertram, B.C.R. 1973. Lion population regulation. *East African Wildlife Journal*, 11, 215-225.

Björkland, M. 2003. The risk of inbreeding due to habitat loss in the lion (*Panthera leo*). *Conservation Genetics*, 4, 515-523.

Bolker, B.M. 2008. *Ecological models and data in R*. Princeton: Princeton University Press.

Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S. & Colson, T. 2006. Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology*, 75, 1393-1405.

Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multimodal Inference: A Practical Information-Theoretic Approach, 2nd ed*. New York: Springer-Verlag

Bygott, J.D., Bertram, B.C.R. & Hanby, J.P. 1979. Male lions in large coalitions gain reproductive advantages. *Nature*, 26, 839-841.

Celesia, G.G., Peterson, A.T., Peterhans, J.C.K. & Gnoske, T.P. 2009. Climate and landscape correlates of African lion (*Panthera leo*) demography. *African Journal of Ecology*, 48, 58-71.

Chase, M. & Landen, K. 2011. A view from the top. *Africa Geographic*, 19, 38-47.

Clark, A.B. 1978. Sex ratio and local resource competition in a prosimian primate. *Science*, 201, 163-165.

Crawshaw, P.G. Jnr & Quigley, H.B. 1991. Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. *Journal of Zoology, London*, 223, 357-370.

Creel, S. & Creel, N. M. (1997) Lion density and population structure in the Selous Game Reserve: evaluation of hunting quotas and offtake. *African Journal of Ecology*, 35, 83-93.

De Boer, W.F., Vis, M.J.P, De Knegt, H.J., Rowles, C., Kohi, E.M., Van Lagevelde, F., Peel,M., Pretorius, Y., Skidmore, A.K., Slotow, R., Van Wieren, S.E. & Prins, H.H.T. 2010. Spatial distribution of lion kills determined by water dependency of prey species. *Journal of Mammalogy*, 91, 1280-1286.

Devenish-Nelson, E.S., Harris, S., Soulsbury, C.D., Richards, S. & Stephens, P.A. 2012. Demography of a carnivore, the red fox, *Vulpes vulpes*, what have we learnt from 70 years of published studies? *Oikos*, 122, 705-716.

Dybala, K.E., Eadie, J.M., Gardali, T., Seavy, N.E. & Herzog, M.P. 2013. Projecting demographic responses to climate change: adult and juvenile survival respond differently to direct and indirect effects of weather in a passerine population. *Global Change Biology*, 19, 2688-2697.

Emlen, S.T., Emlen, J.M. & Levin, S.A. 1986. Sex-ratio selection in species with helpers-at-the-nest. *American Naturalist*, 127, 1-8.

Emmerson, L. & Southwell, C. 2011. Adélie penguin survival: age structure, temporal variability and environmental influences. *Oecologia*, 167, 951-965.

Forcada, J., Trathan, P.N. & Murphy, E.J. 2008. Life history buffering in Antarctic mammals and birds against changing patterns of climate and environmental variation. *Global Change Biology*, 14, 2473-2488.

Fuller, T.K. & Sievert, P.R. 2001. Carnivore demography and the consequences of changes in prey availability. In: *Carnivore Conservation*. (Ed by J.L. Gittleman, S.M. Funk, D.W.Macdonald and R.K. Wayne) pp. 163-178. Cambridge: Cambridge University Press and the Zoological Society of London.

Funston, P.J. & Hermann, E. 2001. Kalahari Transfrontier Lion Project. *Population ecology and demography of lions in the Kgalagadi Trasfrontier Park –adaptations and prospects of survival in a harsh environment.* Endangered Wildlife Trust, Upington, South Africa.

Funston, P.J., Mills, M.G.L., Richardson, P.R.K. & Van Jaarsveld, A.S. 2003. Reduced dispersal and opportunistic territory acquisition in male lions (*Panthera leo*). *Journal of Zoology, London,* 259, 131-142.

Gaillard, J.M., Festa-Bianchet, M. & Yoccoz, N.G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution,* 13, 58-63.

Getz, W.M., Fortmann-Roe, S., Cross, P.C., Lyons, A.J., Ryan, S.J. & Wilmers, C.C. 2007. LoCoH: Non-parametric kernel methods for constructing home ranges and utilization distributions. *PLoS One,* 2, e207. doi: 10.1371/journal.pone.0000207.

Gimenez, O., Lebreton, J-D., Gaillard, J-M., Choquet, R & Pradel, R. 2012. Estimating demographic parameters using hidden process dynamic models. *Theoretical Population Biology,* 82, 307-316.

Grosbois, V., Gimenez, O., Gaillard, G.M., Pradel, R., Barbraud, C., Clobert, J., Møller, A.P. & Weimerskirch, H. 2008. Assessing the impact of climatic variation on survival in vertebrate populations. *Biological Reviews,* 83, 357-399.

Gumbricht, T.P., Wolski, P.F. & McCarthy, T.S. 2004. Forecasting the spatial extent of the annual flood in the Okavango Delta, Botswana. *Journal of Hydrology,* 290, 178-191.

Guthery, F.S., Brennan, L.A., Peterson, M.J. & Lusk, J.J. 2005. Information theory in wildlife science: critique and viewpoint. *Journal of Wildlife Management,* 69, 457-465.

Haber, G.C. 1996. Biological, conservation and ethical implications of exploiting and controlling wolves. *Conservation Biology,* 10, 1068-1081.

Hanby, J. P., Byggot, J.D. & Packer, C. 1995. Ecology, demography, and behaviour of lions in two contrasting habitats: Ngorongoro Crater and the Serengeti plains. In: *Serengeti II: dynamics, management, and conservation of an ecosystem.* (Ed. By A.R.E. Sinclair and P. Arcese) pp. 315-331. Chicago: Chicago University Press.

Hanby, J.P. & Bygott, J.D. 1987. Emigration of sub-adult lions. *Animal Behaviour,* 35, 161-169.

Hanby, J.P. & Bygott, J.D. 1979. Population changes in lions and other predators. In: *Serengeti: Dynamics of an Ecosystem* (Ed by A.R.E. Sinclair and M. Norton-Griffiths) pp. 249-262. Chicago: Chicago University Press.

Hanby, J.P. & Bygott, J.D. 1991. Lions. In: *Great Cats.* (Ed by J. Seidensticker and K. Lumpkin) pp.80-93. Pennsylvania: Rodale Press.

Hayward, M. W., O'Brien, J. & Kerley, G. I. H. 2007. Carrying capacity of large African predators: predictions and tests. *Biological Conservation*, 139, 219-229.

Hayward, M.W. & Kerley, G.I.H. 2005. Prey preferences of the lion (*Panthera leo*). *Journal of Zoology*, 267, 309-322.

Heinsohn, R., Packer, C. & Pusey, A.E. 1996. Development of co-operative territoriality in juvenile lions. *Proceedings of the Royal Society of London, Series B*, 263, 475-479.

IUCN. 2006. Regional conservation strategy for the lion *Panthera leo* in eastern and southern Africa. IUCN SSC Cat Specialist Group, Yaounde, Cameroon.

Junk, W. J., Bayley, P. B. & Sparks, R. E. 1989. The flood-pulse concept in river-floodplain systems. *Canadian special publication of fisheries and aquatic sciences*, 106, 110-127.

Kelly, M.J., Laurenson, M.K., Fitzgibbon, C.D., Collins, D.A., Durant, S.M., Frame, G.W., Bertram, B.C.R. & Caro, T.M. 1998. Demography of the Serengeti cheetah (*Acinonyx jubatus*) population: the first 25 years. *Journal of Zoology, London*, 244, 473-488.

Kéry, M., Masden, J., Lebreton, J-D. 2006. Survival of Svalbard pink-footed geese *Anser brachyrhynchus* in relation to winter climate, density and land-use. *Journal of Animal Ecology*, 75, 1172-1181.

Kie, J.G. 2013. A rule-based *ad hoc* method for selecting a bandwidth in kernel home-range analyses. *Animal Biotelemetry*, 2013, 1-13.

Kiffner, C., Meyer, B., Muhlenberg, M., & Waltert, M. 2009. Plenty of prey, few predators: what limits lions *Panthera leo* in Katavi National Park, western Tanzania. *Oryx*, 43, 52-59.

Laake, J.L. 2013. *RMark: An R Interface for Analysis of Capture-Recapture Data with MARK.* ASFC Processed Report 2013-01. Alaska Fisheries Science Centre, NOAA, National Marine Fisheries Service, Seattle, WA.

Lebreton, J.D., Burnham, K.P, Clobert, J. & Anderson, D.R. 1992. Modelling survival and testing biological hypothesis using marked animals: a unified approach with case studies. *Ecological Monographs*, 62, 67-118.

Lindholm, M., Hessen, D. O., Mosepele, K. & Wolski, P. (2007) Food webs and energy fluxes on a seasonal floodplain: the influence of flood size. *Wetlands*, 27, 775-784.

Loveridge, A.J., Searle, A.W., Murindagomo, F. & Macdonald, D.W. 2007. The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biological Conservation,* 134,548-558.

Loveridge, A.J., Valeix, M., Davidson, Z., Murindagomo, F. Fritz, H. & Macdonald, D. 2009. Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savannah. *Ecography,* 32, 953-962.

Mazvimavi, D., & Wolski, P. 2006. Long-term variations of annual flows of the Okavango and Zambezi Rivers. *Physics and Chemistry of the Earth, Parts A/B/C,* 31, 944-951.

McCarthy, T. S., Cooper, P.D., Tyson, P. D. & Ellery, W. N. 2000. Seasonal flooding in the Okavango Delta, Botswana – recent history and future prospects. *South African Journal of Science,* 96, 25-33.

McCarthy, T.S. & Ellery, W.N. 1998. The Okavango Delta. *Transactions of the Royal Society of South Africa,* 53, 157-182.

Midlane, N. 2013. The conservation status and dynamics of a protected African lion *Panthera leo* population in Kafue National Park, Zambia. PhD Thesis. University of Cape Town.

Miller, S.M. & Funston, P.J. 2014. Rapid growth rates of lion (*Panthera leo*) populations in small, fenced reserves in South Africa: a management dilemma. *South African Journal of Wildlife Research,* 44, 43-55.

Mills, L. S., Doak, D. F. & Wisdom, M. J. 1999. Reliability of conservation actions based on elasticity analysis of matrix models. *Conservation Biology*, 13, 815–829.

Mills, M.G.L., Wolff, P., Le Riche, E.A.N. & Meyer, I.J. 1978. Some population characteristics of the lion *Panthera leo* in the Kalahari Gemsbok National Park. *Koedoe,* 21, 163-171.

Mosser, A. 2008. Group territoriality of the African lion: behavioural adaptation in a heterogeneous landscape. PhD Thesis. University of Minnesota.

Mosser, A. & Packer, C. 2009. Group territoriality and the benefits of sociality in the African lion, *Panthera leo. Animal Behaviour,* 78, 359-370.

Murray-Hudson, M. 2009. Floodplain vegetation responses to flood regime in the seasonal Okavango Delta, Botswana. PhD Thesis. University of Florida.

Murray-Hudson, M. M., Wolski, P., Murray-Hudson, F., Brown, M. T. & Kashe, K. 2014a. Disaggregating hydroperiod: componenets of the seasonal flood pulse as drivers of plant species distribution in floodplains of a tropical wetland. *Wetlands,* 34, 927-942.

Murray-Hudson, M.M, Wolski, P., Cassidy, L., Brown, M.T., Thito, K., Kashe, K. & Mosimanyana, E. 2014b. Remote sensing-derived hyrdoperiod as a predictor of floodplain vegetation composition. *Wetlands Ecology and Management*, 23, 603-616.

O' Kochanny, C.O., Delgiudice, G.D. & Fieberg, J. 2009. Comparing global positioning system and very high frequency telemetry home ranges of white-tailed deer. *Journal of Wildlife Management*, 73, 779-787.

Ogutu, J. O. & Dublin, H.T. 2002. Demography of lions in relation to prey and habitat in the Masai Mara National Reserve, Kenya. *African Journal of Ecology*, 40, 120-129.

Ogutu, J.O., Piepho, H-P., Dublin, H.T., Reid, R.S. & Bhola, N. 2006. Application of mark-recapture methods to lions: satisfying assumptions by using covariates to explain heterogeneity. *Journal of Zoology*, 269, 161-174.

Orford, H.J.L., Perrin, M.R. & Berry, H.H. 1988. Contraception, reproduction and demography of free-ranging Etosha lions (*Panthera leo*). *Journal of Zoology, London*, 216, 717-733.

Ordiz, A., Støen, O.G., Swenson, J.E., Kojola, I. & Bischof, R. 2008. Distance-dependent effect of the nearest neighbour: spatiotemporal patterns in brown bear reproduction. *Ecology*, 38, 3327-3335.

Owen-Smith, N. 2015. Mechanisms of coexistence in diverse herbivore-carnivore assemblages: demographic, temporal and spatial heterogeneities affecting prey availability. *Oikos*, 124, 1417-1426.

Packer, C., Herbst, L., Pusey, A.E., Bygott, J.D., Hanby, J.P., Cairns, S.J. & Borgehoff-Mulder, M. 1988. Reproductive success of lions. In: *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems* (Ed by T.H. Clutton-Brock) pp 363-383. Chicago: University of Chicago Press.

Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, J., Mduma, S. & Sinclair, A.R.E. 2005. Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science*, 436, 927-928.

Packer, C., Pusey, A.E. & Eberly, L. E. 2001. Egalitarianism in female African lions. *Science*, 293, 690-693.

Packer, C., Scheel, D. & Pusey, A.E. 1990. Why lions form groups: food is not enough. *American Naturalist*, 136, 1-19.

Patterson, B.D. 2007. On the nature and significance of variability in lions (*Panthera leo*). *Evolutionary Biology*, 34, 55-60.

Pennycuick, C.J. & Rudnai, J. 1970. A method of identifying individual lions *Panthera leo* with an analysis of the reliability of identification. *Journal of Zoology, London,* 160, 497-508.

Portier, C., Gaillard, J., Jorgenson, J.T. & Yoccoz, N.G. 1998. Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). *Journal of Zoology,* 245, 271-278.

Pusey, A.E. & Packer, C. 1987. The evolution of sex-biased dispersal in lions. *Behavior,* 101, 275-310.

R Core Development Team. 2014. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Vienna, Austria.

Ramberg, L., Hancock, P., Lindholm, M., Meyer, T., Ringrose, S., Silva, J., Van As, J. & Vanderpost, C. 2006. Species diversity in the Okavango Delta, Botswana. *Aquatic Sciences,* 68, 310-337.

Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., Funston, P., Groom, R., Henschel, P., De Iongh, H., Lichtenfeld, L. & Pimm, S. 2013. The size of savannah Africa: a lion's (*Panthera leo*) point of view. *Biodiversity Conservation,* 22, 17-35.

Roelke-Parker, M.E., Munson, L., Packer, C., Kock, R., Cleveland, S., Carpenter, M., O'Brien, S.J., Popsichil, A., Hofmann-Lehmann, R., Lutz, H., Mwamengele, G.L.M., Mgasa, M.N., Machange, G.A., Summers, B.A. & Appel, M.J.G. 1996. A canine distemper virus epidemic in Serengeti lions (*Panthera leo*). *Nature,* 379, 441-445.

Ruggiero, L.F., Hayward, G.D. & Squires, J.R. 1994. Viability analysis in biological evaluations: concepts of population viability analysis, biological population, and ecological scale. *Conservation Biology,* 8, 364-372.

Schaller, G. B. 1972. *The Serengeti lion: a study of predator prey relations*. Chicago: Chicago University Press.

Schielzeth, H. 2010. Simple means to improve interpretability of regression coefficients. *Methods in Ecology and Evolution,* 1, 103-113.

Skalski, J.R. 1996. Regression of abundance estimates from mark-recapture surveys against environmental covariates. *Canadian Journal of Fisheries and Aquatic Sciences,* 53, 196-204.

Smuts, G.L. 1976. Population characteristics and recent history of lions in two parts of the Kruger National Park. *Koedoe,* 19, 153-164.

Smuts, G.L. 1982. *Lion*. Johannesburg: Macmillan.

Smuts, G.L., Hanks, J. & Whyte, I.J. 1978. Reproduction and social organisation of lions from the Kruger National Park. *Carnivore,* 1, 17-28.

Spong, G. 2002. Space use in lions, *Panthera leo,* in the Selous Game Reserve: social and ecological factors. *Behavioural Ecology and Sociobiology,* 52, 303-307.

Stander, P.E. 1991. Demography of lions in the Etosha National Park, Namibia. *Madoqua,* 18, 1-9.

Symonds, M.R.E & Moussalli, A. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Aikaike's Information Criterion. *Behavioural Ecology and Sociobiology,* 65, 13-21.

Trinkel, M., Funston, P., Hofmeyr, M., Hofmeyr, D., Dell, S., Packer, C. & Slotow, R. 2010. Inbreeding and density-dependent population growth in a small, isolated lion population. *Animal Conservation,* 13, 374–382.

Trinkel, M., Van Niekerk, R.W., Fleischmann, P.H., Ferguson, N. & Slotow, R. 2007. The influence of vegetation on lion *Panthera leo* group sizes in the Hluhluwe-Umfolozi Park, South Africa. *Acta Zoologica Sinica,* 53, 15-21.

Valeix, M., Loveridge, A.J., Chamaillé-James, S., Davidson, Z., Murindagomo, F. Fritz, H. & Macdonald, D.W. 2009. Behavioural adjustments of African herbivores to predation risks by lions: spatiotemporal variations influence habitat use. *Ecology,* 9, 23-30.

Van Der Waal, K.L., Mosser, A. & Packer, C. 2009. Optimal group size, dispersal decisions and post-dispersal relationships in female African lions. *Animal Behaviour,* 77, 949-954.

Van Orsdol, K.G. 1984. Foraging behaviour and hunting success of lions in Queen Elizabeth National Park, Uganda. *African Journal of Ecology,* 79-99.

Van Orsdol, K.G., Hanby, J.P. &Bygott, J.D. 1985. Ecological correlates of lion social organisation (*Panthera leo*). *Journal of Zoology, London,* 206, 97–112.

Van Vuuren, J.H., Hermann, E. & Funston, P.J. 2005. Lions in the Kgalagadi Transfrontier Park: modelling the effects of human-caused mortality. *International Transactions in Operational Research,* 12, 145-171.

Vincent, J.P., Gaillard, J.M. & Bideau, E. 1991. Kilometric index as biological indicator for monitoring forest roe deer populations. *Acta thereologica,* 36, 315-328.

Wallach, A.D., Izhaki, I., Toms, J.D., Ripple, W.J. & Shanas, U. 2015. What is an apex predator? *Oikos,* 124, 1453-1461.

Watts, H.E. & Holekamp, K.E. 2009. Ecological determinants of survival and reproduction in the spotted hyena. *Journal of Mammalogy,* 90, 461-471.

White, G.C. & Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. http://www.cnr.colostate.edu/gwhite/software/ht-ml (accessed May 2015).

Whitman, K.L & Packer, C. 2007. *A hunter's guide to aging lions in eastern and southern Africa*. Huntington Beach, CA: Long Beach Press.

Wolski, P. & Murray-Hudson, M.M. 2006a. Recent changes in flooding in the Xudum distributary of the Okavango Delta, and Lake Ngami, Botswana. *South African Journal of Science*, 102, 173-176.

Wolski, P. & Murray-Hudson, M.M. 2006b. Reconstruction of 1989-2005 inundation history in the Okavango Delta, Botswana, from archival Landsat imagery. In: *Globwetland Symposium*, ESA-ESRIN, Frascati, Italy.

Woodroffe, R. & Frank, L.G. 2005. Lethal control of African lions (*Panthera leo*): local and regional population impacts. *Animal Conservation*, 8, 91-98.

Woodroffe, R. & Ginsberg, J. R. (1998) Edge effects and the extinction of populations inside protected areas. *Science*, 280, 2126-2128.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, 70, 164-168.

Worton, B.J. 1995. Using Monte-Carlo simulation to evaluate kernel-based home range estimators. *Journal of Wildlife Management*, 59, 794-800.

Chapter 4

Conclusion

Context

Determining the local drivers of population change for a species such as the lion is an important first step towards effective management and conservation (Karanth & Chellam 2009, Devenish-Nelson 2012). Establishing baseline demographic rates in relation to ecological conditions grants us important insight into how lion populations should fare 'naturally'. When populations deviate from patterns predicted by local ecological conditions, it is often an indication that confounding factors are at work, and more often than not these are anthropogenic in nature (Fuller & Sievert 2001, Kiffner et al. 2009, Everatt et al. 2014). Even within protected areas, activities on park borders such as snaring, illegal baiting for hunting purposes, retaliatory killing for depredation on livestock or diseases contracted from domestic dogs such as rabies or canine distemper, can have far reaching consequences reflected in demographic rates or social organisation of lions even well within the park's boundaries (Funston & Hermann 2001, Kissui & Packer 2004, Loveridge et al. 2007, Kiffner et al, 2009, Everatt et al. 2014).

Collection of baseline demographic data for long-lived and far-ranging species such as lions, however, requires considerable effort and resources (Kelly et al. 1998). The longest running lion project, the Serengeti Lion Project in Tanzania, has collected data continuously on lions since the 1960s (Schaller 1972, Bertram 1973, Hanby & Bygott 1979, Van Orsdol 1985, Pusey & Packer 1987, Packer et al. 1990). Much of what we know about lion social organisation, demographic processes and general ecology stems from this research (Patterson 2007). However, studies in other ecosystems have revealed that there is also considerable variability in lion ecology as a result of adaptation to local ecological conditions (Patterson et al. 2007). The aim of this study was to determine the extent to which inundation patterns, which are unique to wetland systems, affect lion social organisation and demographic rates in the Okavango Delta, as well as determine the relative role of other ecological factors and social factors such as prey availability and competition from conspecifics. The effects of flooding on lion behaviour and ecology have not yet been investigated, and in light of recent genetic

evidence that savannah lions may be descendants of ancestral wetland specialists (Moore et al. 2015), the results of this study may offer important insight into ancestral lion ecology and sociality.

Synopsis and discussion

In large, apex predators such as lions, there is no natural top-down population regulation resulting from predation (Wallach et al. 2015). As a result, populations of large carnivores can be regulated in only two ways – either from resource limitation, or by self-regulation (Kissui & Packer 2004, Wallach et al. 2015). In this study, there is little evidence of bottom-up regulation of lion density and population demographics. While prey availability was identified as an important influence on cub survival, we suggest that this is largely driven by within-pride density dependence, similar to what has been observed in gray wolves (*Canis lupus,* Hayes & Harrestad 2000, Cariappa et al. 2011). At high densities, young females are recruited into prides due to the high costs of dispersal, explaining why pride sizes increased, albeit marginally, despite the decline in prey availability. Extra competition for food within prides, particularly from older cubs and sub-adults, could lead to lower per capita intake for cubs (Bertram 1975, Van Orsdol et al. 1985), ultimately leading to lower cub survival. The lack of further demographic and group size responses to prey availability indicate that the population was more likely intrinsically regulated.

In the absence of resource limitation, apex predators can therefore only be self-regulated. In these cases, mortality, reproductive rate, population density and other demographic processes which determine population growth are limited by social interactions such as territoriality, infanticide, dispersal and reproductive suppression (Hestbeck 1982, Wolff 1997, Wallach et al. 2015). This intrinsic regulation is evident in a number of large carnivore populations including brown bears (*Ursus arctos,* Støen et al. 2005, Ordiz et al. 2008), gray wolves (Messier 1985, Mech 1994), cheetah (*Acinonyx jubatus,* Eaton 1970), Ethiopian wolf (*Canis semensis*, Sillero-Zubiri 1996) and wild dog (*Lycaon pictus,* Malcom & Martin 1982). In this study, intrinsic regulation is clearly evident given that competition with conspecifics regulated pride sizes, led to increased cub mortality, as well as suppressed reproductive rate. Increased cub mortality with more neighbours suggests that the risk of infanticide was a strong driver for females to suppress reproduction until conditions were more

favourable (Wolff 1997, Packer et al. 2001). Alternatively, in the absence of pride males, and likely as a result of the high female to male ratio in the population, some of the young adult males remained in their natal territory until five years of age, which could have resulted in further reproductive suppression to avoid inbreeding (Mech 1970, Sillero-Zubiri 1996, Creel & Waser 1991).

Recent genetic analyses suggest that ancestral lions may have been wetland specialists and that lions spread out and adapted to savannah habitat during arid periods of the Pleistocene (Moore et al. 2015). This study is therefore an important insight into how wetlands, and floods in particular, have shaped lion social behaviour and ecology. In a wetland environment such as the Okavango Delta, dry season flooding of the study area allows for resident prey species, such as lechwe (*Kobus leche*) and reedbuck (*Redunca arundinum*), which would otherwise be absent within the Kalahari ecosystem. The ubiquitous distribution of water as well as the 'green flush' of grass created by receding floods attracts herbivores such as zebra (*Equus burchelli*) and buffalo (*Syncerus caffer*) in large herds in the dry season, resulting in year-round prey availability, and therefore a high density of lions. If the species did indeed evolve in wetland environments, we can tentatively posit that the resulting high densities could have led to the development of sociality in the species. Given such high densities, frequent contact with neighbouring conspecifics would result in high rates of infanticide, as observed in other large carnivore populations such as brown bears (Zedrosser et al. 2009). However, if females were to communally raise cubs under such circumstances, they would increase their chance of reproductive success by reducing the risk of infanticide. Furthermore, by communal hunting, females could also increase individual fitness through higher hunting success rates, and better defence of carcasses against competing conspecifics (Schaller 1972, Bertram 1975, Van Orsdol 1981, Stander 1991). These group benefits not only increase individual fitness directly, but also indirectly through enhanced survival and reproduction of close kin. In such a system, the sex ratios observed in our study, which were skewed towards females, would be advantageous as females would enhance pride success more than males (Pusey & Packer 1987).

In such a high density area, the necessity for defending cubs and pride members would be more important than defence of a strict territory. This would explain why competition is not an important predictor of sub-group sizes in the Okavango Delta. Furthermore, given the ubiquitous distribution of

water during the dry and wet season, and the variable distribution of prey, exclusive territory maintenance would have little advantage, resulting in high home range overlap in the study area. Similar behaviour has been observed in jaguar in the Pantanal in Brazil, where territorial defence is believed to be of little consequence given the complexity of the landscape and the resulting variable distribution of prey caused by seasonal flooding (Crawshaw & Quigley 1999). In the Pantanal, home range overlap is also extensive, but individuals exhibit strong temporal avoidance facilitated by scent marking (Crawshaw & Quigley 1991). We suggest that lions in the Okavango Delta show a similar response to flooding, and most likely achieved temporal avoidance through scent marking and vocalisations (Heinsohn 1997). In contrast, in more arid and mesic systems such as the Serengeti, the variable seasonal distribution of prey in relation to rainfall patterns and the unequal distribution of water sources would make defence of exclusive territories beneficial (McLoughlin et al. 2001). Indeed, prides with the best access to water in savannah habitats have been shown to have higher reproductive success, as herbivores tend to congregate around waterholes and rivers during the dry season (Hanby & Bygott 1979, Mosser 2008, Valeix et al. 2009).

Given this evidence, one could argue that water distribution has played an important role in the development of social behaviour of lions in wetland systems, and that this social behaviour, coupled with territorial behaviour, allowed lions to become successful in savannahs as well. The lack of exclusive territorial defence in the Okavango Delta thus contradicts Mosser and Packer's (2009) assertion that numerical advantage in territorial competition may have been important to the evolution of sociality, particularly if lions were originally wetland specialists. In their investigation of sub-grouping behaviour, they concluded that it would be difficult to distinguish between the relative importance of cub defence and territorial defence, since competition would increase group size in both cases. However, in our study, the opposite effect of competition on number of adult females, and the tendency for group sizes to increase with larger cub cohorts indicates that territorial disputes in the Okavango Delta are indeed secondary to cub defence. Therefore, in this system, communal rearing of cubs, with the aim of reducing infanticide rates, was more likely to play a role in the development of social behaviour.

Conservation implications

The structure of the western Okavango Delta lion populations, in particular the sex ratio, may have important implications for the conservation of the Okavango Delta lion population, especially with regards to offtake and hunting quotas. While the male-depleted population may have been as a result of hunting quotas, sex ratios of cubs were not skewed in favour of males, typical of areas with high offtake (Funston & Hermann 2001, Loveridge et al. 2007). An alternative natural explanation for fewer males may be the extensive overlap in home ranges between competing prides. In this case, male coalitions could easily defend more than one pride simultaneously from other coalitions, again making a sex ratio skewed towards females more beneficial. Whatever the cause, future high offtake of males could have potentially disastrous consequences for the population. Particularly if coalitions cover more than one pride in such a high density area, the loss of a coalition partner could result in the loss of territory by the remaining resident male, resulting in increased infanticide and reduced reproductive success across more than one pride (Loveridge et al. 2007).

Additionally, recent genetic analyses of lions across northern Botswana have revealed that Okavango Delta lions are more isolated than other populations in Botswana (Simon Dures pers. communication). This isolation suggests limited genetic immigration, even from close Kalahari populations less than 500km south of the Okavango Delta (Moore et al. 2015). High human population densities in local communities surrounding the Okavango Delta and high levels of retaliatory killing for cattle depredation further limit dispersal potential (Elliot 2014), and thus increase the chance of inbreeding. If male offtake was unsustainable, and given the tendency of young males to remain in their natal territory until adulthood in the absence of pride males in the Okavango Delta, inbreeding may be further enhanced. While lion hunting was banned in Botswana in 2007, and hunting of all species in 2013, the resumption of lion hunting would require quotas set for adult males to be low for the Okavango Delta in comparison to other systems, and a strict age limit enforced to prevent young males from being killed before successfully rearing their cubs to adulthood (Whitman & Packer 2007).

While prey did not limit lion densities during the study period, the overall decrease in prey availability revealed by recent aerial surveys of the Okavango Delta would be a cause for concern (Chase & Landen 2011). The Okavango Delta lion population is currently in decline (Bauer et al. 2015), with a decline in prey availability believed to be the main cause. Increasing flood levels have been one of the major factors contributing to population declines of large grazing herbivores (Burger et al., in press), which fall within the lions preferred prey weight range. This may cause a shift from competition to prey density as the main regulator of lion population growth in the Okavango Delta. Similar declines have been observed in other wetland habitats such as Busanga Plains in Kafue National Park, Zambia (Midlane et al. 2013). In Zambia, while the floodplains are highly productive resulting in year-round prey base, the proximity of human populations to the park and the resultant snaring from bush-meat poaching keeps lion densities well below their carrying capacity (Midlane 2103). As increasing floods result in lower cub survival in Kafue (Midlane 2013), and as we posit there is a similar trend in the Okavango Delta, wetland lion populations are particularly vulnerable to extra anthropogenic pressure during phases of high flood. While lion and prey populations should theoretically recover again with drier flood years, their rebound may be suppressed by anthropogenic pressure. The erection of the veterinary fence around the Delta, while vital in preventing overgrazing from cattle, has similarly prevented the supplementation of resident herbivore herds by migration from surrounding drier areas (Bartlam-Brooks et al. 2013). Increased encroachment by local villagers into the edges of the Delta increases human-lion conflict and thus retaliatory killings of lions (pers. observation). This edge effect could result in a decline of the Okavango Delta population as a whole, and requires further investigation.

Study limitations and future areas of research

This study has presented clear results on the influence of social and ecological factors on lion demography and group structure, but it is not without its drawbacks. Firstly, the use of VHF telemetry, although the most reliable long-term method of tracking lions at the time, could underestimate the extent of home ranges used, and so over-estimate overlap. Furthermore, while there is annual overlap which seems suggestive of low overall territorial behaviour, an examination of VHF derived locations reveals that there is temporal, seasonal exclusivity of range use. However, VHF

points collected and herbivore counts were not extensive enough for a comprehensive seasonal comparison. Secondly, the use of social and ecological predictors, calculated on an annual basis, may underestimate the importance of seasonal drivers of social behaviour and population demographic processes. Furthermore, while prey availability proved important in shaping social behaviour and cub survival, its effect may have been diluted by using data of prey counting in August to November, when in fact the leanest season occurs from February to April. Again, this is the result of difficulty in consistent sampling in wetland environments, and so the season where sampling was most consistent was chosen. However, we maintain that prey availability would remain secondary to competition in influencing population demographics and overall pride sizes. Annual measures of predictors also limited survival analyses to only six recapture events. If seasonal data was more extensive, capture histories could have been divided into shorter intervals, allowing for more accurate estimations of survival rates.

The seasonal effects of shifting water and prey distribution remain lacking in the investigation of the effects of flooding on lion ecology in wetland systems, and should be an area of research for the future. Additionally, a comparison in lion social behaviour and population demographics in current, lower density conditions would be important in revealing the current ranking of ecological and social factors in determining lion social behaviour and population dynamics. Furthermore, given the low densities of males in the system, and the reported genetic isolation of the Okavango Delta, future studies should focus on how males fare in wetland systems, and whether the sex ratio is still largely in favour of females. Studies should also focus on how social, ecological and anthropogenic factors impact on their dispersal patterns and decisions. This is emerging as an important area of research to ensure connectivity between increasingly isolated populations of large carnivores, and thus their long-term viability (Elliot 2014).

Conclusion

This study has provided the first evidence of how flooding patterns can have a large influence on lion social behaviour, and in turn demographics. The wetland system with year-round prey base allows for high lion densities, and this agrees with other studies that have shown how landscape-scale abiotic

factors such as rainfall, soil nutrients and annual mean temperature are important determinants of lion population demographics (see Celesia et al. 2009). At such high lion densities, lion survival and reproduction is largely driven by competition from neighbouring conspecifics, and the population is therefore self-regulated. Competition is also the main determinant of pride size, and to a small extent, sub-group size. This system therefore differs from other lion populations where these social and demographic processes are mostly limited by prey availability or by anthropogenic influences (Schaller 1972, Van Orsdol et al. 1985, Kiffner et al. 2009, Everatt et al. 2014). As lions are now believed to have been wetland specialists before diversifying into savannah specialists (Moore et al. 2015), this study provides important insight into ancestral lion ecology and behaviour. The high densities resulting in wetland habitats may have played a significant role in causing lion sociality, as co-operation would lead to enhanced reproductive success in an environment with such a high threat of infanticide. Given the potential of this wetland habitat to support high densities of lions, the recent decline in lion populations in the Okavango Delta should be investigated, as it may be one of the most important refuges for lion survival in Africa. Also, given the genetic differences between wetland and savannah lions, considerable conservation effort should be made to maintain this genetically unique population (Moore et al. 2015).

References

Bartlam-Brooks, H.L.A., Beck, P.S.A., Bohrer, G. & Harris, S. 2013. In search of greener pastures: using satellite images to predict the effects of environmental change on zebra migration. *Journal of Geophysical Research: Biogeosciences,* 118, 1427-1437.

Bauer, H., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L.T.B, Macdonald, D. & Packer, C. 2015. Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proceedings of the National Academy of Sciences,* 112, 14894-14899.

Bertram, B.C.B. 1975. Social factors influencing reproduction in wild lions. *Journal of Zoology, London,* 177, 463–482.

Bertram, B.C.R. 1973. Lion population regulation. *East African Wildlife Journal,* 11, 215-225.

Cariappa, C.A., Oakleaf, J.K., Ballard, W.B. & Breck, S.W. 2011. A reappraisal of the evidence for regulation of wolf populations. *The Journal of Wildlife Management,* 75, 726-730.

Celesia, G.G., Peterson, A.T., Peterhans, J.C.K. & Gnoske, T.P. 2009. Climate and landscape correlates of African lion (*Panthera leo*) demography. *African Journal of Ecology,* 48, 58-71.

Chase, M. & Landen, K. 2011. A view from the top. *Africa Geographic,* 19, 38-47.

Crawshaw, P.G. Jnr & Quigley, H.B. 1991. Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. *Journal of Zoology, London,* 223, 357-370.

Creel, S.R. & Waser, P.M. 1991. Failure of reproductive suppression in dwarf mongooses (*Helogale parvula*): accident or adaptation? *Behavioral Ecology,* 2, 7-15.

Devenish-Nelson, E.S., Harris, S., Soulsbury, C.D., Richards, S. & Stephens, P.A. 2013. Demography of a carnivore, the red fox, *Vulpes vulpes,* what have we learnt from 70 years of published studies? *Oikos,* 122, 705-716.

Eaton, R.L. 1970. Group interactions, spacing and territoriality in cheetahs. *Zeitschrift für Tierpsychologie,* 27, 481-491.

Elliot, N.B. 2014. The ecology of dispersal in lions (*Panthera leo*). DPhil. University of Oxford.

Everatt, K.T., Andersen, L. & Somers, M.J. 2014. Trophic scaling and occupancy analysis reveals a lion population limited by top-down anthropogenic pressure in the Limpopo National Park, Mozambique. *PLoS One,* 9, e99389.

Fuller, T.K. & Sievert, P.R. 2001. Carnivore demography and the consequences of changes in prey availability. In: *Carnivore Conservation*. (Ed by J.L. Gittleman, S.M. Funk, D.W.Macdonald

and R.K. Wayne) pp. 163-178. Cambridge: Cambridge University Press and the Zoological Society of London.

Funston, P.J. & Hermann, E. 2001. Population ecology and demography of lions in the Kgalagadi Trasfrontier Park - adaptations and prospects of survival in a harsh environment. *Kalahari Transfrontier Lion Project*. Endangered Wildlife Trust, Upington, South Africa.

Hanby, J.P. & Bygott, J.D. 1979. Population changes in lions and other predators. In: *Serengeti: Dynamics of an Ecosystem* (Ed by A.R.E. Sinclair and M. Norton-Griffiths) pp.249-262. Chicago: Chicago University Press.

Hayes, R. D. & Harestad A. S. 2000. Demography of a recovering wolf population in the Yukon. *Canadian Journal of Zoology*, 78, 36-48.

Heinsohn, R. 1997. Group territoriality in two populations of African lions. *Animal Behaviour*, 53, 1143-1147.

Hestbeck, J.B. 1982. Population regulation of cyclic mammals: the social fence hypothesis. *Oikos*, 39, 157-163.

Karanth, K. & Chellam, R. 2009. Carnivore conservation at the crossroads. *Oryx,* 43, 1-2.

Kelly, M.J., Laurenson, M.K., Fitzgibbon, C.D., Collins, D.A., Durant, S.M., Frame, G.W., Bertram, B.C.R. & Caro, T.M. 1998. Demography of the Serengeti cheetah (*Acinonyx jubatus*) population: the first 25 years. *Journal of Zoology, London*, 244, 473-488.

Kiffner, C., Meyer, B., Muhlenberg, M., & Waltert, M. 2009. Plenty of prey, few predators: what limits lions *Panthera leo* in Katavi National Park, western Tanzania. *Oryx,* 43, 52-59.

Kissui, B.M. & Packer, C. 2004. Top-down regulation of a top predator: lions in the Ngorongoro Crater. *Proceedings of the Royal Society of London, B. Biological Sciences*, 271, 1867-1874.

Loveridge, A.J., Searle, A.W., Murindagomo, F. & Macdonald, D.W. 2007. The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biological Conservation*, 134,548-558.

Malcom, J.R. & Martin, K. 1982. Natural selection and the communal rearing of pups in African Wild dogs (*Lycaon pictus*). *Behavioral ecology and sociobiology*, 10, 1-13.

McLoughlin, P. D., Ferguson, S. H. & Messier, F. 2001. Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations. *Evolutionary Ecology*, 14, 39–60.

Mech, L.D. 1970. *The Wolf*. Chicago: University of Chicago Press.

Mech, D. L. 1994. Buffer zone of territories of gray wolves as regions of interspecific strife. *Journal of Mammalogy*, 75, 199-202.

Messier, F. 1985. Social organization, spatial distribution, and population density of wolves in relation to moose density. *Canadian Journal of Zoology,* 63, 1068-1077.

Midlane, N. 2013. The conservation status and dynamics of a protected African lion *Panthera leo* population in Kafue National Park, Zambia. PhD Thesis. University of Cape Town.

Moore, A.E., Cotterill, F.P.D., Winterbach, C.W., Winterbach, E.K., Antunes, A. & O'Brien, S.J. 2015. Savannah habitat specializations in different populations of lions. *Journal of Heredity*, esv097.

Mosser, A. 2008. Group territoriality of the African lion: behavioural adaptation in a heterogeneous landscape. PhD Thesis. University of Minnesota.

Mosser, A. & Packer, C. 2009. Group territoriality and the benefits of sociality in the African lion, *Panthera leo. Animal Behaviour*, 78, 359-370.

Ordiz, A., Støen, O.G., Swenson, J.E., Kojola, I. & Bischof, R. 2008. Distance-dependent effect of the nearest neighbour: spatiotemporal patterns in brown bear reproduction. *Ecology*, 38, 3327-3335.

Packer, C., Pusey, A.E. & Eberly, L. E. 2001. Egalitarianism in female African lions. *Science*, 293, 690-693.

Packer, C., Scheel, D. & Pusey, A.E. 1990. Why lions form groups: food is not enough. *American Naturalist,* 136, 1-19.

Patterson, B.D. 2007. On the nature and significance of variability in lions (*Panthera leo*). *Evolutionary Biology*, 34, 55-60.

Pusey, A.E. & Packer, C. 1987. The evolution of sex-biased dispersal in lions. *Behavior,* 101, 275-310.

Schaller, G. B. 1972. *The Serengeti lion: a study of predator prey relations*. Chicago: Chicago University Press.

Sillero-Zubiri, C., Gottelli, D. & Macdonald, D.W. 1996. Male philopatry, extra-pack copulations and inbreeding avoidance in Ethiopian wolves, Canis simensis. *Behavioral Ecology and Sociobiology*, 38, 331-340.

Stander, P.E. 1991. Demography of lions in the Etosha National Park, Namibia. *Madoqua,* 18, 1-9.

Støen, O. G., Bellemain, E., Sæbø, S. & Swenson, J. E. 2005. Kin-related spatial structure in brown bears *Ursus arctos*. *Behavioral Ecology and Sociobiology*, 59, 191-197.

Valeix, M., Loveridge, A.J., Chamaillé-James, S., Davidson, Z., Murindagomo, F. Fritz, H. & Macdonald, D.W. 2009. Behavioural adjustments of African herbivores to predation risks by lions: spatiotemporal variations influence habitat use. *Ecology*, 9, 23-30.

Van Orsdol, K. G. 1981. Lion predation in Rwenzori National Park. PhD Thesis. Cambridge University, Cambridge.

Van Orsdol, K.G., Hanby, J.P. & Bygott, J.D. 1985. Ecological correlates of lion social organisation (*Panthera leo*). *Journal of Zoology, London*, 206, 97–112.

Wallach, A.D., Izhaki, I., Toms, J.D., Ripple, W.J. & Shanas, U. 2015. What is an apex predator? *Oikos*, 124, 1453-1461.

Whitman, K.L & Packer, C. 2007. *A hunter's guide to aging lions in eastern and southern Africa*. Huntington Beach, CA: Long Beach Press.

Wolff, J.O. 1997. Population regulation in mammals: an evolutionary perspective. *Journal of Animal Ecology*, 66, 1-13.

Zedrosser, A., Dahle, B., Støen, O.G. & Swenson, J.E. 2009. The effects of primiparity on reproductive performance in the brown bear. *Oecologia*, 160, 847–854.