The Ecology of Dispersal in Lions

(*Panthera leo*)

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> *"There are two species of lions: The Bhubesi and the Ilawu. Bhubesis are the big ones, with big manes. You don't need to worry about them. The Ilawus are the small ones, with little manes. These ones are too cheeky and will kill your livestock".*
>
> - Paraphrased from a conversation with Miti

Many Ndebele people believe that there are two types of lions. The Bhubesi, despite being big and powerful is not to be feared, for he will rarely attack either man or livestock. The Ilawu is small, with little mane. He is the one that people fear because he is "too cheeky". That the Ilawu grows up to become a Bhubesi is not recognised, simply because the Ilawu is bad and cannot change. Generations of livestock herders have realised that it is the Ilawus, the young lions, the dispersers, that cause problems and kill their livestock and thus two different types of lions are engrained in the culture. People living with wildlife often have an intrinsic awareness of ecological systems that academics ignore at their peril.

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Abstract

As ecosystems become increasingly fragmented, there has been a proliferation of research into fields such as resource use, movement ecology and habitat connectivity. To understand how species may adapt to threats associated with habitat fragmentation it is necessary to study these processes in dispersing individuals. However, this is seldom done. Dispersal is one of the most important life-history traits involved in species persistence and evolution, but the consequences of dispersal are determined primarily by those that survive to reproduce. Although dispersal is most effectively studied as a three-stage process (departure, transience and settlement), empirical studies rarely do so and an investigation into the entire process has probably never been carried out on any one species. Here I investigate the survival, resource use, movement ecology and connectivity of African lions (*Panthera leo*) in all three dispersal phases in addition to adulthood. I make use of a long-term dataset incorporating radio-telemetry and observational data from lions in Hwange National Park, Zimbabwe. Dispersal is inherently risky and my results show that male lions that disperse while young suffer high mortality, young dispersal being brought about by high off-take of territorial males. Dispersing males may be aware of risks associated with territorial adults as they position themselves far from them and utilise habitats and resources differently. However, dispersers, compared to adult males and females, are far less averse of risky, anthropogenic landscapes, suggesting they are the demographic most prone to human-lion conflict. The ontogenetic movement behaviour of lions reflects a transition from directional movement during transience, suggestive of sequential search strategies, to random or periodic use of a fixed territory after settlement. In terms of habitat connectivity, I show that radically different conclusions emerge depending on which demographic is used to parameterise connectivity models. Understanding the shifting mechanisms that species adopt throughout ontogeny is critical to their conservation in an increasingly fragmented world.

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Glossary

DISPERSAL

Natal dispersal:
An active or passive attempt to move from a natal site to a breeding site (Clobert *et al.* 2009)

Breeding dispersal:
The movement between two successive breeding areas (Clobert *et al.* 2001)

Philopatry:
Residence in the natal home range beyond the age of independence (Waser and Jones 1983)

Dispersal rate:
The rate of individuals leaving a habitat patch (Ronce 2007)

Dispersal kernel:
A function that describes the probability of dispersing different distances (Nathan 2006)

Local adaptation:
The higher fitness of residents in their native environment compared to immigrants in the same environment (Ronce 2007)

Kin competition:
Competition between individuals with the same allele (Ronce 2007)

Condition dependence:
The relationship between internal and external factors and behaviour at each dispersal stage (Bowler and Benton 2005, Clobert *et al.* 2009)

Phenotype dependence:
The observed correlation between morphological, behavioural and life-history traits with dispersal behaviour at each stage (Clobert *et al.* 2009)

Dispersal syndrome:
A suite of characters related to dispersal behaviour. For example, phenotypic attributes of a disperser may be different to those of a resident (Clobert *et al.* 2009)

Informed dispersal:
A dispersal decision based on social or non-social cues (Clobert *et al.* 2009).

Density-dependent dispersal:
The production of dispersing forms or increased dispersal rates brought about by crowded conditions (Lambin *et al.* 2001, Matthysen 2005)

Habitat selection:
Behavioural processes that result in a biased selection of specific habitats and occurs during all dispersal stages (Clobert *et al.* 2009, Stamps *et al.* 2009)

Dispersal-distance function:
Explains the majority of dispersal distances for a particular species, sex and environment (Wiens 2001)

Perceptual range:
The distances at which animals can perceive cues in the environment (Stamps 2001)

Conspecific attraction:
The presence of conspecifics in a patch increases the probability that transient individuals will settle in that patch (Stamps 1988)

Natal habitat preference induction (NHPI):
Experience of a natal habitat increases the preference for a settlement habitat similar to the natal habitat (Davis and Stamps 2004)

Habitat training:
Experience in a type of habitat prior to dispersal improves performance in a settlement habitat if the habitat is similar (Stamps 2001)

DISPERSAL COSTS

Dispersal costs may be incurred directly or differed during all dispersal stages

Energetic costs:
Includes lost metabolic energy due to movement and costs related to development of dispersal morphology (e.g. wings) (Bonte *et al.* 2012)

Time costs:
Relate to time that cannot be invested in other activities since it is invested in dispersal (Bonte *et al.* 2012)

Risk costs:
Direct costs that include mortality risk (e.g. increased predation) and deferred costs through damage (e.g. wounding) (Bonte *et al.* 2012)

Opportunity costs:
Costs incurred by giving up prior residence advantages or advantages from being locally adapted (Bonte *et al.* 2012)

CONNECTIVITY

Metapopulation:
Discrete populations connected by dispersal (Kokko and López-Sepulcre 2006, Ronce 2007)

Habitat fragmentation:
A landscape-scale process involving habitat loss and break-up of habitat (Fahrig 2003)

Wildlife corridor:
Areas in a landscape that facilitate the movement of organisms (Chetkiewicz *et al.* 2006)

Resistance surface:
Indicate the cost of movement as a function of landscape features. Resistance surfaces are the foundation of most modern connectivity models (Zeller *et al.* 2012)

Functional connectivity:
The extent to which a landscape facilitates movement among habitat patches (Chetkiewicz *et al.* 2006)

Scale: The spatial or temporal dimension of a process, characterised by grain (resolution) and extent (Chetkiewicz *et al.* 2006)

Resistant kernel:
The expected density of transient organisms at any location in a landscape (Cushman *et al.* 2013)

Least cost path:
A prediction of the location of movement routes of minimum cumulative cost value between source and target cells (Cushman *et al.* 2013).

Factorial least cost path:
Calculates a vast number of least cost paths to show synoptic connectivity across large and complex landscapes (Cushman *et al.* 2013)

Landscape genetics:
The extent to which landscape features affect the spatial genetic structure of a population (Manel *et al.* 2003)

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Chapter 1

General Introduction

What is Dispersal?

Every living organism occupies the space it does because it has moved or been moved there (Begon *et al.* 2006). Indeed, the distribution of all species observed today reflects age-old patterns of dispersal and isolation (Kokko and López-Sepulcre 2006). The term dispersal then encompasses all such movements of individuals or propagules that may have consequences on gene flow across space (Ronce 2007). Such broad terminology leads to the word 'dispersal' being used to describe other processes such as foraging or migration which has been bemoaned in recent reviews of dispersal since it hinders the formulation of general conclusions relating to patterns and processes of dispersal ecology (Bowler and Benton 2005, Ronce 2007). It is therefore useful to distinguish between two broad types of dispersal: breeding dispersal and natal dispersal. Breeding dispersal is the movement between two successive breeding areas (Clobert *et al.* 2001) while natal dispersal is an active or passive attempt to move from a natal site to a breeding site (Clobert *et al.* 2009). Three separate stages of natal dispersal are recognised: Departure (initiation of the eventual departure from a natal site), transience (the transfer phase) and settlement (the selection of a new breeding habitat; Ims and Yoccoz 1997, Clobert *et al.* 2001, Bonte *et al.* 2012). Recent studies show that it is important to investigate the dispersal process in the context of these stages rather than as a single parameter as each stage may reveal behavioural variation and condition dependencies (Bowler and Benton 2005, Baguette and Van Dyck 2007). Natal dispersal is the focus of this thesis and while much of this introduction applies to both breeding and natal dispersal, the subsequent chapters pertain solely to natal dispersal.

The importance of dispersal

Dispersal is probably the most important life-history trait involved in both species persistence and evolution (Clobert *et al.* 2001), having implications in population biology, behavioural ecology and conservation (Ronce 2007). Dispersal plays a crucial role in the maintenance of social systems having consequences not only for the individual, but also for population dynamics (Macdonald and Johnson 2001) as it affects distribution, abundance and gene flow (Barton 2001). Through dispersal, species may continue to persist despite local extinctions (Ronce 2007). From a perspective of genetic diversity, dispersal can affect the proportion of diversity contained within a population (Wright 1969) thereby mitigating the effect of drift through genetic rescue and reducing the risk of extinction (reviewed in Tallmon *et al.* 2004). In terms of evolution, dispersal affects speciation and can both aid and hinder local adaptation (Barton 2001, Ronce 2007). Thus, there are important genetic and evolutionary consequences of dispersal which may drive patterns of dispersal or even the tendency to disperse at all (Begon *et al.* 2006). Dispersal also plays a central role in many aspects of applied ecology, such as re-establishment in recovery programmes, colonisation of new habitats and species response to habitat fragmentation and climate change (Bullock *et al.* 2002, Berg *et al.* 2010).

It is important to note however, as did Macdonald and Johnson (2001), that although dispersal can positively influence populations in a multitude of ways, under certain conditions, particularly in fragmented populations or those with anthropogenic interference, dispersal may have adverse consequences and even help to drive a species to extinction. For example, dispersing individuals may carry pathogens to non-resistant populations which may be more detrimental to small populations (Castillo-Chavez and Yakubu 2001, Macdonald and Johnson 2001, McCallum and Dobson 2002). Alternatively, alien species may evolve rapidly to colonise new areas, the best known example being cane toads (*Bufo marinus*), which are invading Australia at a rapid rate, aided by adaptation that has produced longer-legged individuals at the invasion front (Phillips *et al.* 2006). A high dispersal rate may also cause synchronous local population fluctuations, thereby increasing the extinction probability of the whole metapopulation (Macdonald and Johnson 2001). Where anthropogenic alteration of the environment has occurred, dispersers may be misled as to habitat quality. For example, dragonflies are drawn to open surfaces of crude oil and tarmac rather than rivers (Horváth *et al.* 1998). Dispersal processes can also lead to the evolutionary suicide of a species (for theoretical examples see Gyllenberg *et al.* 2002) as was reported for a rare endemic plant (*Centaurea corymbosa*), which counter-selected for long distance dispersal due to high risk and thus is unable to exchange or form new populations (Colas *et al.* 1997).

Understanding the causes and consequences of dispersal is therefore crucial to our understanding of ecology and to improving the management of populations and predicting how they will respond to increased fragmentation and climate change (Bowler and Benton 2005, Kokko and López-Sepulcre 2006, Ronce 2007). For example, changes to climate may result in species' range shift from trees in Sweden (Kullman 2001) to coral in the Gulf of Mexico (Precht and Aronson 2004), from birds in the United States (Hill *et al.* 1998) to dragonflies and damselflies in the United Kingdom (Hickling *et al.* 2005). However, if changes occur such that favourable habitats are beyond the dispersal capabilities of a population or species it may become extinct (Walther *et al.* 2002). Throughout history organisms have faced changes to their environment and evolved ways of adapting to them, including local adaptation, selection and phenotypic plasticity (Clobert *et al.* 2012). Such processes however, are relatively slow, especially when compared to the current rapid rate of climatic change and habitat fragmentation (Kokko and López-Sepulcre 2006). Indeed, as ecosystems become more fragmented the importance of dispersal is increasingly apparent as it is often the only mechanism by which organisms move between populations, thus maintaining population viability and genetic diversity (Clobert *et al.* 2012). As a result, habitat connectivity has become a cornerstone of modern conservation (Chetkiewicz *et al.* 2006), resulting in an increased interest in identifying and creating corridors to facilitate inter-patch movement (for reviews see Sawyer *et al.* 2011, Zeller *et al.* 2012, Cushman *et al.* 2013).

In light of this it is not surprising that the literature abounds with theoretical and empirical studies of this crucial life-history trait, resulting in numerous reviews (Waser and Jones 1983, Hansson 1991, Levin *et al.* 2003, Clobert *et al.* 2004, Bowler and Benton 2005, Ronce 2007, Benard and McCauley 2008, Bonte *et al.* 2012), a special issue in *Science* (2006, Volume 313, issue 5788) and entire volumes devoted to the subject of dispersal (Dingle 1996, Clobert *et al.* 2001, Bullock *et al.* 2002, Clobert *et al.* 2012). Simply put, understanding dispersal is critical to understanding population persistence in the modern world. However, despite its importance and increasing interest in dispersal, this complex ecological process is understudied with respect to its overall significance in ecology and still represents a substantial knowledge gap since it is poorly understood for many taxa (Delgado *et al.* 2010, Clobert *et al.* 2012). This is largely due to a lack of empirical data, the intrinsic complexity of dispersal and great variation among species.

Dispersal mechanisms

It is now widely recognised that individuals that disperse are not a random subset of the population as they frequently have behavioural, physiological and morphological attributes to make them more efficient at colonising or integrating into existing populations (Clobert *et al.* 2001, Bowler and Benton 2005, Ronce 2007). Dispersers therefore may develop a suite of characters related to dispersal ('dispersal syndromes'; Clobert *et al.* 2009).

Organisms can disperse either passively or actively. In plants and most sessile organisms, dispersal is generally passive. Seeds and other dispersal units (diaspores), which are unable to move themselves, rely on dispersal vectors. These units, or diaspores, are often adapted for dispersal by specific agents such as wind, or another animal that will transport the diaspores to a new habitat. Organisms which are passively dispersed generally do not have the capacity to choose their destination site (Murren *et al.* 2001) but are very important in colonisation processes such as of islands, a good example being the sea sandwort (*Honckenya peploides*), which was dispersed by ocean currents and colonised a volcanic island 4.8 km from the nearest land mass (Nathan 2006). Wind is a prolific dispersal agent and atmospheric dust usually consists of between a quarter and a third organic matter (Maguire 1963) carrying a variety of organisms from pollen to freshwater invertebrates (Vanschoenwinkel *et al.* 2008).

Active dispersal involves the dispersing organism moving through its own ability, and may also involve adaptations to better enable dispersal. Many insects, such as the parasitoid wasp (*Melittobia australica*), have a dispersal dimorphism wherein individuals which disperse have longer wings than those that do not. Similar dimorphism is seen in water striders (*Hemiptera gerridae*; Andersen 1993, Andersen 2000), whereas in *Cardiocondyla* ant colonies only dispersing males grow wings (Cremer and Heinze 2003). Some mammals too display a dispersal dimorphism, such as the naked mole-rat (*Heterocephalm glaber*), where on rare occasions dispersing individuals emerge with distinct morphology, physiology and behaviour from their colony members (O'Riain *et al.* 1996).

In some cases, passive and active dispersal can be mixed. For example, Delgado *et al.* (2010) found that the movement of dispersing eagle owls (*Bubo bubo*) had a marked directionality, which was largely influenced by dominant winds. Ferrer (1993) reported similar findings in dispersing Spanish imperial eagles (*Aquila adalberti*) while Walls *et al.* (2005) showed that fledgling common buzzards (*Buteo buteo*) were more likely to disperse when the wind changed to a southerly direction and when minimum temperatures were lower.

Sex-biased dispersal

In many species one sex will disperse while the other tends to be philopatric: in birds, it is usually females that disperse, whereas in mammals males are typically the dispersing sex (Greenwood 1980). Male-biased dispersal is especially prevalent in polygynous mammals where males are more prone to mortality, particularly with sexually dimorphic species as there may be intense competition by males for territory and mating opportunities (Clutton-Brock and Iason 1986). What causes one sex to disperse and the other to remain is still debated; one view is that sex-biased dispersal evolved as a mechanism to avoid inbreeding – if one sex disperses the chances of inbreeding are reduced, and in those species where both sexes disperse, one sex will usually disperse further than the other, again reducing the chances of inbreeding (Packer 1979, Greenwood 1980, Pusey and Packer 1987, Begon *et al.* 2006, Costello *et al.* 2008, Lebigre *et al.* 2010).

The second view is that sex-biased dispersal arises out of intrasexual competition and that the pattern is explained by the balance between philopatric benefits and intrasexual competition (Moore and Ali 1984). The social system of a species is therefore important in determining which sex disperses (Lawson Handley and Perrin 2007). In polygamous mammals, males compete for mates and therefore will gain from dispersing to an area with a large number of females. While in birds, males typically compete for territories and so if they remain philopatric they benefit from being familiar with the natal area (Begon *et al.* 2006). Both sexes will usually disperse in solitary animals (but not always; Waser and Jones 1983) and also among monogamous or cooperatively breeding mammals. Thus in most canids, mongooses and some primates, both sexes disperse (Smale *et al.* 1997). However, even when a strong sex bias exists, typically philopatric individuals may occasionally disperse (Smale *et al.* 1997).

The dispersal process

Dispersal has traditionally been considered from a perspective of population dynamics at the level of the population. However, the dispersal process is best conceptualised at an individual level and studied as a multi-stage process involving departure (instigation of leaving the natal habitat), transience (the movement phase), and settlement (selection of a settlement site; Clobert *et al.* 2009, Bonte *et al.* 2012).

Departure

Ultimate causes

When closely related individuals breed, their offspring often suffer from inbreeding depression resulting in decreased fitness (Charlesworth and Charlesworth 1987). Dispersal can help to prevent these negative effects and can be triggered as a response to inbreeding avoidance. For example, when meadow voles (*Microtus pennsylvanicus*) were released into plots, Bollinger *et al.* (1993) found that individuals were more likely to disperse if the plot was occupied by siblings than from plots occupied by non-siblings. Similarly, in wild populations, dispersal has been suggested to introduce genetic variation and reduce inbreeding in a variety of species (for examples see Wolff *et al.* 1988, Clutton-Brock 1989, Girman *et al.* 1997, Sterck *et al.* 2005, Costello *et al.* 2008, Szulkin and Sheldon 2008).

Whether dispersal is driven by inbreeding avoidance and evolved as a direct consequence is highly contentious (Perrin and Goudet 2001). While reduced fitness may occur as a result of inbreeding, the negative effects of inbreeding may be outweighed by the benefits of philopatry such that dispersal patterns may not be influenced (Bollinger *et al.* 1993). For inbreeding to occur a structure of kin co-habitation occurs, however, if resources become limiting, dispersal may be triggered in response to kin competition avoidance and where competition occurs as a result of crowded conditions, dispersal may be density dependent. It is difficult to discern competition avoidance from inbreeding avoidance since the result in both cases is the same: close kin avoiding one another. The costs of dispersal may not be adequately compensated for by a lower level of competition. Therefore in terms of individual fitness, dispersal can be detrimental, but somewhat altruistic since relatives may benefit from the release of competition (Perrin and Goudet 2001).

While it is difficult to decipher whether kin competition can be a sole driver of dispersal, Léna *et al.* (1998) found that in common lizards (*Lacerta vivipara*), kin competition in combination with female density was a major factor promoting dispersal. Perhaps the most compelling evidence of kin-induced dispersal is found in grey jays (*Perisoreus canadiensis*) where independent individuals are evicted by their siblings until only one offspring remains (Strickland 1991). Relationships between litter size and dispersal rates have provided evidence that larger litters of red foxes (*Vulpes vulpes*) trigger more frequent dispersal (Harris and Trewhella 1988) and dispersal over short distances when living at higher densities (Lloyd 1980). In the parasitoid wasp it was shown that increased competition for resources resulted in an increased production of females with dispersal dimorphism (dispersing individuals have larger wings) but interestingly found no evidence that high relatedness increases the production of dispersing females (Innocent *et al.* 2010).

Whether any of the above factors alone explains the evolution of dispersal is unclear, and it is possibly more likely that they act together and that this combination of dispersal driving situations is more common than one factor working on its own (Dobson and Jones 1985, Clobert *et al.* 1994, Gandon and Michalakis 2001, Long *et al.* 2008).

Proximate causes

Natal and breeding dispersal have a multitude of proximate causes and may include competition for resources, habitat degradation, competition for mates, predators, parasites or a combination of these factors (Ronce *et al.* 2001). Over the last decade, research has highlighted the implications of climate change on dispersal patterns. For example, under a positive North Atlantic Oscillation (NAO) index, female European shags (*Phalacrocorax aristotelis*) disperse longer distances while in NAO negative years, more male shags disperse (Barros *et al.* 2013). This study suggests that if climate change were to result in long periods of either NAO positive or negative years, long-term maladaptive effects may occur in European shags (Barros *et al.* 2013).

Condition-dependent dispersal

Dispersal strategies are frequently condition-dependant, due to both environmental conditions (e.g. population density, habitat quality, season) and the individual's phenotype (e.g. body size, fat reserves; Ims and Hjermann 2001). It is expected that condition-dependent strategies are generally superior to unconditional or fixed strategies since plastic dispersal can result in the transience phase ensuing when an individual is most suited to doing so (Bowler and Benton 2005). Numerous studies have reported that individuals in good condition depart earlier, disperse over longer distances or disperse at higher rates (Benard and McCauley 2008, Bonte and de la Pena 2009, Delgado *et al.* 2010, Clobert *et al.* 2012). For instance, heavier European roe deer (*Capreolus capreolus*) were reported to disperse earlier than lighter individuals (Debeffe *et al.* 2012) and post-fledgling flamingos (*Phoenicopterus ruber roseus*) in good body condition had a higher movement probability and dispersed over longer distances than those in poorer condition (Barbraud *et al.* 2003). However, in some cases, good body condition may result in individuals being more likely to stay within the natal area (the so-called 'silver spoon effect') as a result of high competitive ability and a decision to stay in a patch that has favourable conditions (Stamps 2006). This scenario would entail smaller and weaker individuals being forced to emigrate by larger, competitively superior individuals (for example, the common shrew *Sorex araneus*; Hanski *et al.* 1991). It can be reasonably assumed that individuals that are forced to disperse prior to attaining a robust physical condition may incur increased costs, but the evidence of this is scarce (Dufty and Belthoff 2001). These inconsistencies in condition dependence are not surprising given the opposing forces acting on dispersal (Gyllenberg *et al.* 2008).

Transience

During transience, organisms use environmental cues to assess the quality of a patch prior to settling in it. These may be assessed by, for example, olfaction or vision and are influenced by food availability and quality, the presence of conspecifics and potential mates (Bowler and Benton 2005). For instance, a disperser may wish to avoid adult conspecifics as shown with dispersing coyotes (*Canis latrans*) that did not howl (Gese 1998) and rarely scent marked, thus maintaining a low profile so as not to attract attention from residents (Gese and Ruff 1997). On the other hand, transient individuals may be attracted to areas with conspecifics (‘conspecific attraction’) as their presence provides an indicator of habitat quality (Stamps 2001). The ability to perceive cues (ie. the perceptual range) varies among species and individuals and remains an area of research that is largely unexplored in most taxa (Lima and Zollner 1996, Bowler and Benton 2005). This is one of the main reasons why the literature pertaining to search strategies is largely the realm of simulation models and theory (e.g. Zollner and Lima 1999, Conradt *et al.* 2003; for a review see, Van Dyck and Baguette 2005).

Search strategies

The importance of search strategies during dispersal lie in their impact upon mortality rates, distances travelled and selection of settlement sites (Conradt *et al.* 2003, Doerr and Doerr 2004, Conradt and Roper 2006). While most simulation approaches model dispersal movement as a random walk or correlated random walk (e.g. Kareiva and Shigesada 1983, Byers 2001), frequently search strategies do not follow this approach as organisms are drawn to and repelled by certain cues in the environment (Bowler and Benton 2005). Non-random search strategies include 'foray search' where an individual searches the environment in loops, returning to a central and favourable habitat before exploring in another loop (Conradt *et al.* 2003). Zollner and Lima (1999) used simulation models to contrast the effectiveness of various dispersal search strategies and found that straighter paths vastly improved the probability of survival and that this type of movement was the most effective search rule as straighter paths avoid redundant search and improve the likelihood of finding a vacant patch quickly. This is similar to what Stamps (2006) termed 'sequential search' strategies whereby individuals either accept or reject patches they encounter; if rejected they continue the search in a directional manner. 'Comparative search' strategies on the other hand involve organisms visiting a number of patches before eventually selecting one from among their sample (Stamps 2006). Meanwhile, Zollner and Lima's (2005) simulations demonstrated that transient individuals can benefit from moving at slower speeds thereby engaging in more effective anti-predator behaviour. This is seemingly at odds with a study on eagle owls which reported that transient owls moved faster than residents (Delgado *et al.* 2009) but their findings did concur with the straighter paths prediction of Zollner and Lima (1999). More generally, Van Dyck and Baguette (2005) argue that dispersal movement can be described by two classes of movement: routine movements which are associated with resource exploitation and are characterised by returning to a location, and special movements which are generally fast and direct, designed for displacement.

Of all three phases, the transience phase is the least documented as there is a paucity of data on dispersal movement stemming from the difficulties associated with tracking organisms during this period (reviewed in Nathan *et al.* 2003, Jacobson and Peres-Neto 2010). This has resulted in most population and evolution models assuming that individuals move at random in heterogeneous environments (for a review see Patterson *et al.* 2008). However, unrealistic representations of dispersal are likely to yield inaccurate predictions regarding dispersal behaviour and processes (Bowler and Benton 2005). A thorough assessment of the ecological and evolutionary implications of dispersal therefore requires robust empirical studies which have been lacking and widely called for by recent reviews (Jacobson and Peres-Neto 2010, Clobert *et al.* 2012, Baguette *et al.* 2013). Such studies will inform conservation strategies (Macdonald and Rushton 2003) and improve the way dispersal is represented in simulation models (Zollner and Lima 2005) and connectivity studies (Schwartz *et al.* 2009).

Settlement

Settlement occurs once an individual has moved into and remains within a patch. The size of a suitable patch is expected to influence the probability that it will be detected and settled in by transient individuals since larger patches are more likely to be found. Patches isolated by long distances are likely to receive few settlers since patch colonisation is often a function of patch isolation (reviewed in Bowler and Benton 2005).

Habitats

Once settlement has occurred, an individual’s fitness is expected to vary depending on habitat quality, conspecifics and heterospecifics (Stamps 2001). Conspecific attraction is thought to be a major driver of settlement site selection and occurs when the presence of conspecifics attracts transient individuals to a patch (Stamps 1988). Empirical studies suggest that residents occurring at low densities are more likely to attract newcomers, whereas at high densities this is less likely (Stamps 2001). More recently the theory of natal habitat preference induction (NHPI) has gained prominence (Davis and Stamps 2004, Benard and McCauley 2008, Mabry and Stamps 2008, Stamps *et al.* 2009). NHPI assumes that experience in the natal habitat will shape the selection of a settlement habitat with individuals more likely to settle in habitats similar to the natal one (Davis and Stamps 2004). While this syndrome has long been assumed (Immelmann 1975), only recently did Mabry and Stamps (2008) find empirical evidence for it, in dispersing brush mice (*Peromyscus boylii*). Finally the silver spoon effect assumes that transient individuals in good condition are more likely to settle in high quality habitats than those in poor condition (Stamps 2006). Thus there are multiple criteria affecting settlement decisions and the decision to settle is often condition-dependent as individuals adjust their dispersal tactics according to external cues (Clobert *et al.* 2009).

Despite the fact that the dispersal process consists of three distinct phases: departure, transience and settlement, the majority of dispersal literature focuses on the first and last phase, departure and settlement, mainly due to the difficulties associated with obtaining data on dispersing individuals as they move, often over long distances, through diverse habitats (Bowler and Benton 2005). However, when only the start and end points of dispersal are known, it appears that the transience phase is a linear process which is seldom the case (Wiens 2001). In addition the spatio-temporal matrix between departure and settlement is not featureless and research should take into account how an animal moves and the landscape through which it is moving (Wiens 2001). Indeed, there is accumulating evidence that dispersing individuals move in a non-random, exploratory manner, visiting several areas and transferring information before returning to a favoured habitat (Begon *et al.* 2006, Clobert *et al.* 2009). While most authorities on dispersal argue that the dispersal process should be split into three stages (departure, transience and settlement), this is rarely taken into account in empirical studies and an investigation into the whole process has probably never been carried out on any one species (Bowler and Benton 2005).

Costs of dispersal

Dispersal is an inherently risky process and may entail a variety of costs such as increased predation, aggression from conspecifics, starvation and reduced breeding opportunities (reviewed in Bonte *et al.* 2012). Thus the costs of dispersal may be direct or deferred and can be levied during departure, transience and settlement. There are four main cost classes: (1) energetic costs refer to lost metabolic energy due to movement and costs associated with the development of dispersal machinery (e.g. wings); (2) time costs relate to time lost during dispersal that could have been invested in other activities; (3) risk costs include mortality risk and deferred costs such as wounding; (4) opportunity costs are incurred by giving up advantages associated with residency or being locally adapted (Bonte *et al.* 2012).

The overall costs of dispersal are difficult to quantify and disentangle, resulting in a paucity of reliable data on the cost of dispersal over philopatry. For example, Bonte *et al.* (2012) pointed out that while many studies have compared fitness-related parameters of philopatric and dispersing individuals in order to infer dispersal costs (e.g. Bélichon *et al.* 1996) only a few explicitly demonstrate mortality during dispersal (e.g. Soulsbury *et al.* 2008). However, since the costs of dispersal will ultimately determine the performance of dispersing individuals and shape the evolution of dispersal it is important to understand dispersal costs. More specifically, survival during dispersal is a critical component for the long-term survival of populations since they depend on having a sufficient number of individuals that successfully disperse and reproduce (Kokko and López-Sepulcre 2006). Indeed the impact of dispersal on the processes described above (see pg. 2, '*The importance of dispersal*') are determined by the survival and fitness of those dispersers (Gillis and Krebs 2000).

Quantifying dispersal

The difficulties associated with quantifying dispersal are well documented (for reviews see Nathan *et al.* 2003, Jacobson and Peres-Neto 2010). Both indirect and direct approaches can be used for investigating dispersal. Indirect measures do not necessarily involve direct observation of dispersal, but inferences can be made by measuring gene flow. For example, examining allele frequency differences can reveal levels of dispersal (Sahlsten *et al.* 2008) and dispersal distances (Spong and Creel 2001). Models can also provide a useful tool to aid our understanding of dispersal, and as a result many have been used to investigate various processes involved in the evolution of dispersal and the different stages (for recent examples see Chaianunporn and Hovestadt 2012, Kuijper and Johnstone 2012, Travis *et al.* 2012, Chaine *et al.* 2013, Imbach *et al.* 2013, Lam and Lou 2013, Lewis *et al.* 2013, Stevens *et al.* 2013). Models are particularly useful since there is a lack of empirical data to answer many dispersal related questions (Macdonald and Johnson 2001) but this lack of data can lead to misrepresentations of dispersal leading to inaccurate and costly predictions (Bowler and Benton 2005).

Direct approaches generally consist of mark-recapture methods (e.g. Moerkens *et al.* 2010) and/or the use of telemetry devices (e.g. Yoder *et al.* 2004). Tracking devices are becoming more advanced and therefore more suitable to study dispersal movements. Thus, the use of direct methods enables researchers to monitor the entire dispersal event, allowing researchers to answer fine-scale questions on the movement and life history characteristics of dispersers (Jacobson and Peres-Neto 2010). Even with these advances in technology it is difficult to quantify dispersal movement and behaviour, especially for cryptic species that live at low densities. However, as landscapes become more fragmented, it is becoming increasingly important to understand large-scale animal movement and particularly dispersal in order to inform conservation and management policies.

A recent paper by Packer *et al.* (2013) illustrates the point: the authors conducted a meta-analysis across 42 lion (*Panthera leo*) populations and related lion density to management practices. Their findings revealed that in fenced reserves lions are closer to their carrying capacities and cost less to manage compared to unfenced reserves. This led the authors to conclude that "physical separation is highly effective for conserving African lions" (Packer *et al.* 2013). However, if the management implications of this study were upheld and lion populations fenced, this would drastically increase habitat fragmentation and eradicate all existing connectivity and dispersal between sub-populations leaving lions, and other species, in genetic isolation. Indeed, a population genetics model predicted that the long-term genetic diversity of lions requires a minimum of 50-100 prides with no limits to dispersal (Bjorklund 2003). It is therefore crucial that more information on lion dispersal and movement during transience is gathered before conclusions and recommendations such as those in Packer *et al.* (2013) are implemented.

The case of the African lion

Current status

The African lion population has almost halved in the last three decades and continued declines have led to their classification as Vulnerable on the IUCN Red List (Bauer *et al.* 2012). In 1980 there were an estimated 75,000 lions (Ferreras and Cousins 1996), while today it is likely that a maximum of 35,000 free ranging lions remain (Riggio *et al.* 2013). It is thought that the causes of their decline are largely anthropogenic (Bauer *et al.* 2012). For instance, a rapidly growing human population has brought lions into closer proximity with humans resulting in high rates of livestock depredation and subsequent retaliatory and preventative killings of lions (Woodroffe and Frank 2005, Kissui 2008). As human populations grow, so too does their demand for land, resulting in another, related cause of decline: increased fragmentation of lion populations (Bauer *et al.* 2012). In the last 100 years lions have lost 75% of their former range (Figure 1.1a), resulting in high levels of habitat fragmentation (Riggio *et al.* 2013). The declines of both lion numbers and habitats has led to numerous range-wide priority setting exercises aimed at identifying ‘Lion Conservation Units’ (Figure 1.1b; IUCN 2006), sub-populations (Figure 1.1c; Chardonnet 2002) and ‘strongholds’ (Figure 1.1d; Riggio *et al.* 2013). The evidence suggests that lion populations are becoming more fragmented, and hence it is critical to understand the consequences of increased isolation. As mentioned above, a population model genetics model suggested that a minimum of 50-100 prides are needed to maintain genetic diversity and avoid the damaging effects of inbreeding (Bjorklund 2003). These conditions are met in only a few populations, increasing the threat of decreased genetic diversity which can increase sperm abnormality and decrease reproductive performance (Packer *et al.* 1991). However, it is unclear whether sub-populations across the African continent are isolated or whether there are certain factors or wildlife corridors that may facilitate dispersal and gene flow between them.

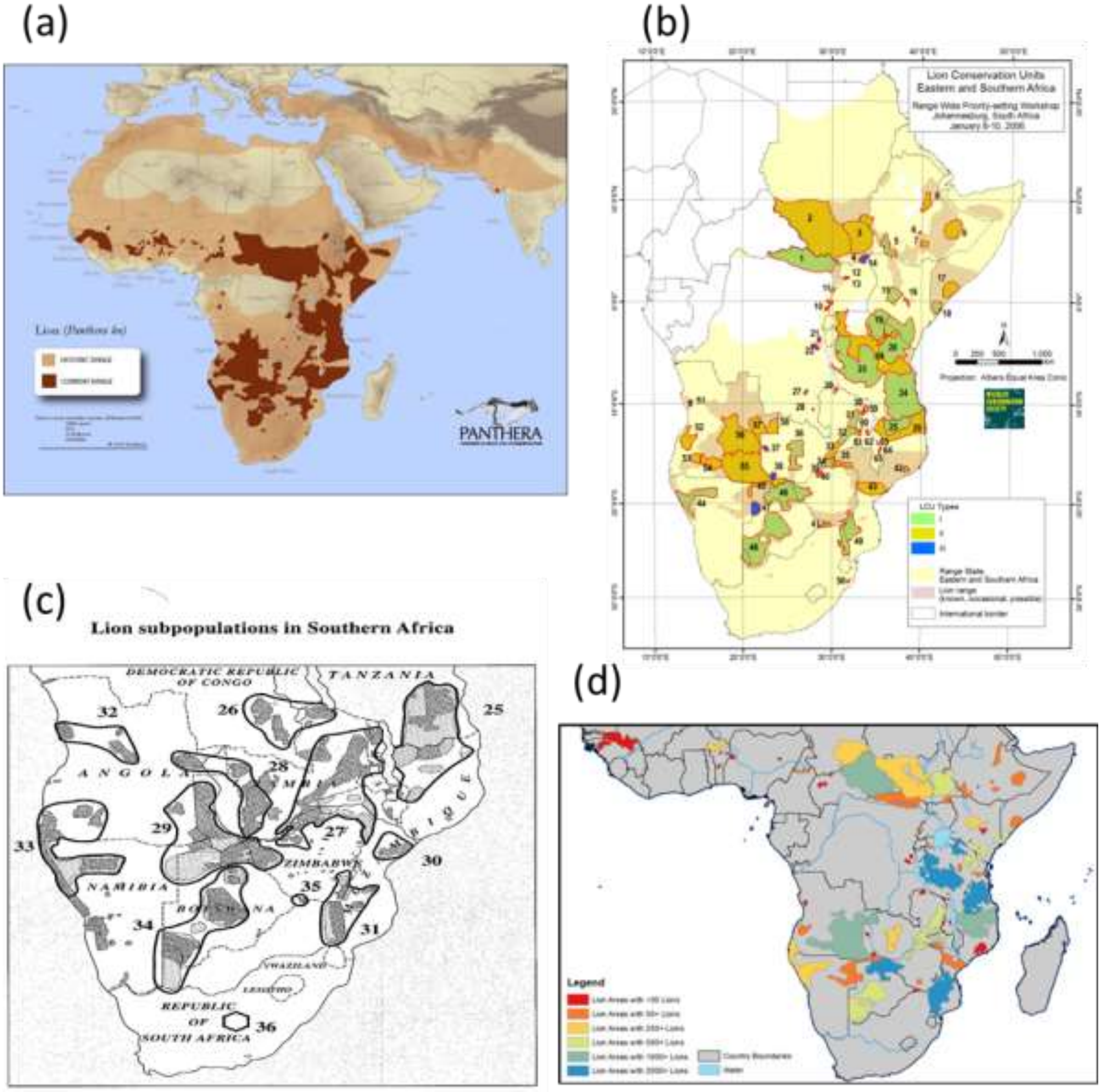

Figure 1.1: Range-wide priority setting exercises for the lion in Africa. The figures show (a) the historic and current range of lions (Panthera 2013), (b) lion conservation units (IUCN 2006), (c) possible sub-populations in Southern Africa (Chardonnet 2002) and (d) the potential 'strongholds' among lion populations. All figures suggest the extent to which lion populations may be isolated but no empirical data supports which populations might be connected.

Lions in the literature

Despite the fact that lions have been a focus of scientific research since the 1960's, there are surprisingly few detailed studies on large-scale lion movement and none on the movement or ecology of dispersing lions. In order to quantify this, I conducted a literature search of peer-reviewed publications that focus on basic ecological variables and noted the demographic categories that were studied. I searched for papers using the Web of Knowledge (Thomson Reuters 2013) with the following search criteria: Topic = *Panthera leo* AND *habitat* OR *space* OR *home-range* OR *connectivity* OR *movement*. The search was thereafter refined to exclude any papers on the Asiatic lion (*P. leo persica*) and any studies that focused on pride composition, genetics or disease. This resulted in a final selection of 26 papers. I classified each article according to which search term it fell under, the demographic group that was used for analysis and method of data collection. The summary of this data is depicted in Figure 1.2.

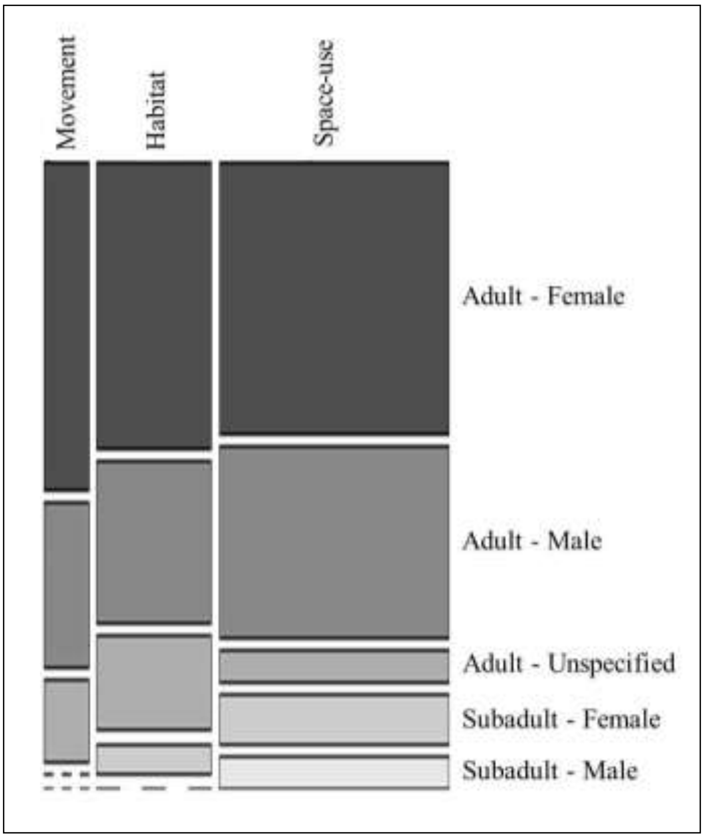

Figure 1.2: Mosaic plot depicting a literature search of papers pertaining to lion movement, habitat, space-use, home range and connectivity. The columns are split according to the demographic category of lions studied. The width of the columns is proportional to the amount of papers found (total N = 26 papers). Space-use and home range papers have been combined in this figure. No peer-reviewed papers we found that dealt with lion connectivity.

The majority of papers were based on data from adult females (20/26) and adult males (24/26) whereas only three papers mentioned sub-adult lions but did not provide detailed ecological data. For example, Funston (2011) used data on adult males and females to calculate spatial distribution in the form of home-ranges. He also monitored sub-adults but provided no ecological information on the sub-adults and in particular on dispersing individuals. VHF or GPS collars were used to collect data in 22 studies and more often than not were deployed on pride females. No studies were found where sub-adults were collared. Given that habitat fragmentation is a key cause of the decline in lions (Bauer *et al.* 2012) it is surprising that no papers were found that dealt with lion connectivity. Habitat and space-use dominated the research on lions and only two papers detailed movement. None of the papers found compared any of these search terms between adults and dispersers. Thus sub-adults and dispersal in particular is under-studied in lions and subsequently there is little knowledge on this crucial life-history stage.

Dispersal in lions

Lions are the most social of all the felids and live in fission-fusion groups, the foundation of which is a group of related females and their offspring (Packer *et al.* 1990). Male lions are transient to the pride and often form single sex coalitions of related males during sub-adulthood and adulthood (Schaller 1972). In general, coalitions do not tolerate the presence of non-coalition members in their territories and encroachment usually results in conflict (Grinnell *et al.* 1995, Packer 2001). Smuts (1982) found that in Kruger National Park, South Africa, male lions become sexually mature at 26 months, but did not mate until they were about five years old.

Apart from the importance of studying dispersal in lions, they are an ideal species to study dispersal for a number of reasons: they are one of the most studied large carnivores and so there is a vast literature pertaining to their social structures and ecology; they are relatively conspicuous compared to other carnivores; their dispersal phase is relatively long (Pusey and Packer 1987), making it possible to acquire large amounts of data; advances in satellite technology enables the collection of data over vast distances. Consistent with recommendations by Clobert *et al.* (2009) and Bonte *et al.* (2012) I consider the dispersal of lions as a three stage process.

Departure

Lions display male-biased dispersal, but some females do disperse (Pusey and Packer 1987), prompting research into why some females disperse and others are philopatric. For instance, VanderWaal *et al.* (2009) reported that in the Serengeti National

Park, 50% of female cohorts dispersed when potential pride size exceeded the habitat optimum. While dispersal occurs at a specific age in many taxa (Matthysen 2012), there is no standard age that lions leave their natal pride and this varies within and between populations; 20 to 65 months in Serengeti National Park and the Ngorongoro Crater, Tanzania (Hanby and Bygott 1987), 36 to 60 months in Kruger National Park, South Africa (Funston *et al.* 2003). In a seminal study on lion dispersal in the Ngorongoro Crater and Serengeti National Park, Hanby and Bygott (1987) sought to establish the reasons that some lions emigrate while others remain philopatric. Many of their results are pertinent to the current study: (1) the authors reported that the emigration of sub-adults was most highly correlated with unfamiliar males entering the pride. Emigration was due to intolerance of the sub-adults by incoming adult males, which effectively evicted all sub-adult males and those sub-adult females which were too young to breed; (2) their results confirmed earlier reports that lions display sex-biased dispersal since all sub-adult male lions left while most (61%) females were philopatric; (3) in sub-adult males, larger groups were more likely to disperse when they were older which was assumed to be due to larger groups being able to better deter eviction. The authors explored other variables in relation to dispersal propensity including relationship with adult females, food availability, inter-pride competition, mating opportunities, pride size and population density. Of these, only population density appeared to have any influence (although it was marginal) over whether or not sub-adults emigrated (Hanby and Bygott 1987). Thus, processes such as density-dependent dispersal and condition-dependent dispersal are seemingly outweighed by the competition posed by incoming adult males. This result is particularly intriguing in lions since their social systems are highly susceptible to disturbances as adult male lions are trophy hunted and killed by agro-pastoralist communities (Woodroffe and Frank 2005, Loveridge *et al.* 2007c, Loveridge *et al.* 2010). The vacuum created by the deaths of males is then filled by incoming males that kill all cubs and evict all sub-adults irrespective of their age (Packer 2001). In populations where the male turn-over is high, it can be reasonably assumed that this has an effect not only on cubs, but also on sub-adults that are forced to disperse before they have attained a physical condition capable of successful dispersal. However, this has not been tested.

Transience

Little is known of the transience stage and lion dispersal has usually been viewed as a linear process. For example Spong and Creel (2001) used genetic data to determine dispersal distances for lions in the Selous Game Reserve, Tanzania, and reported that sub-adults dispersed around 1.3 home ranges away. In Kruger National Park it was reported that lion disperse a small distance of no more than 20km from their natal range (Funston *et al.* 2003). However, the number of transient months for lions in the Serengeti ecosystem was reported to be between 0 and 44 months (Pusey and Packer 1987). Given this, lions may be in the transience phase for up to four years, yet almost nothing is known of the distances travelled, the search strategies they employ, the interactions with conspecifics, the land types they traverse, the habitats they use or the costs they incur.

A number of studies have reported that transient sub-adult lions are potentially the most prolific livestock killers and that lion carcasses recovered from retaliatory killings were frequently sub-adults (Stander 1990, Patterson *et al.* 2003, Patterson *et al.* 2004). This is not surprising given the vast distances lions can move, the rarity of finding a vacant territory, the lack of tolerance by resident males and the increased fragmentation and human encroachment on their range. However, if dispersing lions are indeed prone to livestock raiding, this has important implications for potential connectivity management planning and lion population dynamics.

Settlement

Transient individuals either settle in a vacant area or challenge resident males for pride tenure and territory ownership. Male lions continue to grow until seven years of age but are thought to start to challenge for pride tenure at between four to six years old (Smuts *et al.* 1980, Skinner and Smithers 1990). In the Serengeti, Pusey and Packer (1987) reported that females which dispersed gave birth to surviving cubs later than philopatric females, while in the Ngorongoro Crater, females that dispersed were less likely to survive beyond eight years of age. For males, the authors reported that larger coalitions become resident younger and spent fewer months as transients than those that dispersed in smaller coalitions (Pusey and Packer 1987).

While there are a few papers that deal with lion dispersal, none have looked specifically at the transience phase, focussing instead on the multi-causality of dispersal with particular emphasis on females (Hanby and Bygott 1987, Pusey and Packer 1987, VanderWaal *et al.* 2009) and dispersal distances (Spong and Creel 2001, Funston *et al.* 2003). However, as noted above, the primary reasons for the decline of lions across Africa are increased conflict with people and habitat fragmentation (Bauer *et al.* 2012). Lion dispersal can potentially have a critical role in both of these processes and it is therefore of utmost importance that a thorough understanding of lion dispersal, particularly transience and settlement, is achieved. In addition, dispersal is of particular importance in lions for the following chain of reasons: population size is highly correlated with the number of prides; pride size is limited by density-dependence. Therefore, the only way lion populations can increase is by forming new breeding units which will occur through dispersal (Packer *et al.* 2005a).

Study area

Hwange National Park (HNP) is situated in north-western Zimbabwe (19°00'S, 26°30'E) and covers an area of approximately 14,900km^2 (Figure 1.3). HNP is bordered to the west by Botswana and to the north by the Matetsi Safari Area (MSA) and the Deka Safari Area (DSA). The north-eastern border consists of private land and that owned by the Forestry Commission, making up the Gwai Valley Conservancy (GVC). The south-east borders with agro-pastoralist human settlements. The area is essentially flat, varying in altitude from 800 to 1100 m becoming hillier in the northern areas including Matetsi.

Buffer zones, in the form of hunting areas, make up two thirds of the park boundary separating HNP and areas of human settlement (agro-pastoral/communal lands). Agro-pastoral lands in the area include Tsholotsho to the southeast with Hwange and Lupane Communal Lands to the north of GVC. Under the Communal Areas Management Plan for Indigenous Resources (CAMPFIRE) wildlife can be utilised (i.e. sport hunted) in these areas. HNP is not fenced and so animals can move freely from the park into the surrounding hunting and communal areas. The core study area was located in the northern section of HNP and covers an area of approximately 9000 km^2 incorporating national park, hunting areas and communal lands.

Vegetation and soils

The area is characterised by dystrophic savannah with nutrient poor acidic soils. Deep Aeolian Kalahari sands dominate approximately two-thirds of HNP. Batoka basalts, Karoo sediments and Pre-Cambrian rocks are the three other major geological types that occur (Rogers 1993, Potts *et al.* 1996). The vegetation is primarily woodland and bushland savannah (64%), interspersed with small patches of grassland. More specifically, the vegetation communities are dominated by *Baikiaea plurijuga*, *Colophospermum mopane*, *Combretum* spp., *Acacia* spp. and *Terminalia sericea* (Rogers 1993). The density of woody vegetation was mapped using the Moderate Resolution Imaging Spectroradiometer (MODIS) Vegetation Continuous Fields dataset (Hansen *et al.* 2005), which provides percentage tree cover at a resolution of 500x500m (Figure 1.4).

Water availability

Surface water is available from seasonal waterholes, although only a few hold water in the dry season (Haynes 1996), during which time water is artificially supplied to some (≈50) waterholes (Valeix *et al.* 2010). Figure 1.3 illustrates the pumped and seasonal waterholes within the study area. There are seasonal rivers in the north of HNP as well as in GVC and Matetsi. Daily rainfall was recorded at two weather stations within the study area, approximately 30km apart. These were averaged to give a rainfall profile across the study area. The long-term mean annual rainfall is 613mm and is highly variable (CV≈26%), generally falling between October and April. Annual rainfall was 870mm in 2008, 785mm in 2009, 877mm in 2010, 569mm in 2011 and 589mm in 2012 which are the years corresponding to our study (Figure 1.4).

Seasons

We categorised three seasons consistent with previous studies in this area (Loveridge *et al.* 2009b): early dry season (March – June), late dry season (July – October) and wet season (November – February). During a typical early dry season there is a mean rainfall of 111 ± 73mm with a decrease in the amount of surface water and fodder available. The late dry season has less rainfall (25 ± 27mm) and surface water is restricted to artificially pumped waterholes and a few natural pans which hold water throughout the year. The deciduous trees lose their foliage and fodder is at its lowest quality and quantity compared to the rest of the year. The wet season is characterised by a mean rainfall of 514 ± 160mm and surface water is readily available in the abundant, natural waterholes (Figure 1.3). During the wet season forage is at its highest quality (Holdo 2003, Davidson 2009).

Human impact

HNP is surrounded by hunting concessions and safari areas where trophy hunting takes place (Figure 1.3). In addition, in the adjoining communal lands, animals which either kill livestock or damage crops are occasionally shot in operations of Problem Animal Control (PAC). The impacts of trophy hunting on lions have been extensively documented in this study area, with wide ranging effects including diminished lion density, increased infanticide and alterations to socio-spatial dynamics of the population (Loveridge *et al.* 2007b, Loveridge *et al.* 2007c, Loveridge *et al.* 2009a, Loveridge *et al.* 2009b, Davidson *et al.* 2011). The communal lands to the south east of the park (Tsholotsho) and those to the north of GVC utilise wildlife under the CAMPFIRE programme. Both these areas suffer from crop- and livestock-raiding wildlife and retaliation is not uncommon (Loveridge *et al.* 2010).

Prey species

HNP has a sedentary prey base including a variety of herbivore species. Lions in this study area are known to prey on a wide range of ungulates including buffalo (*Syncerus caffer*), giraffe (*Giraffa camelopardalis*), zebra (*Equus burchellii*), kudu (*Tragelaphus strepsiceros*), sable (*Hippotragus niger*), roan antelope (*H. equinus*), impala (*Aepyceros melampus*), and warthog (*Phacochoerus africanus*; Davidson *et al.* 2012, Davidson *et al.* 2013). At the height of the dry season, and especially in years of drought, lions will also prey on elephants (*Loxodonta africana*), which occur at high densities (Loveridge *et al.* 2006, Chamaillé-Jammes *et al.* 2009). Herbivore populations are generally stable with rainfall and seasonality affecting their dynamics (Valeix *et al.* 2008, Chamaillé-Jammes *et al.* 2009).

Carnivore community

HNP has a range of large carnivores including lions, spotted hyaenas (*Crocuta crocuta*), brown hyaenas (*Hyaena brunnea*), cheetahs (*Acinonyx jubatus*), leopards (*P. pardus*) and African wild dogs (*Lycaon pictus*).

The lions of HNP

The lion population of HNP has been intensively studied since 1999 making it the ideal site to carry out this research since lion social structures are well known. Since 1999, 75 lions (31 adult females, 2 sub-adult females, 29 adult males and 13 sub-adult males) have been fitted with Global Positioning System (GPS) radio-collars in HNP with around 200 known individuals in 50 prides. In the first few years of the study the sex ratio was approximately six females to one male, but is now around two females to one male (Loveridge unplished data, Loveridge *et al.* 2007c). The family lineage of many of the known lions has been documented and an extensive whisker spot library (Pennycuick and Rudnai 1970) is operational allowing for accurate identification of dispersers once they have left their natal pride.

Lion density in the study area is currently estimated at 3.5 lions/100km^2 (Loveridge, unpublished data), a considerable increase from 2007 when the density was estimated at 2.7 lions/100km^2 (Loveridge *et al.* 2007c). The increase in lion density is largely due to changes in management policies pertaining to trophy hunting. Between 1999 and 2004 annual hunting quotas reached 60 lions per year (Loveridge *et al.* 2007c). In 2005 the Zimbabwe Parks and Wildlife Management Authority suspended lion trophy hunting to allow the population to recover (Packer *et al.* 2006, Davidson *et al.* 2011). In 2009 trophy hunting was resumed with a much reduced quota of ten adult males per year in the areas surrounding HNP.

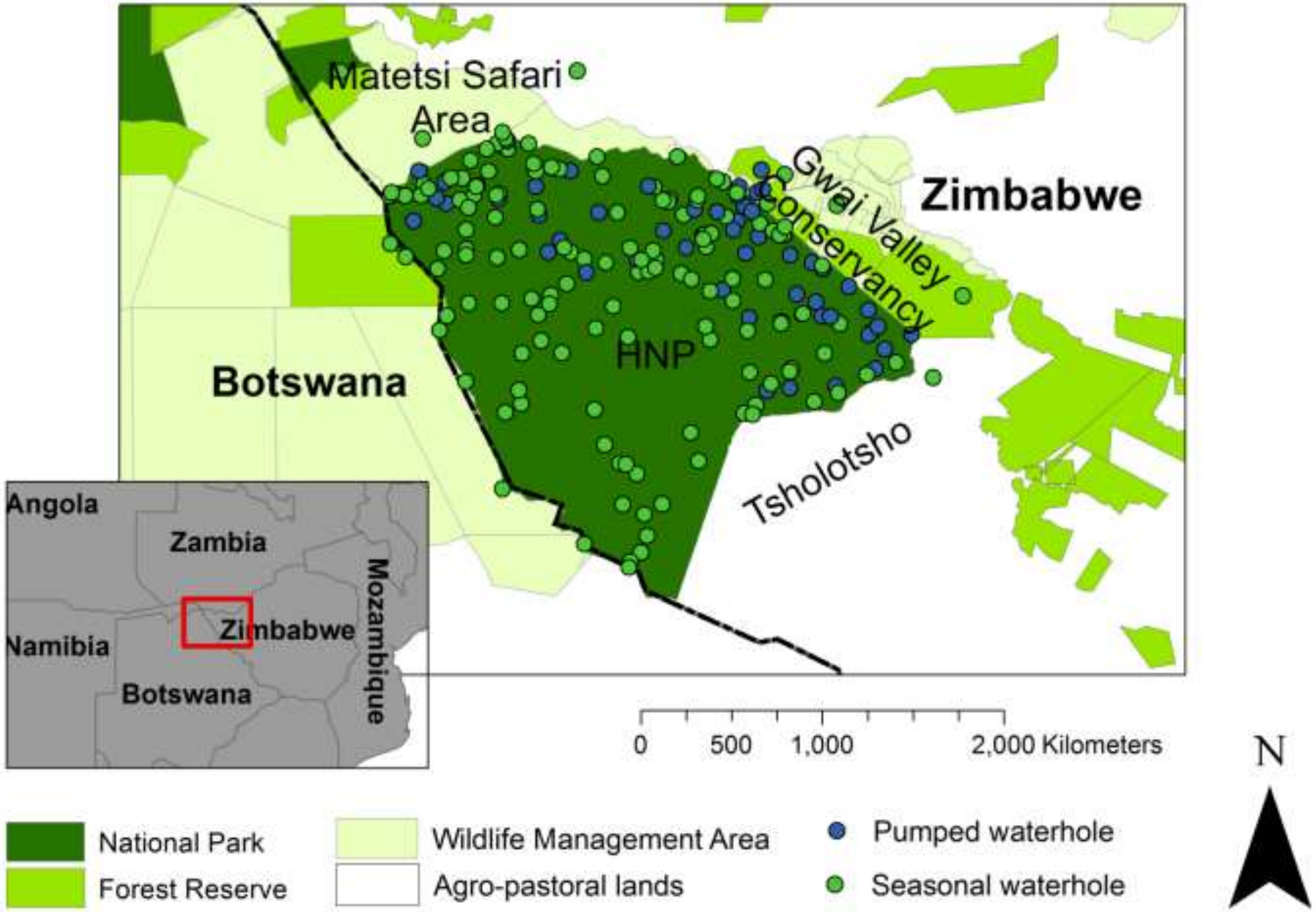

Figure 1.3: The study area Hwange National Park (HNP) is shown in the centre. HNP is bordered by wildlife management areas (WMA's) to the West, forest reserves to the North East and agro-pastoral lands to the South East. Sport hunting of lions is carried out in all forest reserves and WMA's, but not in Botswana. Lions which kill livestock in the agro-pastoral lands are occasionally shot as problem animals. Also depicted are waterholes, most of which do not retain water in the dry season during which time water is artificially pumped to around 50 waterholes.

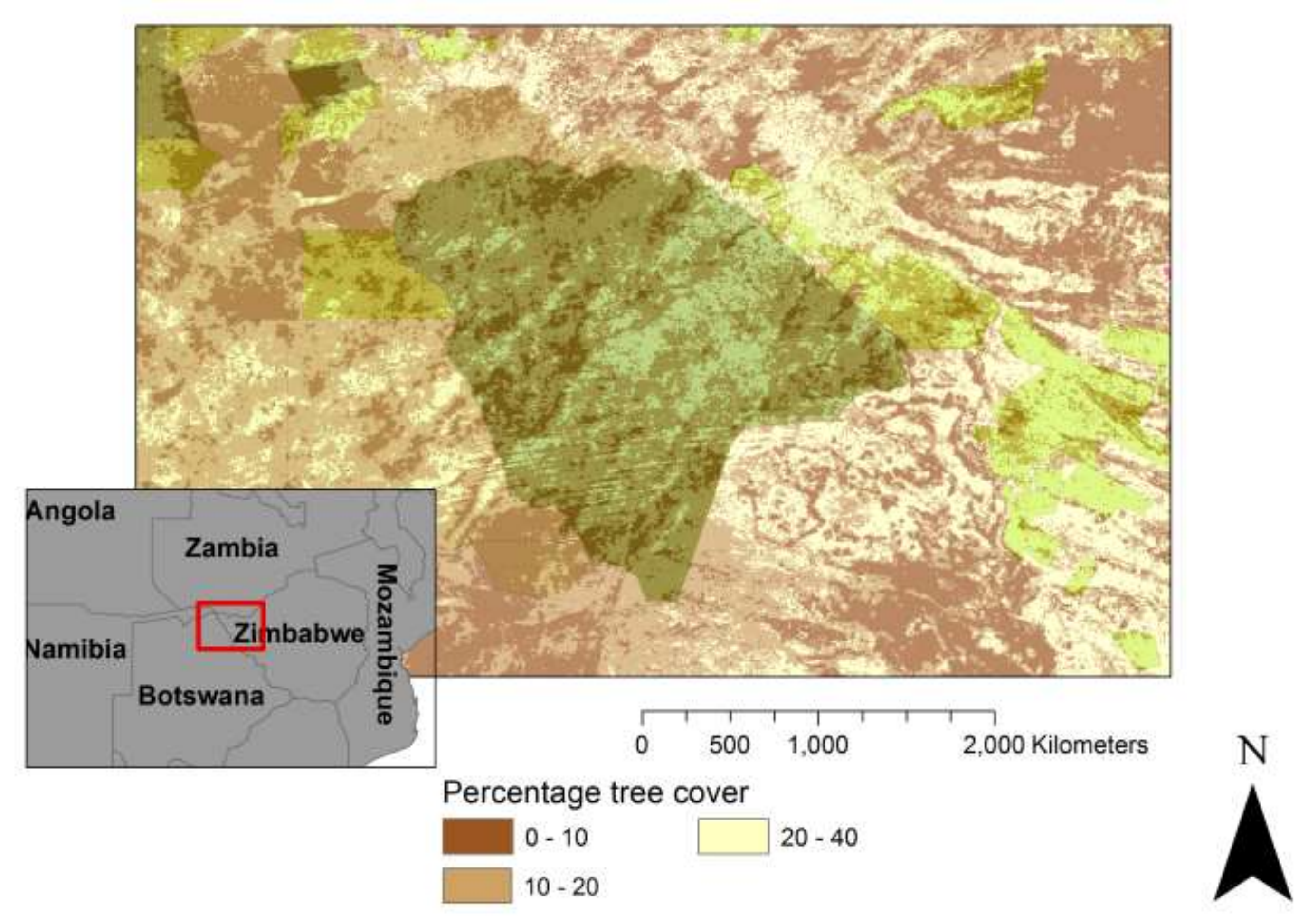

Figure 1.4: The density of woody vegetation as depicted by the Moderate Resolution Imaging Spectroradiometer (MODIS) Vegetation Continuous Fields dataset (Hansen *et al*. 2005), which provides percentage tree cover at a resolution of 500x500m.

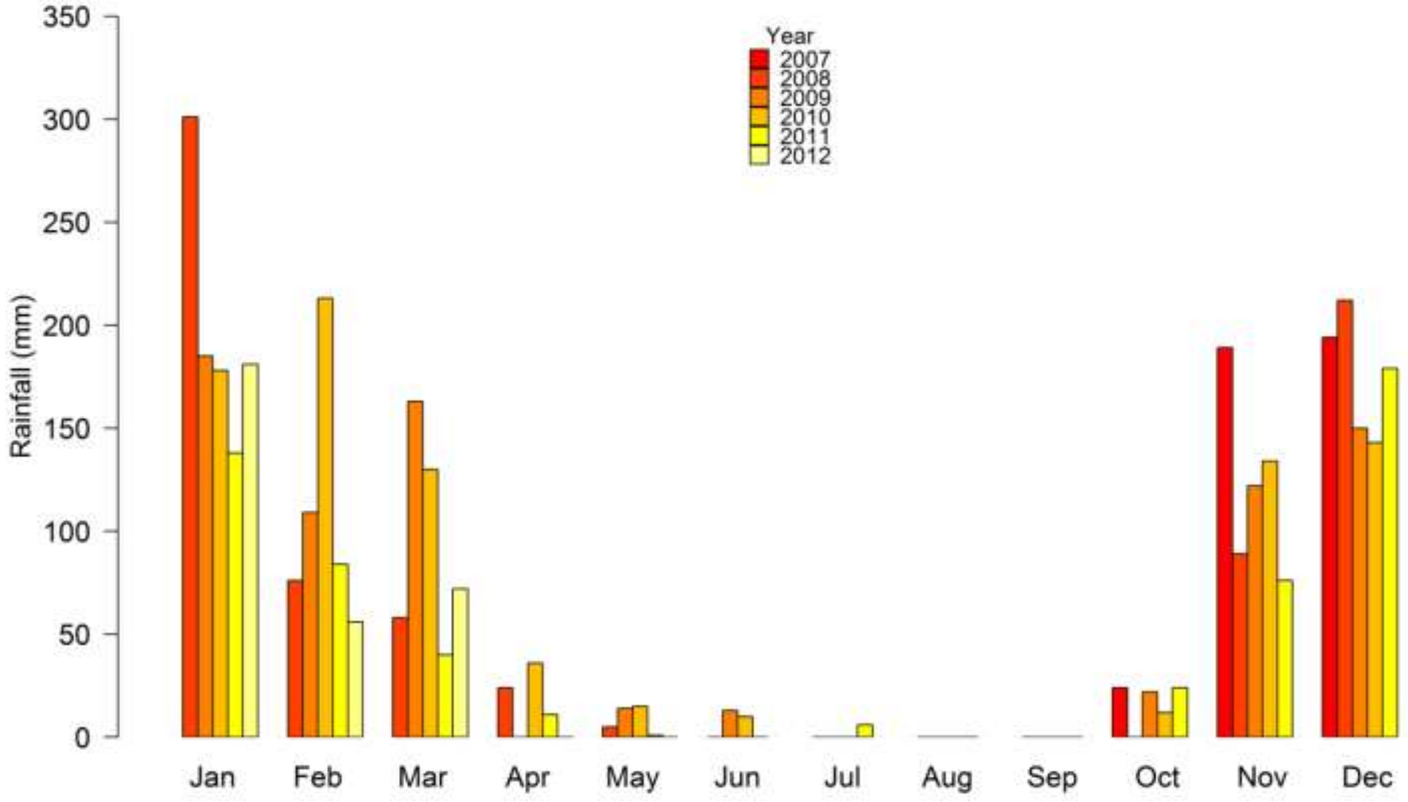

Figure 1.5: Monthly rainfall for the years corresponding to this study

General methods

This section details the general methods that have been used to obtain the data for the chapters of this thesis. More detailed methods are provided in each chapter.

Whisker spots

Each individual lion has a unique combination/array of whisker spots that are commonly used for identification. Lions have long whiskers arranged in parallel rows on either side of the upper lip. Each whisker arises from a black spot and based on the patterns of these spots individual lions can be identified (Pennycuick and Rudnai 1970). This method has been applied in the current study site since 1999 providing an extensive database that allows for the identification of dispersal events prior to the deployment of the radio-collars. Based on sighting data and whisker spots the dispersal timing and lineages have been calculated for 66 individuals.

GPS collars

Lions typically live at low densities and are cryptic, nocturnal animals making them difficult to study by pure observation. For this reason Global Positioning System (GPS) collars with satellite communication were deployed for the collection of spatio-temporal data. The GPS satellite collars automatically collect GPS points during the night and so data is collected regardless of whether the animal is in an inaccessible area which is of vital importance in the current study area as it consists of multiple land use policies and practices. The collars were scheduled to take GPS points at regular intervals allowing for robust data collection. These points are then transmitted via satellite and stored on a server enabling the researcher to remotely download the data and follow an animal’s movements on a daily basis. This also ensures that data loss is minimal as dispersing lions can be difficult to locate due to the distances they travel.

A variety of different collars have been used in this study (Table 1.1), with decisions on type of collar dependent on a variety of factors pertaining to each individual to be collared. All collars used weigh less than 3% of the animal's body mass and so are acceptable to research ethics committees.

Table 1.1. Summary of the collars used in this study. The varying number of fixes per day varied due to differing costs and battery life calculations

Collar Type	Weight (g)	Fixes per day	Manufacturer
VHF	875	None	Sirtrack Ltd. Havelock North, New Zealand
GPS Simplex	950	12	Followit Holding AB, Lindesberg, Sweden
GPS Iridium	1500	11	Vectronic Aerospace GmbH, Berlin, Germany
GPS Argos	1500	8	Sirtrack Ltd. Havelock North, New Zealand
GPS Iridium	1030	12	African Wildlife Tracking cc, South Africa

Lion immobilisation

Under Zimbabwean law, laypersons possessing a Dangerous Drugs License are permitted to use drugs in order to immobilise animals. All lion captures were therefore carried out by qualified personnel. A 2ml dart filled with drugs (Table 1.2) is fired from a Dan-inject JM Special, CO_2 dart rifle (Dan-inject RSA, Skukuza, South Africa) from a distance of 10-30m. While immobilised a collar is fitted and a blood sample taken. Extreme care is taken to monitor the vital signs of the immobilised animal and recovery typically occurs after 172 ± 64min (Loveridge *et al.* 2007c).

Table 1.2. Summary of the drugs used to immobilise lions in this study.

Drugs	Standard dosage
Tiletamine hydrocloride/Zolazepam hydrochloride *(Zoletil; Virbac RSA, Halfway house, RSA)*	250mg
Xylazine *(Rompun; Bayer, Leverkusen, Germany)*	100mg
Atipamezole (reversal) *(Antisedan, Farmos, Orion Corp., Finland)*	10mg per 100mg Xylazine

Thesis overview

Chapter 2: '*In the name of the father: dispersal mortality reveals a delayed infanticide in African lions*'

In this chapter I investigate the average age at which a lion leaves its natal pride and how this affects survivorship during dispersal. Lion social systems are particularly susceptible to anthropogenic perturbations such as trophy hunting and conflict with pastoralists, both of which afflict the study population. Such perturbations lead to a high turn-over of territorial males, resulting in increased levels of infanticide. This chapter explores whether the turn-over of pride males has a knock on effect, as sub-adults are forced to emigrate regardless of age or condition. Evidence is presented to show that age at dispersal has a marked bearing on whether or not sub-adult males (but not females) survive transience. The timing of dispersal was most closely related to the presence of unfamiliar adult males within the natal pride. This chapter has been submitted to *American Naturalist.*

Chapter 3: '*Differences in rest site selection by dispersers and adults: The case of the African lion*'

Resource selection and space use are frequently studied at a species level, ignoring individual variation and changing life stages. In this chapter I investigate fine-scale space use in lions by examining rest site selection of both dispersing males and territorial adult males. The results suggest that individual needs vary in accordance with life stage and this may be reflected in space use. This chapter has been submitted to *Behavioral Ecology and Sociobiology*.

Chapter 4: '*Movements vary according to dispersal status, group size and rainfall: the case of the African lion*'

Movement data during dispersal are rare, and even more so in large mammalian carnivores. I present in-depth analyses of a fine-scale GPS dataset to compare the movement ecology of lions during different stages of natal dispersal (departure, transience and settlement) with that of territorial adults of both sexes and investigate how this varies in relation to rainfall and group size. The results suggest that movement behaviour reflects a transition from directional movement during transience to random or periodic use of a fixed territory after settlement. Thus I highlight the importance of examining the interaction between environmental conditions and the state of the organism to understand the drivers of biologically-based transition processes. This chapter has been resubmitted to *Ecology*.

Chapter 5: '*The devil is in the dispersers: predictions of landscape connectivity change with demography*'

This chapter investigates how connectivity metrics (resistance surfaces) vary depending on the data from which they are parameterised. Dispersal is recognised as being the principal natural mechanism for connecting sub-populations, yet most studies that investigate connectivity rely on data collected from adult individuals. The results demonstrate that the demographic category used to parameterise resistance surfaces may lead to radically different results and that a failure to include dispersing individuals when parameterising resistance surfaces intended for connectivity modelling may lead to erroneous conclusions and subsequently, unsound management strategies. This chapter has been resubmitted to *Journal of Applied Ecology.*

Chapter 6: General discussion

This concluding chapter summarises and discusses the results from the preceding chapters and puts them into a wider context. In addition, future work and recommendations are made.

Appendices

Appendix I - Despite many studies conducted on the effect of predation risk on prey behaviour, very little is known on how the actual presence of the predator in the vicinity affect prey vigilance behaviour. We studied how 2 species with different body-size and ecology, impala and zebra in Hwange National Park, Zimbabwe react to the presence of lions depending on group size, distance to cover and season. We assessed the presence of lions using radio-collars. We measured two types of vigilance: routine vigilance can be conducted while chewing, while intense vigilance is a more acute process forcing the animal to stop any other activity and is therefore more costly. We expected intense vigilance to increase in the presence of lions. Indeed, this is what we observed for zebras but impalas seem to adjust their vigilance to cues less specific, such as group size. Zebras also react differently to lions depending on the season, showing that the response to predation risk differs between species and within species. This manuscript has been published in *Behavioral Ecology*.

Appendix II – This study is the first to investigate the genetic diversity of the lion population in Hwange National Park. Understanding the population genetic diversity of a species is of crucial importance for managing and protecting biodiversity. The present study investigates the gene flow and population genetic structure of HNP lions. We sampled 87 individuals and used the genotypes from 17 microsatellite loci in our analyses. We present evidence of the presence of 14 immigrants (11 males, 3 females). In addition we describe a weak genetic structure, high gene flow within HNP and the lack of any major genetic division. Thus the lion population of HNP is genetically healthy. This manuscript has been re-submitted to *Conservation Genetics*.

Chapter 2

Social relationships affect dispersal timing revealing a delayed infanticide in African lions

This manuscript has been accepted for publication in *Oikos*

Authors: Nicholas B. Elliot, Marion Valeix, David W. Macdonald, Andrew J. Loveridge

Statement of authorship: NE collected data, performed modelling work and analysed output data; MV assisted in analysis; AL collected data, AL and DM oversaw this project, NE wrote the first draft of the manuscript and all authors contributed to revisions

Abstract

Successful dispersal is a critical parameter for species persistence and evolution. Despite this, factors determining successful dispersal are poorly understood, particularly in wide-ranging species. Condition-dependent dispersal strategies tend to be more successful than fixed ones since they can entail dispersal occurring when an individual is most suited to doing so. However, the juvenile's family group or conspecifics may initiate premature dispersal, which could influence whether or not dispersal is successful. We studied dispersal in African lions (*Panthera leo*) and investigated a) whether dispersal age affects dispersal success and b) factors determining dispersal timing. We found that all males that dispersed before 31 months died during transience and that dispersal coincided, regardless of age or body condition, with the arrival of unfamiliar adult males. Whereas a high turn-over of territorial males is known to result in infanticide and eviction of sub-adults, our results indicate it can also induce a previously undescribed, 'delayed infanticide'.

Introduction

Dispersal, the movement from a natal to a breeding site, is inherently risky and can entail a variety of costs such as increased predation, aggression from conspecifics, starvation and reduced breeding opportunities (reviewed in Bonte *et al.* 2012). Despite this, some individuals do disperse, and those that survive to reproduce in a new social group influence a range of processes including population dynamics, gene flow and species distribution (Gillis and Krebs 2000). In light of increased habitat fragmentation and global warming, the importance of successful dispersal is increasingly apparent as it is often the primary mechanism by which metapopulations are sustained and new ones founded (Ronce 2007, Clobert *et al.* 2012). Successful dispersal is therefore a critical component for both species persistence and evolution. Despite its importance, the factors determining whether or not dispersal is successful are still poorly understood, particularly in large, wide ranging species.

The ultimate causes shaping the evolution of dispersal are thought to involve inbreeding avoidance, competition (from kin and conspecifics) and habitat variability (Bowler and Benton 2005). However, the timing of dispersal may be condition-dependant, triggered by individual phenotype (e.g. body size, fat reserves), or environmental conditions (e.g. population density, habitat quality, season), or a combination of both (Ims and Hjermann 2001). Condition-dependent strategies tend to be more successful than unconditional or fixed strategies since plasticity in dispersal timing can entail dispersal occurring when an individual is most suited to doing so (Bowler and Benton 2005). For instance, European roe deer (*Capreolus capreolus*) and Belding’s ground squirrels (*Spermophilus beldingi*) may only initiate dispersal once a critical mass has been attained (Holekamp 1984, Holekamp 1986, Debeffe *et al.* 2012). It follows then that dispersing before attainment of a robust physical condition may incur increased costs (Stamps 2006). Indeed there is considerable literature on body size and its influence on dispersal which points towards a positive correlation between body size and dispersal ability (reviewed in Benard and McCauley 2008). In many species, body size is related to age and thus the age at which an individual disperses may also be a predictor of whether or not dispersal is successful (e.g. Waser *et al.* 1994).

If survival probability during dispersal increases with age, juveniles should delay dispersal (Tarwater and Brawn 2010). However, for this to occur their family group or conspecifics must allow them to remain (Ekman 2006). Parent-offspring conflict and kin competition can affect the timing of dispersal, with more intense competition when resources are limited or when population density reaches a critical threshold. For instance, kin competition in combination with adult density has been shown to promote dispersal in common lizards (*Lacerta vivipara*; Léna *et al.* 1998). If density-dependence is a limiting factor, it follows then, that juveniles from large litters are more likely to disperse (e.g. Harris and Trewhella 1988), and to disperse young (e.g. Hanby and Bygott 1987). In territorial species, the potential risks associated with early dispersal may be counter-balanced for bigger groups of dispersers, since larger groups usually overcome smaller groups, thus enhancing the likelihood of territory acquisition (Clutton-Brock 2002).

Parent-offspring conflict can entail parents forcing the dispersal of their offspring even under conditions where dispersal is risky (Johnson and Gaines 1990). In territorial species, such competition may be manifest with the arrival of unfamiliar adult males into the family group. For instance, in African lions (*Panthera leo*), a male take-over of a pride results in the eviction or death of resident adult males and the infanticide of cubs (Packer and Pusey 1984, Loveridge *et al.* 2007c). Incoming males will also kill or evict sub-adult males and those females that have not yet reached sexual maturity (Hanby and Bygott 1987). Indeed, Hanby and Bygott (1987) found that the arrival of new males was highly correlated with dispersal initiation and it is likely that the unpredictable timing of pride take-overs resulted in the wide range of dispersal ages reported (20-65 months). However, the frequency at which pride take-overs occur could be exacerbated by anthropogenic perturbations such as conflict with pastoralists and trophy hunting. While high levels of anthropogenic mortality have been shown to result in increased infanticide (e.g. Swenson *et al.* 1997), it is plausible that it may also result in young, and therefore risky dispersal.

In this study, we investigated whether the turn-over of territorial male lions would have a knock on effect, a ‘delayed infanticide’, as sub-adults are forced to disperse regardless of age or condition, which may compromise their survival during dispersal. We examined the factors determining successful lion dispersal in Hwange National Park, Zimbabwe, an ecosystem where the lion population has been impacted by trophy hunting and is characterised by a high turn-over of territorial males (Loveridge *et al.* 2007c, Loveridge *et al.* 2010, Davidson *et al.* 2011). The goals of this study were twofold: first, to assess whether the probability of surviving dispersal is a function of dispersal age, sex and/or group size; second, to investigate factors related to the timing of lion dispersal, with a specific focus on the role of pride males and incoming males.

Methods

Study area and population

The study area (≈7,000km^2) was located in the northern section of Hwange National Park (HNP), Zimbabwe (19°00´S, 26°30´E). Vegetation consists primarily of woodland and bushland savannah (64%) and communities are dominated by

Baikiaea plurijuga, *Colophospermum mopane*, *Combretum* spp., *Acacia* spp. and *Terminalia sericea*. The long-term mean annual rainfall is 613 mm (CV≈26%) and generally falls between October and April. Surface water is available from seasonal waterholes, although only a few hold water year round. In the dry season water is artificially supplied to some (≈50) waterholes. We categorised three seasons consistent with previous studies in this area: early dry season (March-June), late dry season (July-October) and wet season (November-February).

Approximately 6,000 km^2 of the study area is within HNP with the remainder in safari areas and agro-pastoral lands (Figure 2.1). There is no restriction of lion movements between protected areas and agro-pastoral lands as evidenced by the trajectories of two singleton dispersing sub-adult males shown in Figure 2.1. Trophy hunting occurs in the surrounding safari areas, with annual quotas reaching 60 lions between 1999 and 2004 (Loveridge *et al.* 2007c). In 2005 lion trophy hunting was suspended to allow population recovery (Davidson *et al.* 2011). Trophy hunting resumed in 2009 with annual quotas of around 10 adult male lions. In addition, lions which kill livestock in the surrounding agro-pastoral lands are occasionally shot in management operations of Problem Animal Control. Alternatively they may be snared or poisoned by local agro-pastoralists (Loveridge *et al.* 2010). The source population has been monitored without interruption since 1999 and lion density is estimated around 3.5 lions/100 km^2 (Loveridge, unpublished data). The data used here were recorded from observations during the period 1999-2012 during which time 33 females and 43 males were fitted with GPS radio collars (see Loveridge *et al.* 2007c for details). Lion prides were regularly sighted and details of group composition and location recorded. Care was taken to individually identify lions during all sightings using whisker vibrissae spots and other distinguishing marks (Pennycuick and Rudnai 1970).

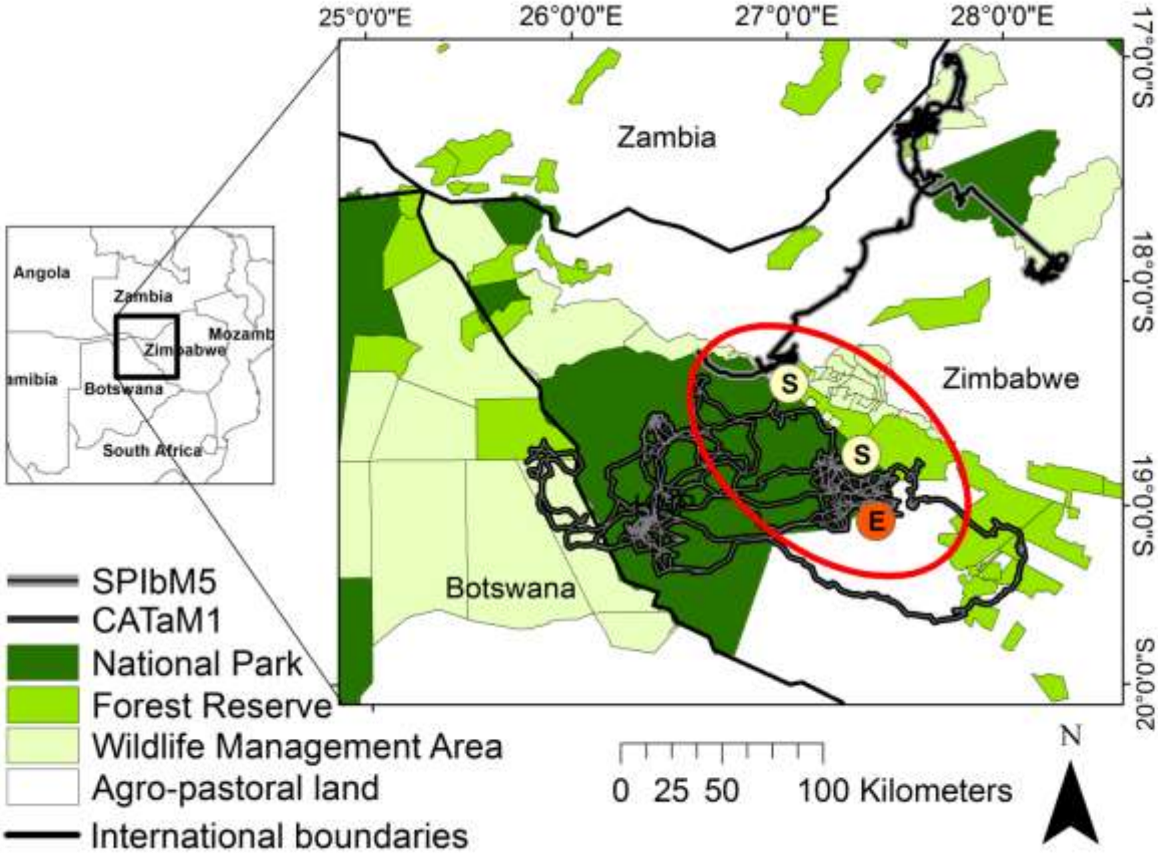

Figure 2.1: Map showing Hwange National Park (HNP) and surrounding forest reserves, wildlife management areas and agro-pastoral lands. The red ellipse indicates the study area. Controlled lion hunting occurs in forest reserves and wildlife management areas (but not in Botswana). Lions that venture into agro-pastoral lands may sometimes be shot by management and frequently poached by communities. The trajectories detail the movement paths of two dispersing male lions (SPIbM5 and CATaM1 - both singletons). The letters in the circles denote start (S) and end (E) points for transience. CATaM1 was still dispersing at the time of writing this article.

Dispersal data

Sub-adults were defined as individuals between 18 and 48 months old (consistent with Pusey and Packer 1987). The age of sub-adults was based on sightings of them soon after birth, enabling accurate estimation of their age (within one month). A total of 66 sub-adults (33 males and 33 females) in 28 different age-sets were observed to disperse from their natal pride. Dispersing lions were allocated a dispersal group identity (N=28), and fifteen of these groups contained at least one collared individual. In two cases there was only one sub-adult in a pride, while in all other cases they dispersed together in groups (up to 13 individuals) that broke up, males and females splitting first, then into smaller groups. Dispersal group identity and dispersal group size were based on these subsequent splinter groups and not the original group that dispersed from the natal pride.

Age at dispersal was calculated as the mid-point between the last time a sub-adult was seen with its natal pride and the first time either was seen alone (mean time interval ± SD = 1 ± 1.5 months). A dispersing individual was deemed to have established a territory and therefore survived dispersal when it had been observed in an area for a minimum period of two months and reproduced thereafter.

Adult males

Consistent with Hanby and Bygott (1987) we considered two aspects of adult males as being important to the timing of sub-adult emigration: the death or departure of the pride males and the arrival of unfamiliar adult males within the natal pride. We were interested in investigating whether the protection lost due to the absence of pride males resulted in sub-adult dispersal or whether this was more likely to occur once unfamiliar males made contact with the natal pride.

First we calculated the number of months between the death or departure of the pride male and the dispersal of sub-adults. Where coalitions of multiple pride males were present and died intermittently we used the timing of the last adult male to depart or be killed. In all dispersal groups where dispersal occurred in the absence of pride males the last remaining male of the coalition was collared and thus the accuracy of the date for their death or departure is estimated as (mean ± SD = 1 ± 0.9 month). We use the term ‘pride male’ to refer to territorial males which are presumed to be the fathers of all sub-adults within the pride, since they had been in attendance at the time of their birth.

Second we calculated the number of months between when an incoming male was first seen with adult females of the natal pride and the subsequent dispersal of sub-adults. We were able to accurately determine when unfamiliar adult males first came into contact with each natal pride through the use of radio collars. In all but one instance at least one adult female from the natal pride was collared in addition to at least one adult male from the incoming coalition. In the case of one dispersal group, the incoming male was not collared but one of the adult females from the natal pride was. The use of radio collars enabled frequent sightings and the pairing of GPS data to establish first contact between the natal pride and incoming males.

Statistical analyses

Factors affecting survival during dispersal

We performed general linear models with a binomial error structure where our response variable was survived (1) or died (0). We created ten *a priori* candidate models to test whether survival during dispersal was a function of age at dispersal, sex of disperser, dispersal group size and combinations and interactions therein.

Determinants of dispersal age

We performed linear models with age at dispersal as the response variable. Our explanatory variables consisted of (1) a class variable for pride male present or absent at the time of each dispersal event; (2) a class variable for incoming male present or absent at the time of each dispersal event; (3) the number of sub-adults in the natal pride at the time of each dispersal event; (4) sex of dispersers; (5) natal pride biomass – we used field data for adult weight (Loveridge *et al.* 2009b) and growth equations for cub and sub-adult weight (Smuts *et al.* 1980); (6) the age of individual sub-adults when new cubs were born. Of the 66 recorded dispersal events, 21 occurred while the pride males were still in attendance and 45 occurred when the pride males had died or been evicted. Of these 45 events, 40 occurred after an incoming male had been sighted with the sub-adult's natal pride. We therefore did not consider the variables pride male present/absent and new male present/absent as independent and used new male present/absent in the subsequent analyses. We created 24 *a priori* candidate models including each of the main effects and combinations and interactions therein.

Relative roles of pride males or incoming males

To determine whether dispersal was triggered by the departure of pride male(s) or the arrival of new males we performed a paired *t*-test comparing the number of months between both scenarios and the commencement of dispersal.

For all models, dispersal group identity was used as a blocking factor. To identify the best model we used model selection based on Akaike Information Criterion corrected for small sample size (AICc). Where one model was clearly superior (w_i>0.9) this was used, otherwise we obtained parameter estimates and unconditional confidence intervals by averaging across the models, correcting for model weights using R package AICcmodavg v.1.30 (Burnham and Anderson 2002, Mazerolle 2013). Finally, we performed separate chi-square tests to determine the distribution of dispersal timing across seasons. All statistical analyses were performed in R 2.15.1 (R Core Team 2012).

Results

Factors affecting survival during dispersal

Of the 66 recorded dispersal events, 49 individuals (28 males, 21 females in 21 age-sets), were recorded from emigration to settlement or death. The remaining 17 individuals (5 males, 12 females in seven age-sets) were observed to emigrate from their natal prides and disappeared. We therefore could not confirm whether or not they established a new territory and thus they were not included in this analysis. Of the 49 individuals that were observed to settlement or death, 65% survived to establish a territory (17 males, 15 females) while 16% (N=8) were poached and 10% (N=5) were shot as ‘problem animals’. One dispersing male lion died of natural causes (probably killed by an adult male) and three deaths were undetermined.

The top model consisted of an interaction between dispersal age and sex, followed by a model with the same interaction and the additive group size (Table 2.1). Given that both these models had substantial support we averaged across them to provide estimates and unconditional confidence intervals (CI). For males, successful completion of dispersal increased with the individual’s age at dispersal (estimate ± SE = 0.685 ± 0.289; CI = 0.118 – 1.252; Figure 2.2). The age at which sub-adult females dispersed had no effect on whether or not they survived to establishment (estimate ± SE included 0 and 95% CI included 0). There was a slight tendency of higher survival probability for dispersers in bigger groups (estimate ± SE = 0.029 ± 0.233; CI = -0.428 – 0.486) but since the estimate ± SE included 0 and 95% CI included 0, we considered the interaction between dispersal age and sex as the main factor influencing successful dispersal.

Table 2.1. Summary statistics for models of survival to establishment during dispersal for African lions in Hwange National Park. Explanatory variables consisted of (1) 'disp.age' – age at dispersal; (2) sex of disperser; (3) 'G.S.' – number of individuals per dispersing group. Models in bold indicate the two top models which were averaged correcting for model weights. Included are the log likelihood, the AICc differences (Δ*i*), the Akaike weights (w_i) and the number of parameters (K).

Response variable	**Rank**	**Model**	**log likelihood**	**AICc**	**Δ*i***	**w_i**	**K**
Survived dispersal (1) vs died during dispersal (0)	**1**	**disp.age * sex**	**-19.91**	**51.21**	**0**	**0.77**	**5**
	2	**disp.age * sex + G.S.**	**-19.90**	**53.80**	**2.59**	**0.21**	**6**
	3	disp.age + G.S.	-26.35	61.61	10.40	0.00	4
	4	disp.age	-28.11	62.76	11.54	0.00	3
	5	G.S.	-28.39	63.32	12.11	0.00	3
	6	disp.age + sex	-27.28	63.47	12.26	0.00	4
	7	disp.age + sex + G.S.	-26.27	63.93	12.72	0.00	5
	8	sex	-28.91	64.36	13.15	0.00	3
	9	Null	-31.63	65.35	14.14	0.00	1
	10	sex + G.S.	-28.39	65.70	14.48	0.00	4

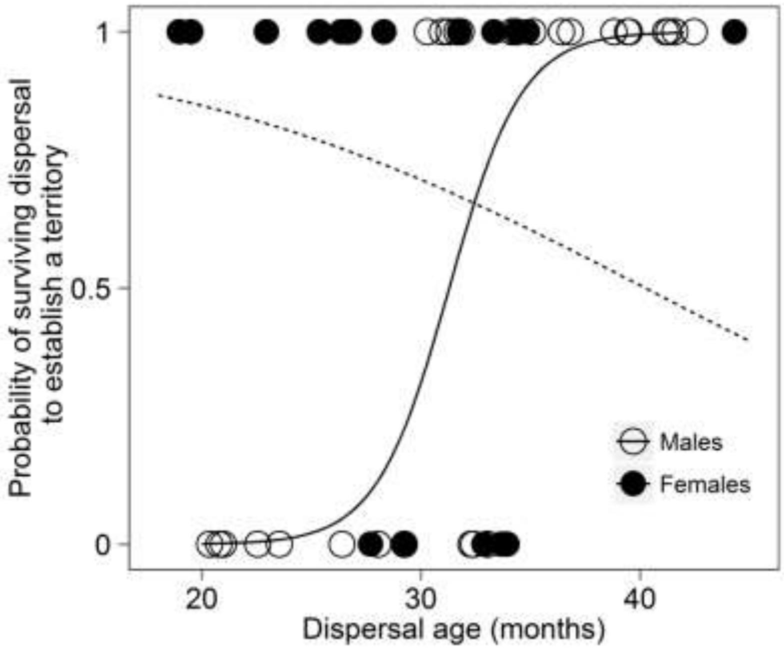

Figure 2.2: Logistic regression curve showing the effect of dispersal age on the probability of surviving to establish a territory for both male and female sub-adult lions in Hwange National Park, Zimbabwe.

Determinants of dispersal age

The variables that were most influential in determining the timing of dispersal included the sex of sub-adult, presence of new males, and pride biomass (Appendix 2.1). Overall there was a wide distribution of dispersal ages spanning over two years with sub-adult males dispersing when they were older (mean ± SD = 34.1 ± 7.4 months, range = 20-45, Figure 2.3) compared to sub-adult females (mean ± SD = 30.2 ± 6.5 months, range = 18-45, Figure 2.3; estimate ± SE = 3.001 ± 1.291; 95% CI = 0.471 – 5.532). Sub-adult males dispersed in smaller groups (mean ± SD = 2.6 ± 1.1, range = 1-6) compared to females (mean ± SD = 4.5 ± 2.6, range = 1-8) but neither group size, nor the birth of new cubs, had a bearing on the timing of dispersal.

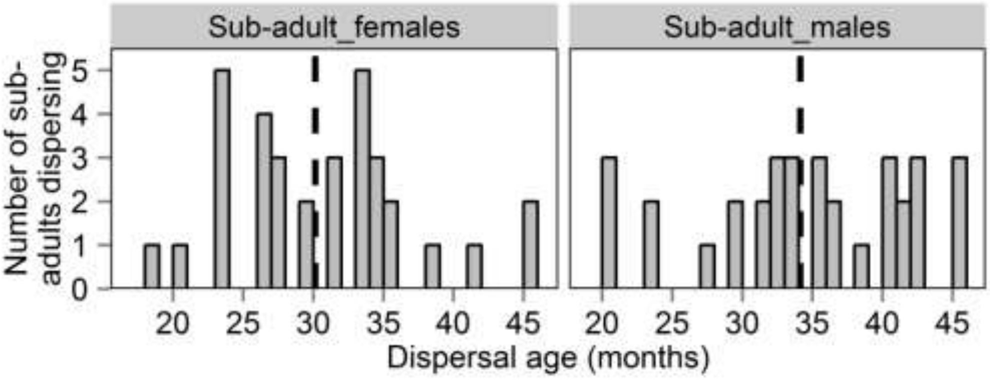

Figure 2.3: Dispersal ages for male and female sub-adult lions in Hwange National Park, Zimbabwe. The dashed line indicates the mean dispersal age for each sex.

Sub-adults dispersed earlier if incoming males were present (mean ± SD = 28.6 ± 6.1 months) compared to when no new male was present (mean ± SD = 37.6 ± 5.2 months; estimate ± SE = -4.554 ± 1.737; CI = -7.959 – -1.150; Figure 2.4). Pride biomass appeared in the top model, revealing a tendency for lower dispersal age with increased pride biomass (estimate ± SE = 0.003 ± 0.002; 95% CI = -0.8.35E-05 –

0.007). However the estimate ± SE included 0 as did the 95% CI; thus we considered the arrival of immigrant males as the main factor influencing dispersal age.

A separate chi-squared test revealed that dispersal was markedly seasonal with more emigration occurring during the wet season than in either the early dry or the late dry season (χ^2=7.363, d.f.=2, p=0.025). Sub-adults of both sexes dispersed younger during the wet season (mean ± SD = 29 ± 5.8 months) compared to the early dry season (mean ± SD = 36 ± 4.6 months) or late dry season (mean ± SD = 34 ± 8.5 months).

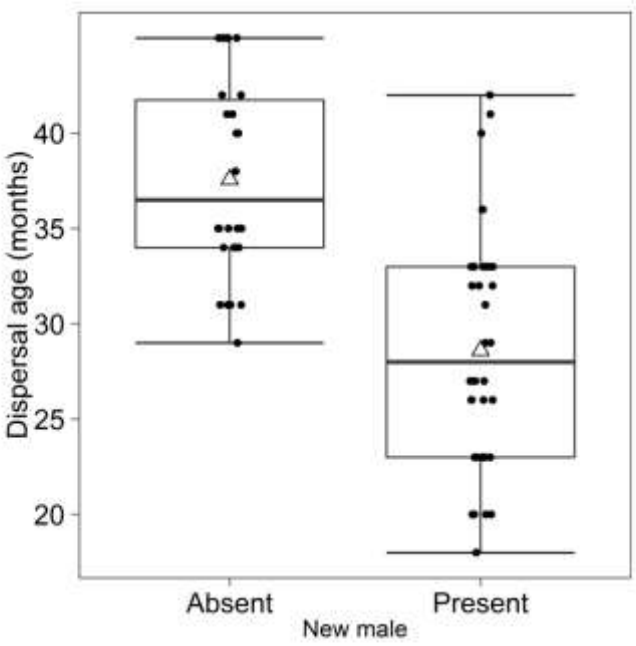

Figure 2.4: The age at which lions dispersed relative to the presence or absence of incoming males. Boxes show medians, 25% and 75% quartiles. Triangles indicate means. Whiskers indicate 10-90 percentiles. Dots represent the raw data.

Relative roles of pride males or incoming males

In the case of 34 dispersers, pride males were trophy hunted, and for 11 dispersers, pride males were evicted by incoming males (always when the coalition had been weakened either through trophy hunting or illegal killings). Sub-adult age at the time of pride male's death or eviction ranged from 1 to 37 months (mean ± SD = 15 ± 10.2 months). In order to determine whether new males encountering the pride or the death or emigration of the pride males was more likely to determine the timing of dispersal we analysed the subset of individuals which dispersed after the pride male died and new males were seen with the natal pride (N=40). The number of months between the death or eviction of resident males and new males being sighted with the natal pride ranged from 0 to 19 months (mean ± SD = 12 ± 8 months). A paired-samples *t*-test showed that there was a significant difference between the number of months to dispersal after the pride males had died or emigrated and after a new male was seen with the natal pride ($t_{1,39}$=8.97; $p<0.001$, Figure 2.5). Once the pride males had died or been evicted the time to dispersal for the sub-adults was highly variable (mean ± SD = 14.6 ± 8.9 months, range: 2-40 months) while dispersal occurred far sooner after a new male was first seen with their natal pride (mean ± SD = 1.6 ± 3.2; range: 0-10 months). In fact, 63% (N=25) dispersed within the same month that incoming males were first seen, and 26% (N=9) dispersed a month later. Finally, a chi-squared test showed that the season during which dispersal most frequently occurred shifted from the late dry season when incoming males were absent to the wet season when incoming males were present (χ^2=17.271, d.f.=2, $p<0.001$).

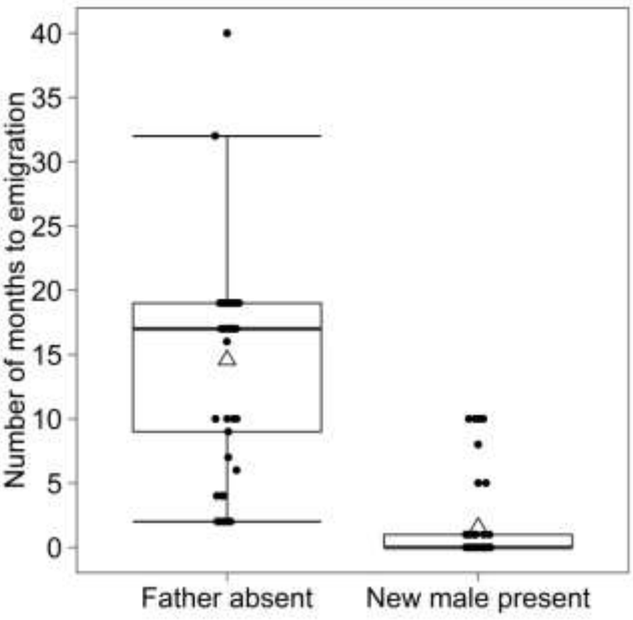

Figure 2.5: The number of months to emigration for sub-adult lions after the death/departure of the pride males and after a new male was first seen with their natal pride. Boxes show medians, 25% and 75% quartiles. Triangles indicate means. Whiskers indicate 10-90 percentiles. Dots represent the raw data.

Discussion

Our results show that for sub-adult male lions the probability of successful dispersal increases with dispersal age as those that dispersed young generally did not survive. Males dispersed between 20 and 42 months of age, but all those that dispersed under 31 months of age died during dispersal. Interestingly, the regression curve linking survival probability with dispersal age was very steep indicating that dispersal delayed by even a few months can drastically increase survival probability. In contrast, the age at which female sub-adults dispersed had no bearing on whether or not they survived dispersal.

That sub-adult males suffered high mortality if they dispersed when young is most likely due to their relatively small body size and inexperience. Lion body mass for males and females has a strong linear relationship with age ($r^2 = 0.98$ and 0.99

respectively) up until 36 months (Smuts *et al.* 1980). Thus lions that disperse when they are relatively young are at a competitive disadvantage and are likely unable to compete for territory with older, larger males. This may prolong the amount of time and increase the distance travelled as vulnerable transients which in itself could escalate mortality risk as reported for American martens (*Martes americana*; Johnson *et al.* 2009). Since not all dispersing lions were collared, we could not accurately determine the date of establishment for all individuals and thus did not analyse the time length of dispersal. However, our data provide some support for this hypothesis: for instance, a lone male lion that dispersed at the age of 27 months was transient for 848 days and travelled some 4,223 kilometres during the 16 months he was radio collared (Figure 2.1). During his transience phase he spent considerable time outside the protected area and was subsequently shot for raiding livestock. A similar fate was recorded for 27% (N=9) of our dispersing male study animals which were either shot as problem animals or subject to retaliatory killings. Thus our results are typical of a system impacted by trophy hunting and retaliatory killing, and hence characteristic of a population under anthropogenic pressure (Loveridge *et al.* 2010). In addition, increasing energy demands, coupled with hunting inefficiency and inability to compete for occupied territories, may result in dispersing lions taking more risks than do adults. Indeed, studies in Namibia and Kenya have reported that dispersing sub-adult lions are more prone to stock-raiding than adults (Stander 1990, Patterson *et al.* 2003, Patterson *et al.* 2004). Furthermore, studies that have reported mortalities during dispersal in other species frequently note that the cause is anthropogenic (e.g. Kenward *et al.* 1999, Real and Mañosa 2001, Klar *et al.* 2009, Smallwood *et al.* 2009).

Our findings are consistent with studies in other taxa that reported increased costs among young male dispersers (Waser *et al.* 1994, Ekman *et al.* 1999, Tarwater and Brawn 2010, Sparkman *et al.* 2011). For instance, Waser *et al.* (1994) reported that the survival rate of dispersing male dwarf mongooses (*Helogale parvula*) increased with age. While mongooses of both sex dispersed, only males had increased survival with dispersal age. Indeed, the costs of dispersal are expected to vary at an individual level according to sex (Bowler and Benton 2005). It is likely that female lions dispersed younger than males since sexually mature females are likely to remain and mate with immigrant males (Hanby and Bygott 1987). That female dispersal age had no bearing on their survival is typical of polygynous mammals, where females are less prone to mortality, particularly in sexually dimorphic species (Clutton-Brock and Iason 1986).

The range of male dispersal ages (20-45 months) was similar to that reported in the Serengeti National Park and the Ngorongoro Crater, Tanzania (20-65 months; Hanby and Bygott 1987), whereas in Kruger National Park, South Africa, sub-adults tended to disperse older (36-60 months) which may have improved their survival (Funston *et al.* 2003). The timing of dispersal for both sexes was most highly related to the take-over of the natal pride by unfamiliar adult males. This finding is consistent with that of Hanby and Bygott (1987) and behavioural data collected during their study showed that incoming males were intolerant of all lions except females that were sexually receptive and effectively evicted all other sub-adults. This is in line with our field observations and it is likely that a similar mechanism was occurring. Similarly, the role of parental tolerance in delaying dispersal was experimentally shown in Siberian jays (*Perisoreus infaustus*) where the removal of fathers resulted in the dispersal of offspring, particularly when they were replaced by despotic immigrant males (Ekman and Griesser 2002). Our study takes such findings one step further to show that age at dispersal has significant implications for survival, which may be particularly pronounced in ecosystems and species affected by a high off-take of adult males.

We had expected that the benefits of group size (Clutton-Brock 2002) would translate into increased dispersal success for larger groups. While there was a tendency of support for this hypothesis, the relationship between dispersal age and dispersal success had far greater explanatory power. Indeed, as Funston *et al.* (2003) noted, fully mature males can resist younger males, even when outnumbered. Similarly, we had anticipated that dispersal timing may be density-dependent. However, neither the age of sub-adults when new cubs were born nor the number of sub-adults in an age set appeared to influence dispersal timing. Pride biomass did appear in our top candidate models indicating that in the absence of incoming adult males, this variable may have more influence.

While many mammals disperse seasonally, for example the Eurasian badger (*Meles meles*; Macdonald *et al.* 2008), lions dispersed throughout the year and the relationship between season and dispersal timing was not straightforward. Overall, dispersal occurred most frequently in the wet season but this was largely the period when incoming males were present; dispersal most frequently occurred in the late dry season if incoming males were not present. Between 1999 and 2012 we recorded 77 anthropogenically caused adult male mortalities. Of these, 56% occurred during the late dry season (which is typically the trophy hunting season), 29% in the early dry season and 16% in the wet season (Loveridge, unpublished data). It follows then that territorial males killed in the late dry season were frequently replaced in the wet season and dispersal was triggered.

Sub-adults that dispersed in the early and late dry seasons tended to be older than those that dispersed in the wet season, leading us to tentatively propose that the dry season is an optimal dispersal time. In the semi-arid savannah of Hwange, the ecology of lions is heavily influenced by artificial waterholes, particularly in the dry season when lions thrive as prey animals are generally more vulnerable and their distribution more predictable (Valeix *et al.* 2010). It is therefore unlikely that increased competition is driving dispersal in the dry season, but rather it represents an optimal dispersal window.

Free-ranging populations that suffer high levels of anthropogenic mortality, such as our study population (Loveridge *et al.* 2010), experience an increased rate of male turnover, often resulting in infanticide (Swenson *et al.* 1997, Loveridge *et al.* 2007c). Our study reveals a previously undescribed, secondary 'delayed infanticide' that may be amplified in populations that experience a high off-take of resident adult males. In summary, it appears that the timing of lion dispersal is highly related to the presence of incoming males, leading to an increased mortality rate for male lions that disperse younger than 31 months of age. It is plausible then, that in ecosystems with minimal off-take of adult males, dispersal would occur later and be more successful. These results have implications for the management of lions and should be considered in the same way as infanticide when setting hunting quotas for lions (e.g. Whitman *et al.* 2004).

Appendix

Appendix 2.1: Summary of model selection statistics for linear models investigating the timing of dispersal for lions in Hwange National Park. Our explanatory variables consisted of (1) 'new_males' – a class variable for incoming male present or absent at the time of each dispersal event; (2) 'N.S' – the number of sub-adults over 18 months in the natal pride at the time of each dispersal event; (3) 'sex' – sex of dispersers; (4) 'P.B.' – pride biomass; (5) 'ASWCB' – the age of individual sub-adults when new cubs were born. Models were ranked according to Akaike weights (w_i) based on the Akaike Information Criterion for small sample size (AICc). Models in bold indicate the two top models which were averaged correcting for model weights. In all models group identity was entered as a blocking factor. Included are the log likelihood, the AICc differences (Δi) and the number of parameters (K).

Response variable	Rank	Model	log likelihood	AICc	Δi	w_i	K
Age at dispersal (months)	**1**	**new males + sex + P.B.**	**-197.97**	**409.37**	**0.00**	**0.40**	**6**
	2	**new males + sex**	**-199.89**	**410.78**	**1.41**	**0.20**	**5**
	3	new males + sex + ASWCB	-199.09	411.60	2.23	0.13	6
	4	new males * sex	-199.89	413.20	3.82	0.06	6
	5	new males + N.S. + sex	-199.89	413.21	3.84	0.06	6
	6	sex + ASWCB	-201.26	413.51	4.14	0.05	5
	7	new males + N.S. + sex + ASWCB	-199.06	414.05	4.68	0.04	7
	8	N.S. + sex + ASWCB	-200.71	414.83	5.46	0.03	6
	9	sex + P.B. + ASWCB	-201.12	415.66	6.29	0.02	6
	10	sex	-203.96	416.57	7.20	0.01	4
	11	P.B. + sex	-203.37	417.73	8.36	0.01	5
	12	N.S. + sex	-203.48	417.95	8.58	0.01	5
	13	new males	-206.08	420.82	11.44	0.00	4
	14	new males + P.B.	-205.19	421.37	12.00	0.00	5
	15	new males + N.S.	-205.59	422.18	12.81	0.00	5
	16	new males + ASWCB	-205.66	422.33	12.96	0.00	5
	17	new males + N.S. + ASWCB	-204.92	423.27	13.90	0.00	6
	18	new males + P.B. + ASWCB	-205.11	423.65	14.28	0.00	6
	19	N.S. + ASWCB	-206.41	423.82	14.45	0.00	5
	20	ASWCB	-208.59	425.84	16.46	0.00	4
	21	N.S.	-208.76	426.18	16.81	0.00	4
	22	P.B. + ASWCB	-208.58	428.17	18.79	0.00	5
	23	P.B.	-210.66	429.98	20.61	0.00	4
	24	NULL	-223.46	451.10	41.73	0.00	2

Chapter 3

Differences in rest site selection by dispersers and adults: The case of the African lion

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Statement of authorship: NE collected data, performed modelling work and analysed output data; SP collected data; AL and DM oversaw this project; NE wrote the first draft of the manuscript and all authors contributed to revisions

Abstract

Resource selection is frequently studied at a species level, ignoring individual variation and changing life stages. However, individual needs vary throughout ontogeny and this may be reflected in space use. We investigated fine-scale space use in lions by examining rest site selection of both dispersing males and territorial adult males. We visited 104 rest sites and 69 random points in order to examine the effects of habitat, visibility, distance to water, distance to road and distance to territorial males on rest site selection. The primary factor influencing rest site selection for dispersing males was that they be far from territorial males. Their rest sites were randomly selected based on their visibility, distance to roads and water, but they did select for bushed grasslands. The rest sites of territorial males were characterised by high visibility, bushed grassland habitat and close proximity to roads and waterholes. We suggest that these results highlight divergent strategies as dispersers are subordinate to territorial males and thus seek to avoid them. In addition, territorial males have knowledge of their surroundings and select for specific habitats and environmental features that allow them to maximise the resources therein.

Introduction

Resource selection and space use are central themes in ecology, influencing a range of processes from species coexistence to evolution (Morris 2003, Broekhuis *et al.* 2013). Despite its importance, space use is frequently assessed at a species level, under the assumption that individuals do not differ and that preferences remain constant throughout ontogeny (Campioni *et al.* 2012). However, space use may vary intra-specifically, with differences occurring at an individual level (Boydston *et al.* 2003), according to reproductive state (McLoughlin *et al.* 2002, Mackie and Racey 2007), social rank (Ekman and Askenmo 1984), sex (Clutton-Brock *et al.* 1987, McLoughlin *et al.* 2002, Rodway *et al.* 2003) or age (Rodway *et al.* 2003, Pettorelli *et al.* 2009).

Space use by adults has been studied for many species, but much less so during natal dispersal (hereafter dispersal). Consequently, it is still largely unknown for many mammal species whether dispersers and adults utilise their environment in a similar manner (Palomares *et al.* 2000, Selonen and Hanski 2006). Soulé (1991) proposed that residents use habitats that satisfy all life-history requirements, whereas habitats used during dispersal only need to provide resources required by individuals moving through patches. In general, resources in space and time can be utilised more efficiently if an individual is familiar with its surroundings i.e. has ‘a cognitive map’ (Vuilleumier and Perrin 2006, Gautestad *et al.* 2013). While adults may have spatial and temporal knowledge of their surroundings, natal dispersers moving through novel environments may not (Campioni *et al.* 2010). This may be particularly pronounced in territorial species for which the priorities of residents and dispersers are likely different (Delgado *et al.* 2009). Therefore adult space use may not be an accurate predictor of dispersal space use (Selonen and Hanski 2006).

We compared the space use of adult and dispersing African lions (*Panthera leo*). African lions are a revealing model species to study fine-scale space use during dispersal as there is an extensive literature on their resource selection, including use of vegetative cover during hunts (Funston *et al.* 2001, Hopcraft *et al.* 2005), reliance on waterholes (Valeix *et al.* 2010), preference for killing in thick vegetation (Davidson *et al.* 2012) and general habitat selection (Schaller 1972, Davidson *et al.* 2011, Broekhuis *et al.* 2013). Conversely nothing is known of space use by dispersing lions.

Dispersal in lions is sex-biased as sub-adult males always disperse while females rarely do (Pusey and Packer 1987). Two factors likely to influence space use by male dispersers are limited knowledge of their surroundings and the avoidance of territorial adults. Male lions continue to grow until seven years of age and are at their prime between five and seven years old (Smuts *et al.* 1980). In Serengeti National Park and the Ngorongoro Crater, Tanzania sub-adult males had a wide range of dispersal ages (20-65 months; Hanby and Bygott 1987), whereas in Kruger National Park, sub-adults tended to disperse older (36-60 months; Funston *et al.* 2003). Since dispersers are younger, they are morphologically smaller than adult males and thus are at a competitive disadvantage. Furthermore, territorial males do not tolerate the presence of non-coalition members in their territories and encroachment may result in physical conflict (Grinnell *et al.* 1995, Packer 2001). Due to their limited knowledge of surroundings, inexperience and smaller size, we expect dispersers to utilise the landscape differently to territorial males.

In order to investigate fine-scale space use, we examined and compared rest site selection of dispersing males and territorial adult males. Rest sites are important because lions are opportunist, stalk-and-ambush hunters and may be inactive for up to 20 hours per day (Schaller 1972). Since lions rely on vegetative cover for concealment (Funston *et al.* 2001, Hopcraft *et al.* 2005), we expected that both habitat type and visibility would be important factors in rest site selection. In Hwange National Park (HNP), Zimbabwe, where this study was conducted, prey select areas close to waterholes (Valeix *et al.* 2009) and subsequently so do lions (Valeix *et al.* 2010). We therefore expected that territorial males would select rest sites in close proximity to waterholes. Roads inside HNP directly connect perennial waterholes and were historically built along major game trails. Since lions may rotate between waterholes (Valeix *et al.* 2011), we expected that territorial lions would use roads to travel between waterholes and therefore preferentially rest close to them. For dispersing males, we expected that their space use would reflect a motivation to minimise encounters with territorial males while maximising hunting success, thereby displaying a balance between concealment and visibility (Camp *et al.* 2012). In addition, due to lack of familiarity with their surroundings we expected dispersing lions not to show strong environmental selection, consistent with other dispersing predators (Beier 1995, Miller *et al.* 1997). More specifically, we hypothesised that they would select rest sites far from territorial males, in habitats offering concealment and further from waterholes and roads compared to territorial males.

Methods

Study area

HNP is situated in north-western Zimbabwe (19°00'S, 26°30'E) and covers an area of approximately 14,900km^2. The core study area (≈7000km^2) included the northern and central parts of HNP. The vegetation is primarily woodland and bushland savannah, interspersed with small patches of grassland (Rogers 1993). HNP is semi-arid with a wet season from October to April and a dry season from May to September. The long term mean annual precipitation is 613mm, which varies considerably (CV≈26%). Surface water available to animals is primarily from rainwater collected in natural depressions. However, most of these do not hold water in the dry season, when water is artificially supplied to around 50 waterholes (Valeix *et al.* 2010).

Lion data

Between May and October 2011, eight lions (five territorial males and three dispersing sub-adult males) were fitted with Global Positioning System (GPS) radio-collars (see Loveridge *et al.* 2007c for details of capture and handling). All individuals were from different social groups and the data used for dispersing males were from the transience phase of dispersal while individuals were outside their natal range. The transience phase was deemed to have commenced once the sub-adult had left its natal pride and did not return thereafter. GPS collars were programmed to take hourly fixes during the night from 18:00h to 07:00h. Using these GPS data individual rest sites were defined as a cluster of locations where a minimum of two consecutive GPS fixes were in the same location. Only night time rest sites were selected as this is when lions are active and more likely to encounter conspecifics as well as prey. To ensure that rest sites were accessible for observers to collect environmental data (see below) we visited only those rest sites within a 1km buffer of any road. It is unlikely this sampling regime caused a bias as roads did not follow any particular habitat type. In total we visited 157 clusters. On arrival at a cluster, a detailed inspection of the area was carried out to ensure no feeding had occurred. Sites where remains of a kill were found (N=53) were excluded from this analysis, resulting in a total of 104 rest sites, 58 for dispersing males and 46 for territorial males.

To investigate whether rest site selection was random, we compared actual rest sites to randomly selected points (used vs. available). Within the 1km buffer zone along roads, we created 100 random points of which we visited 69. We used the same set of random points for the analysis of rest site selection of dispersing and territorial males, selecting the same number of 'available' sites as there were 'used' sites for each individual lion. Since dispersers do not have defined home-ranges, the available points for each individual were randomly selected from the entire dataset, ensuring that no available point was used twice. The adult males were territorial, potentially restricting the habitat that is available to them. Therefore we randomly selected available sites within each adult male's home-range. Individual home-ranges were created using all the GPS locations collected during this six month study period and were calculated based on the 95% isopleth using a Kernel Density Estimate (KDE) function. Kernel isopleths were calculated using the reference smoothing factor h_{ref} as recommended by Hemson *et al.* (2005).

Environmental variables

For each rest site and random point we calculated the distance to the nearest waterhole, the distance to the nearest road, visibility and habitat type. The distances to the nearest waterhole and road were calculated in QGIS (Quantum GIS Development Team 2012) whilst data on visibility and habitat were collected in the field. To ensure minimal vegetation change during the study period no sites were visited after the first rains.

The visibility at each rest site was assessed using two 50cm x 50cm white boards attached to a pole. The first board was set at 10-60cm and the second was at 100-150cm to roughly represent the heights of a sitting and a standing lion, respectively. One person stood at the rest site holding the visibility board while the second person walked away from it in each of the four cardinal directions. The distance at which each board could no longer be seen was measured using a handheld GPS device (Garmin eTrex Legend Hcx; Garmin, Olathe, Kansas, USA) with an accuracy of ± 4m. The distances in each cardinal direction were then averaged to give a mean visibility measure at each site. As there was a correlation between the mean visibility of the two markers (Pearson: N=104; r=0.96;

$p<0.001$) only the mean visibility for the lower marker was used as it better represents a resting lion.

Habitat type at each rest site was recorded as bushed grassland, bushland, woodland or wooded bushland. Classification was based on the dominant vegetation immediately surrounding the visibility board. Full definitions of these habitat types within HNP can be found in Davidson *et al.* (2012).

In order to test whether dispersing males chose rest sites based on proximity to territorial males we calculated the distance of each dispersal rest site and random point to the nearest territorial male, using contemporaneous GPS data. We included only those dispersal rest sites (N=51) that fell within the 95% home-ranges of GPS collared territorial males to ensure that we included only those where the proximity to the nearest territorial male was known.

Statistical analysis

Characteristics of dispersing and adult male rest sites

Rest site selection was modelled separately for dispersers and territorial males. To determine the characteristics of disperser and adult male rest sites, lion locations (1) were compared to random points (0) using generalised linear mixed models (GLMMs) with a binomial error structure and logit-link function. For dispersing males, we created 31 *a priori* candidate models to assess the probability of a site being selected as a function of visibility, distance to waterholes, distance to roads, habitat type and distance to nearest adult male. For territorial males we created 15 *a priori* candidate models to assess the probability of a site being selected as a function of visibility, distance to waterholes, distance to roads and habitat type.

To identify the best model we used model selection based on Akaike Information Criterion corrected for small sample size (AICc). When one model was clearly superior

(w_i>0.9) this was used, otherwise we obtained parameter estimates and unconditional confidence intervals by averaging across the models, correcting for model weights using R package AICcmodavg v.1.30 (Burnham and Anderson 2002, Mazerolle 2013).

Comparison of rest sites between dispersing and adult males

We tested whether the visibility, distance to water and distance to road varied depending on whether an individual was dispersing or territorial using linear mixed models. A Chi-square test was used to assess the differences in habitat type at rest sites between dispersing and territorial males.

In all models, lion identity was entered as a random effect. Statistical analyses were performed in R 2.15.1 (R Core Team 2012). Models and model comparison statistics for generalised linear mixed models can be found in Appendix 3.1 and 3.2.

Results

Characteristics of dispersing male rest sites

Dispersing male lions primarily selected rest sites based on their lack of proximity to territorial males. The probability of selecting a rest site increased with increasing distance to adult males (estimate ± SE = 0.787 ± 0.197; CI = 0.401– 1.172; Figure 3.1). Dispersing lions also prefered to rest in bushed grassland vegetation compared to bushland (estimate ± SE = -2.236 ± 1.052; CI = -4.297 – -0.175), wooded bushland (estimate ± SE = -3.856 ± 1.722; CI = -7.230 – -0.481) or woodland (estimate ± SE = -3.982 ± 1.517; CI = -6.955– -1.009).

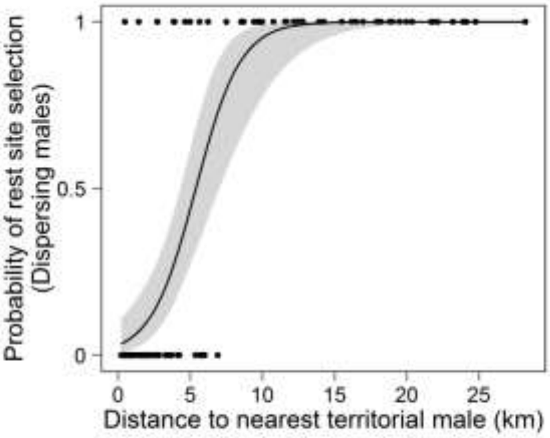

Figure 3.1: The probability of rest site selection by dispersing male lions as a function of the distance to the nearest territorial male lion in Hwange National Park, Zimbabwe.

Characteristics of adult male rest sites

Territorial male lions preferentially rested in areas of higher visibility (estimate ± SE = 0.037 ± 0.011; CI = 0.014 – 0.06; Figure 3.2) and selected rest sites closer to waterholes (estimate ± SE = -0.519 ± 0.186; CI = -0.884 – -0.155; Figure 3.2) and closer to roads (estimate ± SE = -0.002 ± 0.001; CI = -0.004 – -0.001; Figure 3.2) than expected by chance. Territorial males prefered to rest in bushed grassland vegetation compared to wooded bushland (estimate ± SE = -2.353 ± 1.026; CI = -4.364 – -0.342).

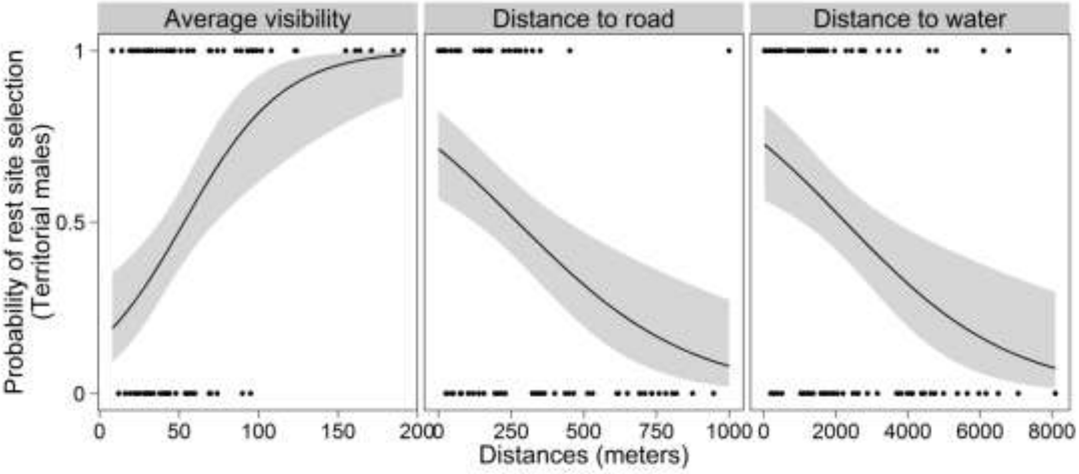

Figure 3.2: The probability of rest site selection by territorial male lion rest sites as a function of mean visibility, distance to water and distance to road

Comparison of rest sites between dispersing and adult males

Dispersing male lions utilised rest sites with lower visibility (mean ± SD = 50 ± 43m) compared to territorial males (mean ± SD = 77 ± 51m; t=-2.45, d.f.=6, p=0.05; Figure 3.3a). Rest sites of dispersing males tended to be further from roads (mean ± SD = 314 ± 338m) than those of territorial males (mean ± SD = 179 ± 272m, t=2.22, d.f.=6, p=0.069; Figure 3.3b). On average, dispersing male rest sites were further from waterholes (mean ± SD = 2,237 ± 1,382m) compared to territorial males (mean ± SD = 1,686 ± 1539m) but this was not significant (t=1.92, d.f.=6, p=0.103). Habitat type at rest sites did not differ between the two statuses (χ^2=1.124, d.f.=3, p=0.771).

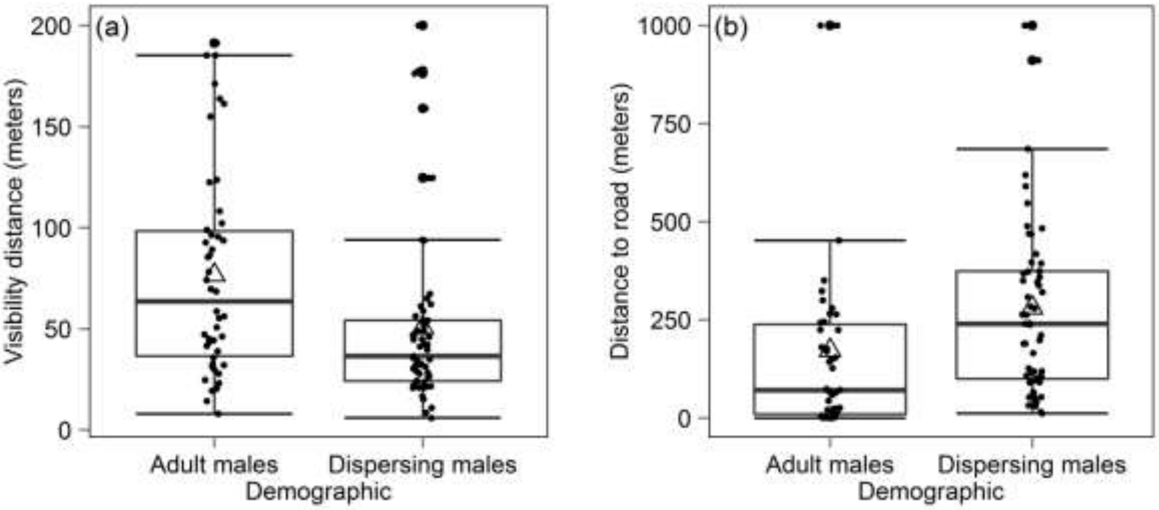

Figure 3.3: Comparison of rest sites between territorial male lions and dispersing male lions in terms of their environmental characteristics in Hwange National Park, Zimbabwe in relation to (a) mean visibility, (b) mean distance to road.

Discussion

Dispersing male lions showed marked differences in their rest site selection compared to territorial males. Dispersing males selected rest sites that were further from territorial males than expected by chance, and in areas of bushed grassland. In contrast, territorial males selected rest sites in areas of high visibility, in bushed grassland and close to waterholes, which are known prey hot-spots (Valeix *et al.* 2010). They also selected rest sites close to roads which provide direct routes between waterholes. We propose that these differences reflect divergent strategies as dispersers are subordinate to territorial males and thus seek to avoid them. In addition, territorial males have spatial and temporal knowledge of their surroundings and thus select for environmental attributes that allow them to maximise the resources therein.

In selecting rest sites, dispersers take into account their proximity to adult males. Indeed only a small proportion (12%, N=6) of disperser rest sites were found within 4km of the nearest adult male. Territorial lions advertise their presence with long distance calls or roars and the listener is able to gauge the group size of those calling (McComb and Packer 1994). Roars also function to intimidate rivals and strengthen bonds within groups (Grinnell *et al.* 1995, Grinnell and McComb 1996). It is likely that dispersers were able to detect their larger territorial counterparts through their roars and avoided resting in close proximity to them. Similarly, cheetahs (*Acinonyx jubatus*), which like dispersing lions, are competitively subordinate to adult lions, positioned themselves further than random from both lions and spotted hyaenas (*Crocuta crocuta*; Broekhuis *et al.* 2013).

Both territorial males and dispersing males preferentially rested in bushed grassland despite 92.1% of HNP being covered by woody vegetation (Rogers 1993). A previous study in HNP showed that while adult lions select bushed grassland, their kills were preferentially made in thicker habitats (Davidson *et al.* 2012). Therefore the results from the present study indicate that lions sit and wait in open areas where they can observe potential prey before moving into thicker habitats where they are more likely to kill (Davidson *et al.* 2012). Open areas have the added advantage of allowing for detection of conspecifics and competitors. Indeed, territorial males selected rest sites with high visibility, vantage points from which they could assess prey and potential competitors. Dispersing males on the other hand, utilised rest sites with lower visibility compared to territorial males. The reasons for this could be three-fold: the use of rest sites with lower visibility provides greater concealment from competitors and prey (Camp *et al.* 2012) and/or dispersers are not yet experienced enough to be able to optimise their space use to the extent that territorial males do. Finally dispersing lions may be out-competed by their territorial counterparts and forced into suboptimal space use. Interestingly, Funston *et al.* (2003) found that in Kruger National Park, sub-adult males dispersed over short distances, sometimes remaining with the natal area, and attributed this in part to the dense vegetation, which enabled the dispersing males to conceal themselves.

In HNP, prey select areas close to waterholes (Valeix *et al.* 2009) and subsequently so do lions (Valeix *et al.* 2010). Water sources are also a key determinant of lion space use in the Serengeti ecosystem (Mosser *et al.* 2009). We therefore anticipated the result from our study that territorial males selected rest sites close to water. In fact 74% (N=34) of territorial male rest sites were within 2km of a waterhole. In contrast, rest site selection of dispersing males did not have a strong relationship with distance to water, probably because it is at waterholes where they are most likely to encounter territorial male lions and therefore dispersers did not rest close to them despite waterholes being associated with high prey densities (Valeix *et al.* 2009).

In addition, our expectation that territorial male lions would select rest sites in close proximity to roads was confirmed. With a lack of vegetation, roads present pathways of little resistance, and thus are easier to walk along. Furthermore, roads in HNP were built along natural game trails, going from one waterhole to another, often providing the shortest route between waterholes. A previous study showed that lions may rotate their hunting effort between waterholes (Valeix *et al.* 2011) and our results suggest a scenario whereby they might do so by utilising roads, stopping to rest either on or close to them. The rest sites of dispersing male lions had no relationship with distance to road. Territorial males frequently scent mark bushes at road verges (N. Elliot, pers. obs.) which could deter dispersing males from resting near roads, where they are also more likely to encounter adults.

While our sample size necessitates cautious conclusions, the present study adds to the growing body of evidence that individual needs vary in accordance with life stage which is reflected in changes of space use (Palomares *et al.* 2000, Campioni *et al.* 2012). In addition, our results support the suggestion of Selonen and Hanski (2006) that adult space use is not necessarily a good predictor of dispersal space use and accords with findings of suboptimal habitat use by dispersing lynx (*Lynx pardinus*) and tigers (*P. tigris*; Smith 1993, Palomares *et al.* 2000). This may be explained by the divergent strategies and constraints associated with territory holders versus dispersers. Territory holders need to defend their territory and access to mates. In addition, they have spatial and temporal knowledge of their surroundings and thus their space use maximises access to the resources within their territory. In contrast a disperser, free from the constraints of territoriality, may adopt a strategy to minimise encounters with territorial males through mechanisms such as spatial avoidance. Furthermore, natal dispersers frequently travel in unfamiliar areas and their space use may reflect an inability to actively select for environmental attributes that will maximise their resource use.

At present the majority of literature pertaining to dispersal habitat selection focus on the departure and settlement stages, mainly due to the difficulties associated with obtaining data on dispersing individuals as they move, often over long distances, through diverse habitats (Bowler and Benton 2005). As a result there is a paucity of information on movements and space use during dispersal. However in order to develop conservation strategies and manage a species in fragmented landscapes, information is needed on requirements during all life stages. Studies such as the present one are therefore crucial in furthering our understanding of how space use can shift depending on life stage.

Appendix

Appendix 3.1. Summary of model selection statistics for generalised linear mixed models (GLMMs) comparing dispersing male lion rest sites (1) with random sites (0). We analysed the probability of a site being selected as a function of distance to nearest territorial male (D.T.A.), visibility (vis), distance to waterholes (D.T.W.), distance to roads (D.T.R.) and habitat type (hab.). Models were ranked according to Akaike weights (w_i) based on the Akaike Information Criterion for small samples (AICc). Included are the log likelihood, the AICc differences (Δi) and the number of parameters (K). In all models the identity of individual lions was entered as a random factor. Since no one model was clearly superior (w_i >0.9) we averaged parameter estimates across those models with AICc differences (Δi<2; shown in bold) correcting for model weights. Model averaged parameter estimates and unconditional confidence intervals are reported in the main text.

Response variable	**Rank**	**Model**	**log likelihood**	**AICc**	**Δi**	**w_i**	**K**
Used (1) vs available (0)	**1**	**hab + D.T.A.**	**-20.21**	**53.29**	**0**	**0.33**	**6**
	2	**vis + hab + D.T.A.**	**-19.49**	**54.15**	**0.86**	**0.21**	**7**
	3	**hab + D.T.W. + D.T.A.**	**-20.05**	**55.28**	**1.99**	**0.12**	**7**
	4	hab + D.T.R. + D.T.A.	-20.21	55.59	2.30	0.10	7
	5	vis + hab + D.T.W. + D.T.A.	-19.40	56.33	3.04	0.07	8
	6	vis + hab + D.T.R. + D.T.A.	-19.47	56.48	3.19	0.07	8
	7	hab + D.T.W. + D.T.R. + D.T.A.	-20.04	57.62	4.33	0.04	8
	8	D.T.A.	-26.25	58.73	5.45	0.02	3
	9	D.T.R. + D.T.A.	-25.80	60.02	6.73	0.01	4
	10	D.T.W. + D.T.A.	-25.86	60.13	6.84	0.01	4
	11	vis + D.T.A.	-26.17	60.74	7.45	0.01	4
	12	D.T.W. + D.T.R. + D.T.A.	-25.57	61.76	8.47	0.00	5
	13	vis + D.T.R. + D.T.A.	-25.66	61.94	8.65	0.00	5
	14	vis + D.T.W. + D.T.A.	-25.71	62.04	8.75	0.00	5
	15	vis + D.T.W. + D.T.R. + D.T.A.	-25.37	63.62	10.34	0.00	6
	16	hab + D.T.W.	-62.33	137.54	84.25	0.00	6
	17	hab + D.T.W. + D.T.R.	-61.80	138.78	85.49	0.00	7
	18	vis + hab + D.T.W.	-62.32	139.82	86.53	0.00	7
	19	hab	-64.67	139.96	86.67	0.00	5
	20	hab + D.T.R.	-63.55	139.98	86.69	0.00	6
	21	D.T.W. + D.T.R.	-65.90	140.21	86.92	0.00	4
	22	vis + hab + D.T.W. + D.T.R.	-61.78	141.08	87.80	0.00	8
	23	D.T.W.	-67.65	141.54	88.25	0.00	3
	24	vis + hab	-64.58	142.04	88.75	0.00	6
	25	vis + hab + D.T.R.	-63.51	142.21	88.92	0.00	7
	26	vis + D.T.W. + D.T.R.	-65.83	142.28	88.99	0.00	5
	27	D.T.R.	-68.41	143.06	89.77	0.00	3
	28	vis + D.T.W.	-67.45	143.31	90.02	0.00	4
	29	vis + D.T.R.	-68.04	144.48	91.19	0.00	4
	30	NULL	-71.39	146.90	93.61	0.00	2
	31	vis	-70.52	147.28	94.00	0.00	3

Appendix 3.2. Summary of model selection statistics for the generalised linear mixed models (GLMMs) comparing territorial male lion rest sites (1) with random sites (0). We analysed the probability of a site being selected as a function of visibility (Vis), distance to waterholes (D.T.W.), distance to roads (D.T.R.) and habitat type (Hab.). Models were ranked according to Akaike weights (w_i) based on the Akaike Information Criterion for small samples (AICc). Included are the log likelihood, the AICc differences (Δi) and the number of parameters (K). In all models the identity of individual lions was entered as a random factor. Since no one model was clearly superior (w_i>0.9) we averaged parameter estimates across those models with AICc differences (Δi<2; shown in bold) correcting for model weights. Model averaged parameter estimates and unconditional confidence intervals are reported in the main text.

Response variable	**Rank**	**Model**	**log likelihood**	**AICc**	**Δi**	**w_i**	**K**
Used (1) vs	**1**	**vis + D.T.W. + D.T.R.**	**-42.79**	**96.29**	**0**	**0.59**	**5**
available (0)	**2**	**vis + hab + D.T.W.**	**-41.32**	**97.97**	**1.69**	**0.25**	**7**
	3	vis + hab + D.T.R.	-42.56	100.46	4.17	0.07	7
	4	vis + D.T.W.	-46.23	100.93	4.64	0.06	4
	5	vis + D.T.R.	-47.63	103.71	7.43	0.01	4
	6	hab + D.T.W. + D.T.R.	-44.56	104.45	8.16	0.01	7
	7	vis + hab	-46.85	106.69	10.40	0.00	6
	8	hab + D.T.W.	-47.10	107.19	10.90	0.00	6
	9	hab + D.T.R.	-47.93	108.84	12.55	0.00	6
	10	vis	-52.92	112.12	15.83	0.00	3
	11	D.T.W. + D.T.R.	-51.91	112.29	16.00	0.00	4
	12	hab	-52.45	115.59	19.30	0.00	5
	13	D.T.R.	-55.57	117.40	21.12	0.00	3
	14	D.T.W.	-57.62	121.52	25.23	0.00	3
	15	(1 | id)	-63.77	131.67	35.39	0.00	2

Chapter 4

Movements vary according to dispersal status, group size and rainfall: the case of the African lion

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Statement of authorship: NE collected data, performed modelling work and analysed output data; SC assisted with modelling techniques; AL and DM oversaw this project; NE wrote the first draft of the manuscript and all authors contributed to revisions

Abstract

Dispersal is one of the most important life-history traits affecting species persistence and evolution and is increasingly relevant for conservation biology as ecosystems become more fragmented. However, movement behaviour during different dispersal stages has been difficult to study and remains poorly understood. We analysed movement parameters and patterns of autocorrelation from GPS data for 20 lions over a five year period. We compared movement behaviour among different stages of natal dispersal (departure, transience and settlement) in addition to that of territorial adults of both sexes. The movement behaviour of lions was influenced by dispersal status, sex, group size and rainfall. During dispersal, lions moved faster and further and in a more directional manner than pre- or post-dispersal. In addition, transient movement was more directional than adult movement, although territorial males moved faster and further per night than did transient males. The effect of group size on movement differed with sex and dispersal status; solitary dispersers moved faster and further than individuals in bigger groups, while territorial males had the opposite trend. Our results suggest that movement behaviour reflects a transition from directional movement during transience to random or periodic use of a fixed territory after settlement. In addition group size may affect the search and settlement strategies of dispersers while seeking a territory in which to settle.

Introduction

Dispersal is one of the most important life-history traits involved in species persistence and evolution (Clobert *et al.* 2001). As ecosystems become more fragmented dispersal is increasingly important as it is often the only mechanism by which organisms can move between populations and thus maintain genetically diverse meta-populations (Clobert *et al.* 2012). Despite its importance, little is known about dispersal movement behaviour or the search strategies employed by dispersing individuals as they move through novel environments. This is largely due to the practical difficulties associated with data collection of this often once-in-a-lifetime event. However mortality rates, distances travelled and selection of settlement sites largely depend on the search strategy of the disperser (Conradt *et al.* 2003, Doerr and Doerr 2004, Conradt and Roper 2006). The paucity of data on dispersal movement has resulted in most population and evolution models assuming that individuals move at random in heterogeneous environments (for a review see Patterson *et al.* 2008). However, recent evidence suggests that dispersal movements are highly complex and may vary depending on the three stages of dispersal (departure, transience, settlement; Clobert *et al.* 2001, Clobert *et al.* 2009, Delgado *et al.* 2009). A thorough assessment of the ecological and evolutionary implications of dispersal thus requires robust empirical studies, which have been lacking and widely called for by recent reviews (Jacobson and Peres-Neto 2010, Clobert *et al.* 2012, Baguette *et al.* 2013). Such studies will inform conservation strategies (Macdonald and Rushton 2003) and improve the way dispersal is represented in simulation models (Zollner and Lima 2005) and connectivity studies (Schwartz *et al.* 2009).

Shifting between dispersal statuses brings about changes in animal behaviour (Gese 1998), particularly in territorial species where territory holders and dispersers show discernible ecological differences (Campioni *et al.* 2012). In addition to dispersers being relatively uninformed of key spatial and temporal characteristics of the new environment, dispersers and territory holders have different goals in that dispersers aim to establish a territory while avoiding conspecifics, whereas established individuals need to maintain their territory and defend access to mates (Campioni *et al.* 2010).

While the study of movement patterns during dispersal is an emerging ecological field, the study of movement ecology is vast and advanced (for reviews see Holyoak *et al.* 2008, Schick *et al.* 2008) and can be integrated into dispersal studies. For example, Schick *et al.* (2008) argue that it is essential to understand the interaction between environmental conditions and the state of the organism to understand the drivers of biologically-based transition processes. Various empirical studies on vertebrates have highlighted behavioural differences between the different dispersal phases in birds (Stutchbury 1991, Delgado and Penteriani 2008), reptiles (Aragón *et al.* 2006) and to a lesser extent mammalian carnivores (Gese 1998); however, there is a lack of research linking these internal states (dispersal stages) to characteristics of the external environment, which is imperative to understanding the drivers of movement (Schick *et al.* 2008). To our knowledge, there has been no research that investigated seasonal movement patterns during dispersal in comparison with territorial adults of the same species and how this varies depending on social grouping. Doing so provides a unique opportunity to evaluate the shifting search strategies of dispersers and obtain insight into the drivers of their movement. To this end, we studied the movement ecology of African lions (*Panthera leo*) in all three dispersal phases in addition to adult lions of both sex.

Lions live in fission-fusion groups (Packer *et al.* 1990) and prides defend their territories. Adult males do not tolerate the presence of non-coalition members, with territorial encroachment usually resulting in conflict (Grinnell *et al.* 1995, Packer 2001). Dispersal in lions is sex-biased as sub-adult males always disperse while females are usually philopatric (Pusey and Packer 1987). During ‘departure’, most individuals conduct prospecting searches outside their natal territory prior to eventual departure (Elliot, unpublished data). Little is known of the ‘transience’ and ‘settlement’ phases, but dispersing lions either settle in a vacant area or challenge resident males for territory. While many mammals, for example the Eurasian badger (*Meles meles*), disperse seasonally and over short periods of time (Macdonald *et al.* 2008), lions may disperse throughout the year and the number of transient months can be relatively prolonged, making it possible to gather substantial quantities of data during dispersal.

In this paper we investigate nine predictions (Table 4.1) relating to the hypothesis that individual needs vary in accordance with life stage, bringing about broad behavioural changes, such as shifting movement patterns and search strategies (Zollner and Lima 1999, Van Dyck and Baguette 2005, Zollner and Lima 2005, Stamps 2006, Schick *et al.* 2008, Penteriani *et al.* 2011). In order to achieve this we utilise an extensive dataset based on five years of fine-scale GPS data collected on 21 lions of varying statuses. We analysed patterns of autocorrelation and classified movement as directional, periodic or random, in addition to calculating various movement parameters. We then examine whether movement behaviour of lions differs depending on their demographic category (pre-dispersal, transient, post-dispersal, territorial adult), sex, group size and rainfall.

Table 4.1. Predictions of hypotheses relating to the movement of lions in different demographic categories and how their movement is influenced by rainfall and group size.

Dataset †	Prediction
Comparing sub-adult dispersal stages	*1. Transient lions move fastest and furthest* [1, 2] **2. Transient lions display most directional movement** [3, 4, 5] **3. Post-dispersal lions cease directional movements and display random and periodic movement**
Comparing transients and territorial adults	*4. Transients move slowest and less far per night* [6] **5. Transient individuals display more directional movement** [3] **6. Territorial adults predominantly display periodic movements** [7] *7. Territorial adults respond to rainfall while dispersers do not* [8, 9, 10] **8. Transients in smaller groups move more per night compared to larger groups** [11, 12] *9. Territorial adults in bigger groups move further per night compared to smaller groups* [8]

Notes: **Bold** = supported predictions, *italics* = partially supported or weak support.

† We analysed two different datasets in order to compare the demographic groups therein: the first consisted of pre-, transient and post-dispersal; the second consisted of transients, territorial males and territorial females.

Predictions based on hypotheses and findings: [1] Delgado *et al.* 2009; [2] Campioni *et al.* 2012; [3] Zollner and Lima 1999; [4] Van Dyck and Baguette 2005; [5] Stamps 2006; [6] Zollner and Lima 2005; [7] Valeix *et al.* 2010; [8] Loveridge *et al.* 2009; [9] Campioni *et al.* 2010; [10] Vuilleumier and Perrin 2006; [11] Packer *et al.* 1988; [12] Baguette and Van Dyck 2007

Methods

Study area

The study area (≈7,000km^2) was located in the northern section of Hwange National Park (HNP), Zimbabwe (19°00′S, 26°30′E). HNP covers ≈15,000km^2 of semi-arid savannah. Vegetation consists primarily of woodland and bushland savannah (64%) and communities are dominated by *Baikiaea plurijuga*, *Colophospermum mopane*, *Combretum* spp., *Acacia* spp. and *Terminalia sericea* (Rogers 1993). The long-term mean annual rainfall of 613mm is highly variable (CV≈26%) and generally falls between October and April. Surface water is available from seasonal waterholes, although only a few hold water in the dry season, during which time water is artificially supplied to some (≈50) waterholes.

Lion movement data

Between 2007 and 2012, we obtained movement data from 20 lions, in different social groups (9 sub-adult males, six territorial adult males and five territorial adult females). Each was fitted with a GPS enabled radio-collar (see Loveridge *et al.* 2007c for details) pre-programmed to take hourly fixes when lions are active (1800-0700).

Data preparation

To ensure accuracy, only fixes with a Dilution of Precision (DOP) <10 were retained for analysis (Frair *et al.* 2010). This resulted in a dataset of 40,669 locations for sub-adult males (93% DOP<5), 72,030 locations for territorial males (96% DOP<5) and 60,139 locations for territorial females (97% DOP<5).

In order to reduce the effects of non-stationarity (Cushman *et al.* 2005) the study period was split into sequential, non-overlapping temporal windows of 30 day intervals. In total we created 56 window periods, the first starting 01 October 2007 and the last on 22 May 2012. The data for each individual lion were split according to these windows, resulting in a total dataset of 446 windows.

Mantel correlograms

Mantel correlograms reveal patterns of spatial and temporal autocorrelation which are highly informative in elucidating scales and patterns of ecological processes and provide a detailed picture of movement variability (Legendre 1993, Cushman *et al.* 2005). To identify different movement patterns for each window and individual we calculated two matrices (distance and time): The distance matrix was produced by calculating geographical distances between each pair of locations and the time matrix was computed by calculating the difference in decimal days between each pair of locations. We then used

Mantel tests to assess the level of association between these two matrices (Mantel 1967). We computed Mantel correlograms (Oden and Sokal 1986) to assess the levels of spatial autocorrelation in lion movements across a range of lag times. Correlograms were plotted for each individual as a surface to provide a visualisation of the patterns and statistical significance of autocorrelation in lion movements. This allowed us to visually classify the ‘shape’ of the correlogram for each of the 446 windows. Cushman (2010) simulated three path types under 18 different movement rules and showed that each path type had a characteristic autocorrelation structure and correlogram shape. Thus, correlogram shapes are diagnostic of broad movement patterns and provide an accurate and repeatable method to classify paths into categories such as directional, random and periodic movement (Cushman *et al.* 2005, Cushman 2010). In the current study, window plots were classified according to the degrees of autocorrelation into three ‘shape’ categories: directional, periodic or random movement (for full explanation see Appendix 4.1; Cushman *et al.* 2005, 2010). Directional movement, akin to a correlated random walk, is typified by a constant cline from positive to negative autocorrelation at increasing time lags indicating a pattern of movement in which successive locations in time become farther apart in space. Periodic movement, resulting from central place random walks or periodic revisits to a collection of locations, is characterised by repeated cycles between strong positive and strong negative autocorrelation. Random movement within a fixed home range is typified by a rapid drop from positive to negative autocorrelation and subsequent fluctuation near zero autocorrelation.

Movement parameters

We calculated three movement parameters: speed, path length and net displacement. Speed (m/h) was calculated by dividing the total distance travelled per night by the number of hours. Path length was the total distance travelled each night and net displacement was the distance between the first and last fix on a given night. Each parameter was then averaged per 30 day window.

Rainfall

Daily rainfall was recorded at two weather stations within the study area, approximately 30km apart. These were averaged to give a rainfall profile across the study area. We did not expect that rainfall in itself would impact lion movements but rather that replenishment of water holes, vegetation growth and subsequent prey dispersion would influence lion movement patterns. We therefore computed total rainfall for 60 days prior to the start of each window.

Demographic categories

The data utilised in this study was from lions in three demographic categories: Territorial males (N=6), territorial females (N=5) and sub-adult males (N=9). To assess changes in movement during dispersal the sub-adult data were further split into the three phases of dispersal (Clobert *et al.* 2001): pre-dispersal (N=4), transient (N=9) and post-dispersal (N=5). Based on field observations we classified demographic categories as follows:

Pre-dispersal: Four sub-adult males were collared while still with their natal pride. We were interested in investigating movements leading up to final departure and so only used data six months prior to dispersal (18 windows).

Transience: The timing of dispersal was calculated as the mid-point between the last time a sub-adult was seen with its natal pride and the first time either was seen alone (mean time interval = one month; SD ± 1.52). Nine individuals made up the transient dataset (58 windows).

Post-dispersal: Establishment of a territory was deemed to have occurred when a transient sub-adult had been in a consistent home-range for a minimum period of two months and continued to have a fixed home-range thereafter. The onset of post-dispersal was then back-dated to the time at which the lion entered the new home range. We were interested in movements shortly after establishment and therefore discarded all data that extended beyond six months. Five transient males were deemed to establish territories (27 windows).

Territorial adults: Lions in the study area have been closely monitored since 2002. All adults in this study were known to be territorial through direct observation and GPS data. In total we utilised 158 windows for territorial males and 135 for territorial females.

A complete breakdown of all 30 day temporal windows for each lion can be found in Appendix 4.2.

Group size

Female prides, male coalitions and sub-adults were closely monitored throughout the study period allowing for accurate recording of group size. Group sizes varied over the study period, being reduced by deaths or increased by the addition of new members into a coalition or pride. For adult group size we only included individuals over 36 months, while transient groups could be younger.

Statistical analyses

The structure of our data necessitated different modelling approaches for Mantel correlogram shape (categorical response) and movement parameters (continuous response). We therefore detail each approach below. In addition, we analysed two different datasets: the first consisted of the sub-adult dispersal stages (pre-dispersal, transient and post-dispersal); the second consisted of the transients, territorial males and territorial females. The data were split in this manner for clarity and due to the relatively small number of windows for pre- and post-dispersal which did not allow for direct comparisons between, for example, post-dispersal and territorial males.

Movement analysis

To assess the relationships between correlogram shape and demographic parameters and rainfall we used generalised linear mixed models (GLMMs) using combinations of two shape types per analysis (i.e. three sets of pairs). An example analysis consists of a response variable, periodic (0) or directional (1) movement with each of the fixed effects (demographic category, group size and rainfall), their interaction terms and lion identity as a random intercept (see Appendix 4.3 for models and model selection statistics). These analyses were performed in R 2.15.1 (R Core Team 2012), package lme4 v.0.9-2 (Bates *et al.* 2012) using a binomial error structure and logit-link function.

In order to analyse the movement parameters we performed mixed effects linear models with a continuous response variable (either speed, path length or net displacement), each of the fixed effects (demographic category, group size and rainfall), their interaction terms and lion identity as a random intercept (see Appendix 4.4 for models and model selection statistics). Models were fitted in R 2.15.1 (R Core Team 2012), package nlme v.3.1 (Pinheiro *et al.* 2012).

Datasets

First we analysed the sub-adult dataset during the three dispersal phases. Our primary interest in this dataset was to assess change in movement depending on demographic category irrespective of group size or rainfall. Furthermore, our dataset of pre- and post-dispersal was relatively small necessitating simple models. Therefore for each movement parameter and type we constructed models with demographic category as the only explanatory variable, and lion identity as a random factor (Table 4.1, predictions 1-3).

Second we analysed the dataset comprising territorial males, females and transient males (without the pre- and post- dispersal data). The parameters considered to affect movement were demographic category, group size and rainfall. To investigate predictions 4-9 (Table 4.1) we created 12 *a priori* candidate models including each of the main effects and their interaction terms (Appendix 4.3 and 4.4). The most complex model considered was ~ demographic * group size + rainfall * demographic. We used the same 12 *a priori* candidate models to analyse all three movement parameters and correlogram shapes. To account for among-individual variation, lion identity was entered as a random factor affecting the intercept in all models. Model selection was used to identify the best model based on Akaike Information Criterion corrected for small sample size (AICc). It was decided *a priori* that if one model was clearly superior (w_i>0.9) this would be used, otherwise we would average parameter estimates across models with AICc differences (Δi<3) correcting for model weights using R package AICcmodavg v.1.30 (Burnham and Anderson 2002, Mazerolle 2013).

Results

Sub-adult male dispersal stages

Transient lions had higher net displacement and moved further and faster per night than either pre- or post-dispersal (Table 4.1, prediction 1). This effect was most apparent when comparing transient to pre-dispersal lions (Table 4.2; Figure 4.1). Post-dispersal lions had the second highest values of these parameters, while pre-dispersers had the lowest. No differences were evident between pre- and post-dispersal movement parameters (estimate ± SE included 0 and 95% CI included 0).

Transient lions were more likely to engage in directional rather than random movement compared to pre- (estimate ± SE = -1.62 ± 0.77; CI = -3.14 – -0.10) and post-dispersal lions (estimate ± SE = -2.72 ± 0.83; CI = -4.35 – -1.09; Table 4.1, predictions 2-3). Similarly, transient lions had more directional than periodic movement compared to pre- (but estimate ± SE included 0 and 95% CI included 0) and post-dispersal lions (estimate ± SE = -1.97 ± 0.82; CI = -3.58– -0.35). See Figure 4.2 for comparisons.

Table 4.2. Estimated parameters and 95% confidence intervals (CI) from mixed models assessing variation in movement between transient, pre- and post-dispersal lions in Hwange National Park, Zimbabwe. In all cases, transient individuals are the reference class. Boldface type indicates CI not including 0. The comparison between periodic and random movement is not included here as estimates ± standard error (SE) all included 0 and 95% CI included 0.

Response variable	Parameter	Value	SE	Lower 95% CI	Upper 95% CI
Net displacement	Intercept	4336.24	304.57	3740.22	4932.27
	Pre-dispersal	**-1225.07**	**460.24**	**-2125.73**	**-324.40**
	Post-dispersal	-743.22	392.94	-1512.19	25.75
Path length	Intercept	5942.57	490.41	4982.87	6902.28
	Pre-dispersal	**-1239.78**	**586.84**	**-2388.20**	**-91.37**
	Post-dispersal	-298.59	498.19	-1273.52	676.33
Speed	Intercept	547.68	33.64	481.84	613.52
	Pre-dispersal	**-105.99**	**45.82**	**-195.66**	**-16.32**
	Post-dispersal	-47.36	39.01	-123.71	28.98
Directional (1) vs random (0)	Intercept	0.77	0.35	0.09	1.46
	Pre-dispersal	**-1.62**	**0.77**	**-3.14**	**-0.10**
	Post-dispersal	**-2.72**	**0.83**	**-4.35**	**-1.09**
Directional (1) vs periodic (0)	Intercept	-0.26	0.30	-0.85	0.32
	Pre-dispersal	1.24	0.74	-0.21	2.69
	Post-dispersal	**1.97**	**0.82**	**0.35**	**3.58**

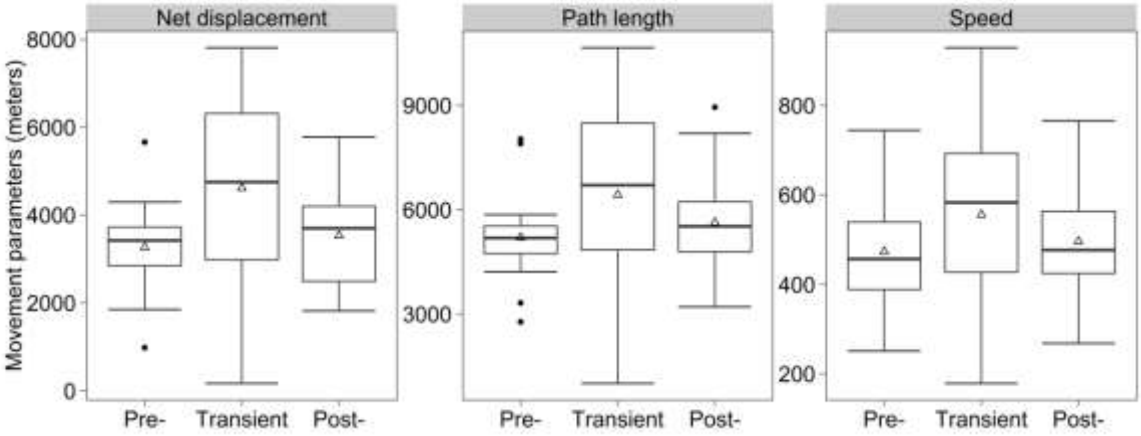


Figure 4.1. Differences in movement patterns between pre-, during and post-dispersal lions in Hwange National Park, Zimbabwe, in relation to net displacement, path length and speed.

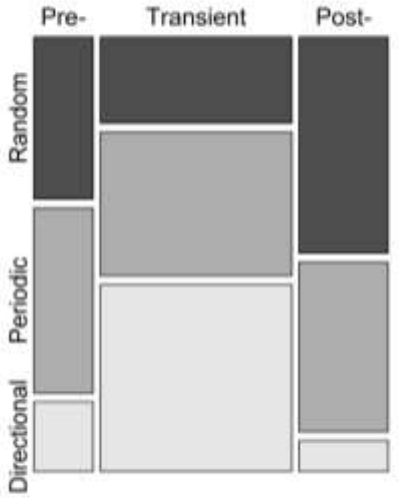


Figure 4.2: Differences in correlogram shape in relation to pre-, during and post-dispersal lions in Hwange National Park. The width of segments is proportional to the amount of data for each dispersal stage.

Transients and territorial adults

Lion movement patterns were highly variable depending on demographic category, rainfall, group size or a combination of these. There was no top model (w_i<0.9) in our analyses of movement parameters (speed, path length, net displacement) or correlogram shape, thus all reported parameter estimates were obtained by averaging across models with AICc differences <3 from the top model, correcting for model weights (see Appendix 4.3 and 4.4 for model selection statistics and model averaging procedure). The most supported candidate models for all movement parameters consisted of the interaction terms group size:demographic and rainfall:demographic in addition to their main effects. The most supported candidate models in our analysis of correlogram shape contained each of the main effects (demographic, rainfall and group size).

Demographic categories

Compared to transient sub-adult males, territorial males moved faster (estimate ± SE = 164.39 ± 49.49; CI = 60.42 – 268.35) and further (estimate ± SE = 2306.52 ± 633.51; CI = 975.66 – 3637.38) per night, while females moved slower (estimate ± SE = -132.92 ±

51.79; CI = -241.71 – -24.13). Similarly, territorial males had higher net displacement (estimate ± SE = 879.93 ± 342.74; CI = 159.91 – 1599.95), while females had lower net displacement (estimate ± SE = -1568.72 ± 356.03; CI = -2316.66 – -820.77) compared to transient sub-adult males (Table 4.1, prediction 4).

Transient males were more likely to engage in directional rather than periodic movement (Figure 4.3) compared to territorial males (estimate ± SE = -1.32 ± 0.51; CI = -2.31 – -0.33). Transient males were also more likely to engage in directional movement rather than random movement compared to territorial males (estimate ± SE = -1.91 ± 0.56; CI = -3.01 – -0.80) and territorial females (estimate ± SE = -1.65 ± 0.57; CI = -2.78 – -0.53; Table 4.1, prediction 5 and 6). Although group size and rainfall were included in the top models (Appendix 4.3), there were no clear trends (estimate ± SE included 0 and Wald 95% CI included 0) and thus we considered demographic category as the main factor explaining variation in movement type.

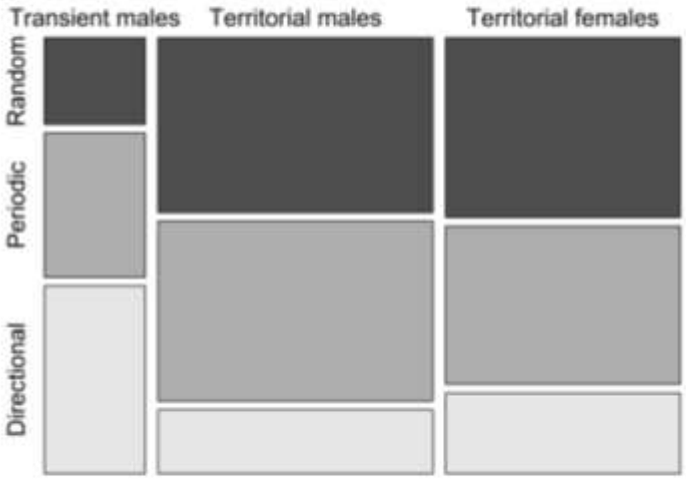


Figure 4.3: Differences in correlogram shape according to lion demographic in Hwange National Park, Zimbabwe. Width of segments is proportional to the amount of data for each demographic.

Rainfall

The way in which lions responded to rainfall depended on an interaction with demographic category. Territorial males and females moved slower with increasing rainfall, with territorial females also decreasing nightly path length (Table 4.3). Meanwhile, the movement parameters of transient males had no relationship with the amount of rainfall (estimates ± SE all included 0 and 95% CI included 0; Table 4.3; Table 4.1, prediction 7).

Group size

Group size ranged from one to four in adults and one to three in transient males. Movement parameters for territorial males, territorial females and transient males differed depending on group size (Table 4.3; Figure 4.4). Transient males in smaller groups moved faster, had higher net displacement and higher path length than those in bigger groups (Table 4.1, prediction 8). In contrast, territorial males displayed the opposite trend: bigger groups moved faster, had higher net displacement and a higher path length than smaller groups. Territorial females exhibited the same tendency as transient males but increasing group size had a less marked effect as there was only substantial decrease in net displacement (Table 4.3; Table 4.1, prediction 9).

Table 4.3. Model averaged slope estimates from results of mixed effects linear models investigating lion movement parameters (net displacement, path length and speed) in Hwange National Park, Zimbabwe. Boldface type indicates confidence intervals (CI) not including 0.

		Model averaged			
Response variable	Parameters	Slope	SE	Lower 95% CI	Upper 95% CI
Net displacement	**group size X transient males**	**-1494.22**	**319.94**	**-2121.30**	**-867.14**
	group size X territorial males	**405.26**	**120.84**	**168.42**	**642.10**
	group size X territorial females	**-394.41**	**156.17**	**-700.5**	**-88.32**
	rain X transient males	-0.29	1.12	-2.47	1.90
	rain X territorial males	-0.09	0.86	-1.78	1.61
	rain X territorial females	-1.51	0.98	-3.44	0.41
Path length	**group size X transient males**	**-2084.63**	**481.93**	**-3029.21**	**-1140.07**
	group size X territorial males	**674.12**	**170.94**	**339.09**	**1009.16**
	group size X territorial females	-129.97	226.13	-573.17	313.22
	rain X transient males	-1.33	1.53	-4.34	1.68
	rain X territorial males	-1.21	1.15	-3.47	1.05
	rain X territorial females	**-2.92**	**1.33**	**-5.52**	**-0.32**
Speed	**group size X transient males**	**-143.56**	**38.8**	**-219.61**	**-67.52**
	group size X territorial males	**36.97**	**13.21**	**11.09**	**62.86**
	group size X territorial females	-11.41	17.71	-46.12	23.31
	rain X transient males	-0.16	0.1	-0.35	0.04
	rain X territorial males	**-0.17**	**0.07**	**-0.30**	**-0.03**
	rain X territorial females	**-0.21**	**0.08**	**-0.36**	**-0.06**

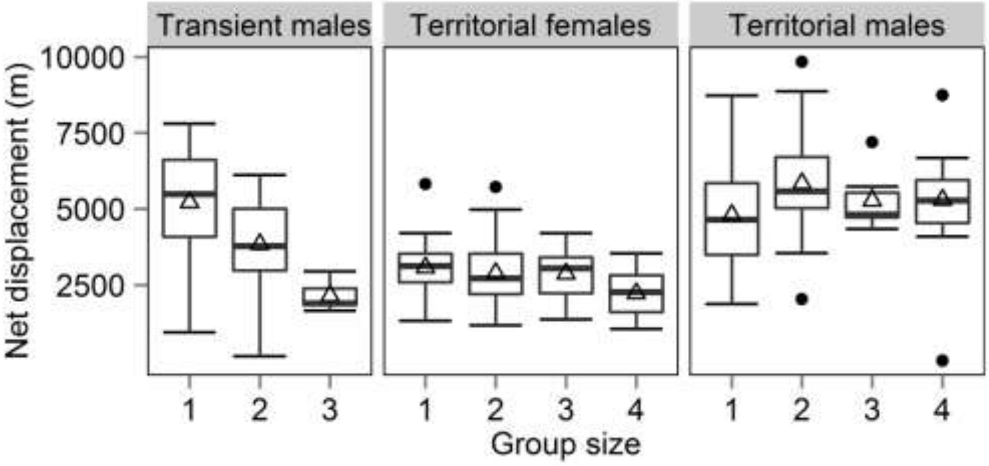


Figure 4.4: Relationship between demographic category and group size in relation to net displacement of lions in Hwange National Park, Zimbabwe. There were no groups of four in transient lions.

Discussion

Our findings show the extent to which lion movement behaviour is influenced by group size and rainfall and how this differs depending on demographic category. By incorporating an environmental variable in addition to the internal state of the organism (Schick *et al.* 2008) we offer a unique insight into differential responses to shifting environmental conditions and social grouping depending on the life stage and sex of a species.

Transient lions exhibited directional movement whilst all adult movement was a composite of random and periodic movements. Differences in movement behaviour are, to a certain extent, determined by an individual's ability to perceive its surroundings and acquire knowledge (Vuilleumier and Perrin 2006). As such, dispersers moving through novel environments may move differently relative to territorial individuals that have learnt to maximise the resources within that patch, as was reported with transient eagle owls (*Bubo bubo*; Delgado *et al.* 2009). The observed periodic movement in adults was expected given that in this ecosystem, waterholes are a key loci for lions; prey select areas close to waterholes (Valeix *et al.* 2009) and subsequently so do lions (Valeix *et al.* 2010), which appear to rotate between waterholes (Valeix *et al.* 2011; Table 4.1, prediction 6).

Pre-dispersal lions exhibited periodic and random movement patterns shifting to high levels of directional movement during dispersal (Table 4.1, prediction 2). This accords with Zollner and Lima's (1999) simulated dispersal experiments and subsequent predictions: they found that straighter paths vastly improved the probability of survival and that this type of movement was the most effective search rule as straighter paths avoid redundant search and improve the likelihood of finding a vacant patch quickly (Table 4.1, prediction 5). With territorial species such as lions, it is plausible that unless a disperser is going to challenge for a territory, he will pass through it in a directional manner, and minimise the chance of an aggressive encounter with the resident adult. Such directional movement suggests a sequential search strategy whereby individuals either accept or reject patches they encounter; if rejected they continue the search in a directional manner, and do not revisit patches (comparitive search strategies; Stamps *et al.* 2005, Stamps 2006). Interestingly, the amount of directional movement declined dramatically once establishment occurred, replaced by random and periodic movements (Table 4.1, prediction 3). In contrast, territorial adults displayed higher proportions of directional movement than did post-dispersal lions. We speculate that during establishment, a sub-adult lion consolidates a patch, around a waterhole for instance, leading to exaggerated patterns of periodic and bounded home-range movements, and then, as it becomes familiar with and secure in its new territory, it transitions to movement patterns similar to those of territorial adult males. Additional data on post-dispersal movements may confirm this.

Our findings concur with what Van Dyck and Baguette (2005) termed ‘special movements’ in relation to directional dispersal movements designed for displacement (Table 4.1, prediction 5). However, ‘special movements’ are associated with high speed as reported for transient eagle owls that moved faster and straighter than established individuals (Delgado *et al.* 2009). In contrast, our results showed that transient males were slower and moved less than territorial males (Table 4.1, prediction 4). One explanation is that by using directional movement at a decreased locomotory rate, transient males effectively search the area while limiting their detection probability. Indeed, Zollner and Lima’s (2005) simulations demonstrated that transient individuals can benefit from slower speeds due to more effective anti-predator behaviour. More tortuous paths covering a larger area would entail leaving more scent which would increase the likelihood of detection by territorial males. Indeed, increased activity has been shown to increase predation susceptibility (Ebenhard 1987) and predation rates (Norrdahl and Korpimäki 1998) in small mammals.

Depending on their demographic, group size influenced how individuals moved. When in small groups transient lions moved faster and farther (Table 4.1, prediction 8), as did territorial females, although the effect was less marked. In contrast territorial males had the opposite trend (Table 4.1, prediction 9). Fluctuations in lion home range size are strongly suggestive of expansionism (Kruuk and Macdonald 1985) as home range size increases with increasing pride biomass (Loveridge *et al.* 2009b). Thus, with larger territories to defend, males in bigger groups have increased movement compared to smaller groups in smaller territories. On the other hand females are not as active as males in patrolling their territories (Schaller 1972) and thus, while bigger groups of females have larger territories, their movements may reflect a strategy of food acquisition (which is concentrated around waterholes) and rearing of offspring. Lions in larger coalitions are more likely to gain residence in a pride (Bygott *et al.* 1979, Packer *et al.* 1988) and among transients it is plausible that a solitary disperser has little chance of displacing the resident males and would benefit from moving directly through an occupied territory. Thus, the decreased locomotion of transient individuals in bigger groups could reflect ‘boldness’ as opposed to ‘shyness’ (Baguette and Van Dyck 2007). While it has been reported that bold individuals dispersed farther (Fraser *et al.* 2001) with larger and straighter movements (Delgado and Penteriani 2008) in our scenario the opposite could apply. Bigger groups may face fewer consequences if detected by resident males and can afford to remain within occupied territories for longer periods. Solitary individuals on the other hand represent the ‘shy’ individuals and move faster, with higher net displacement per night through the landscape while searching for a (often rare) vacant territory, and may be less inclined to challenge for one.

Lions showed differing response to rainfall in the preceding 60 days depending on their demographic (Table 4.1, prediction 7). While the changing of seasons has no effect on lion home range size of either sex in HNP (Loveridge *et al.* 2009b), we show that when using a more fluid approach to climatic data (i.e. rainfall as opposed to pre-defined seasons delineated by calendar months) variation in movement patterns is detected. The slopes defining these relationships are shallow (Table 4.3) and our small sample size necessitates cautious conclusions. However these findings are in line with our expectations. For instance, that females decreased their speed and path length with increased rainfall may be explained by the addition of small cubs, which may constrain the movements of females. Cubs were more common in the wet season during this study. Indeed cubs under six months of age were present in 49% of all female wet season windows compared to 38% of dry season windows.

In summary, our findings reveal that in territorial species such as lions, movement behaviour may be influenced by the demographic category of an individual. This variation may be further explained by incorporating social grouping and environmental variables. Our results indicate that movement behaviour reflects a transition from exploratory strategies during dispersal to reduced movement during settlement, followed by more expansive movement while established. As ecosystems become increasingly fragmented it is crucial to elucidate the patterns and processes of movement behaviour during the different stages of dispersal in order to better understand the associated shifting behaviours. This will improve our understanding of how species may persist in fragmented landscapes and how for example fencing, may curtail and alter the movements described in this paper. Thus we provide the first investigation of seasonal movement patterns during dispersal in conjunction with territorial adults and show how this varies depending on social grouping. In so doing, we deliver a much called-for empirical study on dispersal movements that will improve the way dispersal is represented in simulation models (e.g. Zollner and Lima 2005) and connectivity studies (e.g. Schwartz *et al.* 2009).

Appendix

Appendix 4.1: Rational and methodology for ascribing directional, random, or periodic movement based on the 'shape' of Mantel correlograms.

The first section of this appendix, entitled 'Rationale' explores the background and justification of the methodology based on previous studies incorporating one or more of the elements of the analyses used in this paper. The second section, entitled 'Simulation' presents results of a simulation of three movement paths to demonstrate our methodology and relate it to pre-defined movement types. The final section, titled 'Empirical data', illustrates the application of our methods to empirical data from GPS collars on lions in Hwange National Park, and shows examples of correlogram surfaces for directional, periodic and random movement types.

1. Rationale

The patterns of temporal and spatial autocorrelation of locations are an important part of the information that telemetry data provide (Cushman *et al.* 2005, Cushman 2010). Spatial autocorrelation is an informative ecological parameter that reveals scales and patterns of ecological processes which are often not resolvable through other methods. In terms of animal movements, addressing the details of the strength, scale and patterns of autocorrelation may illustrate details about animal space use and its relationships to changes in the environment in response to perturbations, social interactions or seasonality (Legendre and Fortin 1989, Legendre 1993, Cushman *et al.* 2005). Cushman *et al.* (2010) investigated the structure and range of spatial autocorrelation of sequential relocation points by simulating three path types under 18 different movement rules. The three path types were (1) correlated random walk, (2) bounded correlated random walk, and (3) central place random walk. The correlated random walk represents an unconstrained walk, with the only spatial parameter consisting of the normal random turning angle between steps. The bounded correlated random walk was calculated in the same way, with the additional constraint that the path not exceed a specified distance from the origin. This reflects a correlated random walk within a fixed circular home range. When a walk reached ten distance units from the origin the next step was taken directly toward the origin, with subsequent steps again following a correlated random walk. The central place random walk consisted of correlated random walks of 100 steps, followed by an azmithal return to the origin in the next 100 steps, with this sequence repeated five times over the 1,000 steps of the simulation. This simulates correlated random foraging paths out from a central place, such as a nest or natal den, followed by direct return, such as after capturing prey.

Cushman *et al.* (2010) produced Mantel correlograms for each of the 180 simulated movement paths using the Ecodist library in R (R Core Team 2012). The Mantel test (Mantel 1967) tests the degree of association between two distance matrices (distance and time). The distance matrix was produced by calculating geographical distances between each pair of locations and the time matrix was computed by calculating the difference in decimal days between each pair of locations. From these two matrices it is possible to construct a multivariate correlogram (Oden and Sokal 1986; Sokal 1986), which shows the strength of correlation between the two multivariate matrices across a range of lags between them. Cushman *et al.* (2010) found that each simulated path type had a characteristic autocorrelation structure, or ‘shape’, that enabled reliable classification of the path as a directional, random or periodic movement.

Below we describe the characteristics of each of the correlogram ‘shapes’; directional, random and periodic:

Directional movement

Correlogram shapes of correlated random walks under different movement rules all showed clines of increasing negative spatial autocorrelation between locations as time and distance between them increased.

Random movement

Correlogram shapes of bounded random walks under different movement rules had initial high positive autocorrelation, followed by a drop to near zero autocorrelation and subsequent fluctuation around zero autocorrelation.

Periodic movement

Correlogram shapes of central place random walks under different movement rules all shared a common basic form, characterised by repeated cycles between strong positive and strong negative autocorrelation with a period equal to the time to complete a full cycle of foraging and azmithal return to the central place.

The strong and consistent structure of correlograms resulting from paths generated using different known spatial processes show that correlograms themselves can be highly useful tools to explore movement behaviour and identify dominant movement patterns (e.g. directional, random or periodic), which then can be used to generate or test ecological and behavioural hypotheses. The identification of one of these shapes in correlograms produced from empirical data will invalidate hypotheses about the existence of the process that would generate one of the other two correlogram forms. For example, if we hypothesize that an organism will exhibit random use of a fixed home range, and discover that its movement path produces a cline or periodic shaped correlogram we would be able to safely reject that hypothesis. Similarly, if one proposes that movement during the dry season should be periodic, reflecting regular use of a collection of fixed foraging locations (such as waterholes) and then observe a strongly periodic correlogram, this observation is consistent with the hypothesis of periodic movement.

2. Simulation

In order to further demonstrate our methodology for categorising correlogram shape and how this relates to pre-defined movement types, we simulated three movement paths: Figure A4.1a -- a correlated random walk with a normally distributed turning angle with mean 0 and standard deviation *pi* degrees; Figure A4.1b -- a bounded random walk representing random use of a fixed home range, and Figure A4.1c -- a central place foraging pattern where a correlated random walk with a normally distributed turning angle is taken for 20 steps from the central place, and after 20 steps the path returns directly to the central place in 20 steps. The Mantel correlograms for each of these paths are shown in the panels below the paths. In our classification of correlogram shape we based interpretation on the first half of the correlogram (e.g. 0-250 in the correlograms in Figure A4.1) given that the end of the correlogram should not be interpreted due to decreasing number of lag pairs at long lag distances. We classified correlograms into three classes: (1) directional, (2) random, (3) periodic.

Directional movement

We classified a correlogram as directional if, over the first half of its length, the correlogram declined smoothly with a relatively constant slope and no inflection points (e.g. Figure A4.1d). This pattern indicates that distances between points become larger as the time between points becomes longer in a roughly linear relationship, indicative of directional movement.

Random movement

We classified a correlogram as indicating random movement when, over the first half of its length, there was a rapid initial drop in Mantel correlation to near zero, followed by a period where the correlogram was relatively flat and fluctuating around zero (e.g. Figure A4.1e). This pattern indicates that at short lag distances locations are autocorrelated, but become uncorrelated, at the lag distance of the inflection point.

Periodic movement

We classified a correlogram as indicating periodic movement when, over the first half of its length, there was a rapid initial drop of correlation to negative values, followed by one or more ‘peaks’ of positive correlation, followed by ‘troughs’ of negative correlation (e.g. Figure A4.1f). The distance to the first major peak indicates the period of repeat of the periodic movement (e.g. the average time between revisits of the same location – such as a waterhole).

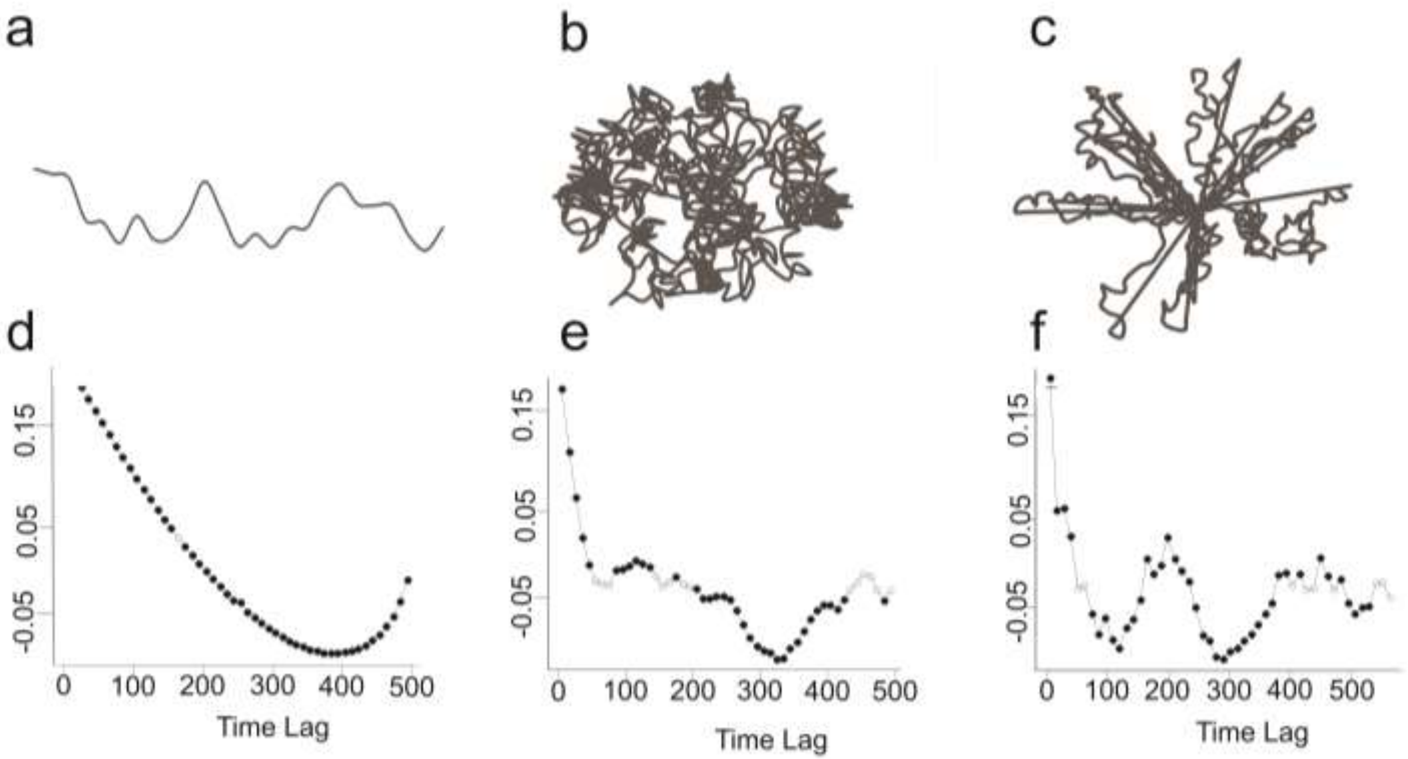


Figure A4.1: Illustration of Mantel correlogram shapes for three simulated paths. The simulated paths are (a) a correlated random walk with 0 mean and *pi* standard deviation of turn angle, (b) bounded random walk, (c) central place random walk. The panels below the simulated paths are the Mantel correlograms produced for those paths. Classifictation of correlogram shape was based on the first half of the correlogram given that the end of the correlogram has a decreasing number of lag pairs at long lag distances. The correlogram for the correlated random walk (d) is a smooth cline without any inflection point, indicating a directional pattern of movement in which successive locations in time become farther apart in space. The correlogram for the bounded random walk (e) shows an initial rapid drop in correlation, followed by an inflection point, after which correlation fluctuates near zero. This indicates that locations are autocorrelated at small lag distances, but become independent at a time lag corresponding to the location of the inflection point. The correlogram for the central place periodic movement path (f) shows an initial drop in correlation from positive to negative, followed by a peak of positive correlation and a trough of negative autocorrelation. This pattern indicates periodic movement, where locations separated by a lag distance corresponding to the location of the peak are closer together than average, and locations separated by lag distances corresponding to the troughs are farther apart than average.

3. *Empirical data*

The following three figures are derived from empirical GPS data from collared lions in Hwange National Park, Zimbabwe. We chose three examples to demonstrate directional, periodic and random movements as identified from Mantel correlogram ‘shape’. Each figure follows the same format: (a) The Mantel correlogram surface displaying all windows together for a particular individual. Time lag refers to lag in days between observations used to calculate autocorrelation. Warm colours indicate positive autocorrelation while cool colours indicate negative autocorrelation. The solid contour indicates the isocline of zero autocorrelation. The oval shape highlights the individual window which is displayed in (b), and was classified as either directional, random or periodic. In our classification of correlogram shape we based interpretation on the first half of the correlogram given that the end of the correlogram should not be interpreted due to decreasing number of lag pairs at long lag distances. Section (c) displays the 3D movement trajectory for the same window in order to relate the correlogram back to GPS data. The colour range indicates the sequence of locations going from bottom to top. The blue vertical lines portray the xy location of waterholes in the vicinity. The correlogram shape is much more meaningful than categorizing the paths themselves by eye. Movement paths are highly complicated trajectories that retrace, overlap, and produce a ‘tangle’ of intersecting ‘spaghetti’ lines. These are very difficult to interpret visually as to the strength of directional, periodic and random movement, particularly with large datasets, while the shapes of the correlograms are diagnostic and readily interpretable.

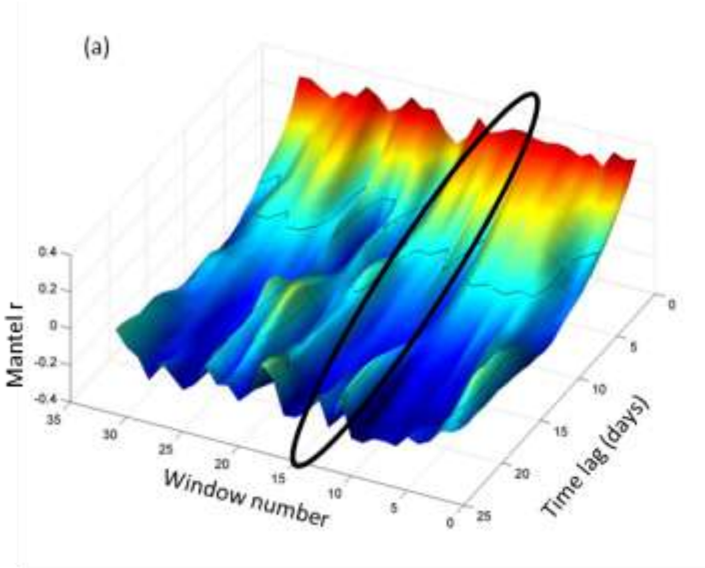
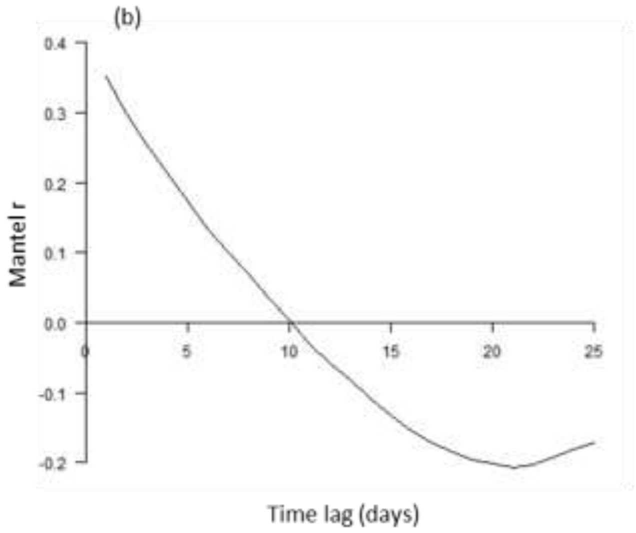
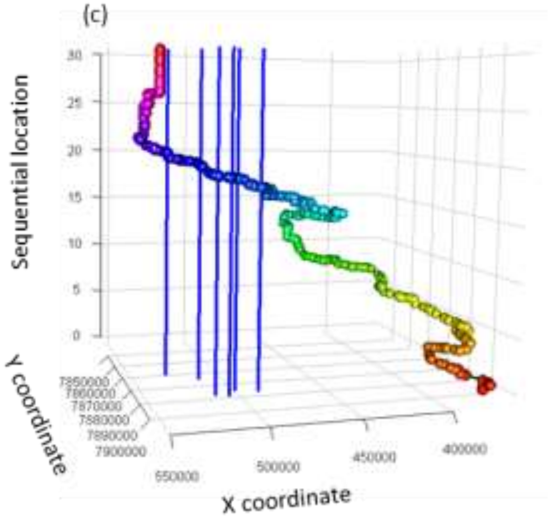


Figure A4.2: Directional movement of disperser SPIbM5 *

Directional movement revealed by analysis of patterns of autocorrelation of GPS data for dispersing lion SPIbM5. The oval shape (a) highlights window 14, displayed alone (b), which shows that the longer apart the locations are in time the farther apart they are in space. Directional movement produces a similar “shape” to a correlated random walk and was classified as directional if, over the first half of its length, the correlogram declined smoothly with a relatively constant slope and no inflection points. The movement trajectory (c) of window 14 confirms a strong pattern of directional movement.





* Refer to text under heading “3. Empirical data” for full description of each figure.

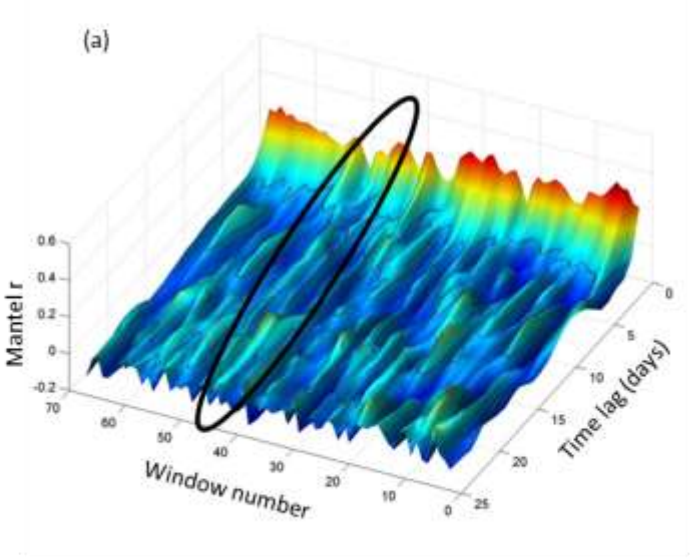
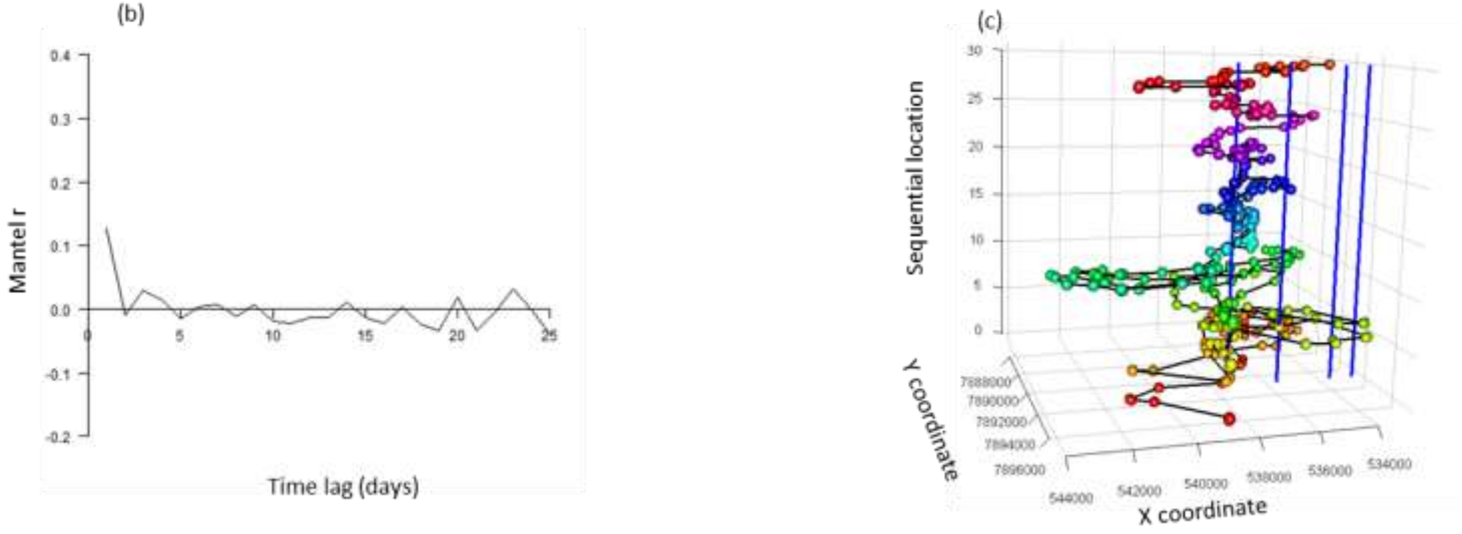


Figure A4.3: Random movement of territorial female BACF2 *

Random movement revealed by analysis of patterns of autocorrelation of GPS data for territorial female BACF2. The oval shape (a) highlights window 48, displayed alone (b), which typifies random use of a home range. We classified a correlogram as indicating random movement when, over the first half of its length, there was a rapid initial drop in Mantel correlation to near 0, followed by a period where the correlogram was relatively flat and fluctuating around zero. The correlogram shape representative of random movement is similar to that of a bounded correlated random walk.



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* Refer to text under heading “3. Empirical data” for full description of each figure.

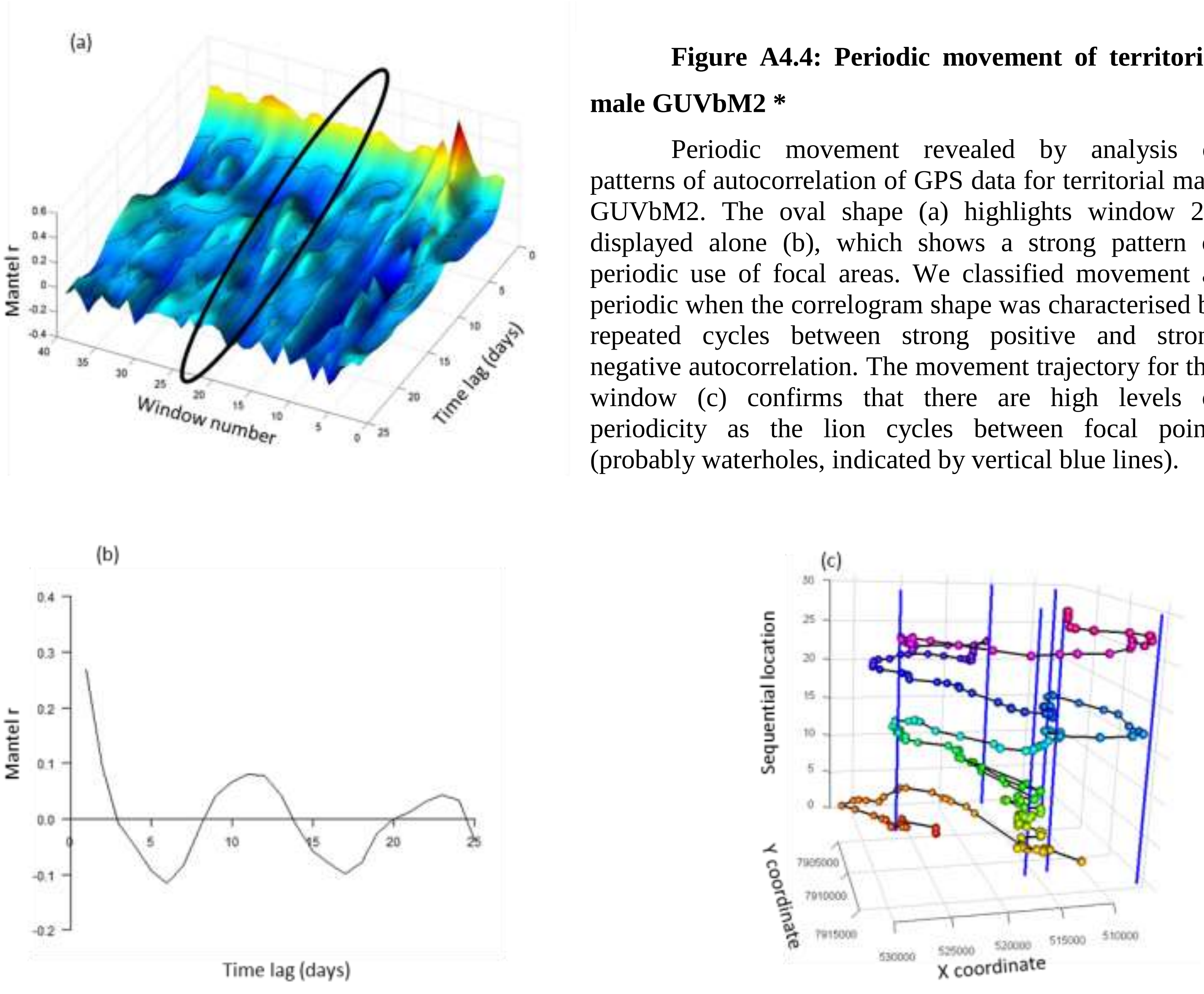

Figure A4.4: Periodic movement of territorial male GUVbM2 *

Periodic movement revealed by analysis of patterns of autocorrelation of GPS data for territorial male GUVbM2. The oval shape (a) highlights window 23, displayed alone (b), which shows a strong pattern of periodic use of focal areas. We classified movement as periodic when the correlogram shape was characterised by repeated cycles between strong positive and strong negative autocorrelation. The movement trajectory for this window (c) confirms that there are high levels of periodicity as the lion cycles between focal points (probably waterholes, indicated by vertical blue lines).

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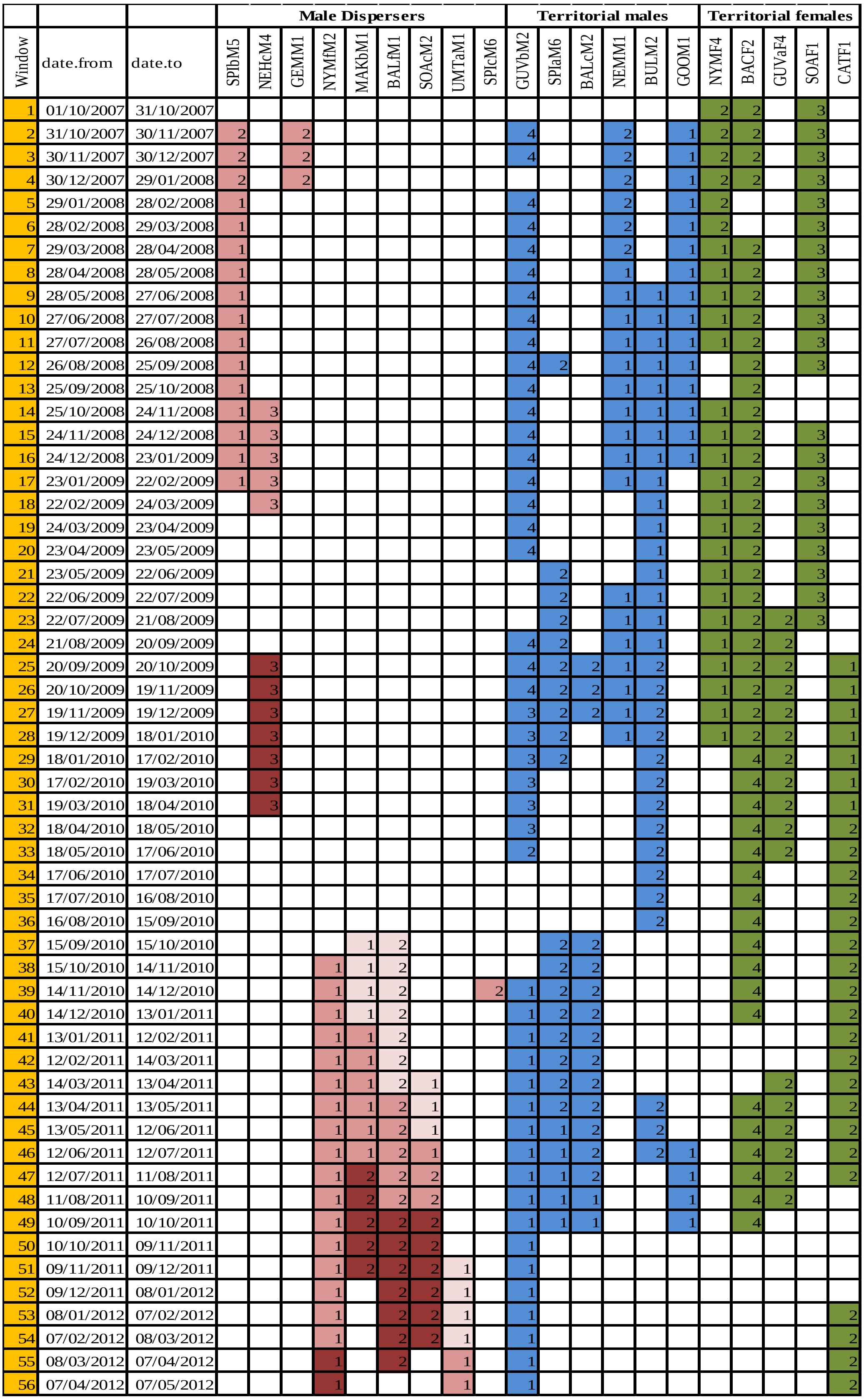
* Refer to text under heading “3. Empirical data” for full description of each figure.

Appendix 4.2. Summary of the GPS data used in this analysis. Nine sub-adult males were fitted with GPS collars. Light purple (pre-dispersal), medium purple (dispersing), dark purple (post dispersal). The numbers in each box represent group size. See Methods for full explanation.



			Male Dispersers									Territorial males						Territorial females				
Window	date.from	date.to	SPIbM5	NEHcM4	GEMM1	NYMfM2	MAKbM1	BALfM1	SOAcM2	UMTaM1	SPIcM6	GUVbM2	SPIaM6	BALcM2	NEMM1	BULM2	GOOM1	NYMF4	BACF2	GUVaF4	SOAF1	CATF1
1	01/10/2007	31/10/2007																2	2		3	
2	31/10/2007	30/11/2007	2		2							4			2		1	2	2		3	
3	30/11/2007	30/12/2007	2		2							4			2		1	2	2		3	
4	30/12/2007	29/01/2008	2		2										2		1	2	2		3	
5	29/01/2008	28/02/2008	1									4			2		1	2			3	
6	28/02/2008	29/03/2008	1									4			2		1	2			3	
7	29/03/2008	28/04/2008	1									4			2		1	1	2		3	
8	28/04/2008	28/05/2008	1									4			1		1	1	2		3	
9	28/05/2008	27/06/2008	1									4			1	1	1	1	2		3	
10	27/06/2008	27/07/2008	1									4			1	1	1	1	2		3	
11	27/07/2008	26/08/2008	1									4			1	1	1	1	2		3	
12	26/08/2008	25/09/2008	1									4	2		1	1	1		2		3	
13	25/09/2008	25/10/2008	1									4			1	1	1		2			
14	25/10/2008	24/11/2008	1	3								4			1	1	1	1	2			
15	24/11/2008	24/12/2008	1	3								4			1	1	1	1	2		3	
16	24/12/2008	23/01/2009	1	3								4			1	1	1	1	2		3	
17	23/01/2009	22/02/2009	1	3								4			1	1		1	2		3	
18	22/02/2009	24/03/2009		3								4				1		1	2		3	
19	24/03/2009	23/04/2009										4				1		1	2		3	
20	23/04/2009	23/05/2009										4				1		1	2		3	
21	23/05/2009	22/06/2009											2			1		1	2		3	
22	22/06/2009	22/07/2009											2		1	1		1	2		3	
23	22/07/2009	21/08/2009											2		1	1		1	2	2	3	
24	21/08/2009	20/09/2009										4	2		1	1		1	2	2		
25	20/09/2009	20/10/2009		3								4	2	2	1	2		1	2	2		1
26	20/10/2009	19/11/2009		3								4	2	2	1	2		1	2	2		1
27	19/11/2009	19/12/2009		3								3	2	2	1	2		1	2	2		1
28	19/12/2009	18/01/2010		3								3	2		1	2		1	2	2		1
29	18/01/2010	17/02/2010		3								3	2			2			4	2		1
30	17/02/2010	19/03/2010		3								3				2			4	2		1
31	19/03/2010	18/04/2010		3								3				2			4	2		1
32	18/04/2010	18/05/2010										3				2			4	2		2
33	18/05/2010	17/06/2010										2				2			4	2		2
34	17/06/2010	17/07/2010														2			4			2
35	17/07/2010	16/08/2010														2			4			2
36	16/08/2010	15/09/2010														2			4			2
37	15/09/2010	15/10/2010					1	2					2	2					4			2
38	15/10/2010	14/11/2010				1	1	2					2	2					4			2
39	14/11/2010	14/12/2010				1	1	2			2	1	2	2					4			2
40	14/12/2010	13/01/2011				1	1	2				1	2	2					4			2
41	13/01/2011	12/02/2011				1	1	2				1	2	2								2
42	12/02/2011	14/03/2011				1	1	2				1	2	2								2
43	14/03/2011	13/04/2011				1	1	2	1			1	2	2						2		2
44	13/04/2011	13/05/2011				1	1	2	1			1	2	2		2			4	2		2
45	13/05/2011	12/06/2011				1	1	2	1			1	1	2		2			4	2		2
46	12/06/2011	12/07/2011				1	1	2	1			1	1	2		2	1		4	2		2
47	12/07/2011	11/08/2011				1	2	2	2			1	1	2			1		4	2		2
48	11/08/2011	10/09/2011				1	2	2	2			1	1	1			1		4	2		
49	10/09/2011	10/10/2011				1	2	2	2			1	1	1			1		4			
50	10/10/2011	09/11/2011				1	2	2	2			1										
51	09/11/2011	09/12/2011				1	2	2	2	1		1										
52	09/12/2011	08/01/2012				1		2	2	1		1										
53	08/01/2012	07/02/2012				1		2	2	1		1										2
54	07/02/2012	08/03/2012				1		2	2	1		1										2
55	08/03/2012	07/04/2012				1		2		1		1										2
56	07/04/2012	07/05/2012				1				1		1										2

Appendix 4.3. Model selection statistics for GLMMs investigating correlogram shape (directional, periodic and random movements) of lion movement paths. Explanatory variables consisted of (1) ‘dem’ – demographic category; (2) ‘G.S’ – number of individuals per group; (3) ‘rain’ – rainfall 60 days prior to the start of each window. In all models lion identity was entered as a random factor. Models were ranked according to Akaike weights (w_i). Included are log likelihood, AICc differences (Δ*i*) and number of parameters (K). We averaged parameter estimates across those models with AICc differences (Δ*i*<3; shown in bold) correcting for model weights.

Response variable	Rank	Model	log likelihood	AICc	Δ*i*	w_i	K
Directional (1) vs random (0)	**1**	**rain + dem**	**-122.83**	**255.95**	**0**	**0.60**	**5**
	2	**rain * dem**	**-121.97**	**258.50**	**2.55**	**0.17**	**7**
	3	dem * rain + G.S.	-121.82	260.35	4.41	0.07	8
	4	dem	-126.15	260.50	4.56	0.06	4
	5	dem * G.S. + rain	-122.38	261.46	5.52	0.04	8
	6	dem + G.S.	-125.62	261.53	5.58	0.04	5
	7	rain	-128.84	263.79	7.85	0.01	3
	8	G.S. * dem + rain * dem	-121.67	264.44	8.49	0.01	10
	9	G.S. * dem	-125.29	265.13	9.19	0.01	7
	10	rain + G.S.	-128.77	265.73	9.78	0	4
	11	Null	-132.16	268.39	12.44	0	2
	12	G.S.	-131.92	269.95	14.00	0	3
Directional (1) vs periodic (0)	1	dem	-131.11	270.40	0	0.29	4
	2	rain + dem	-130.55	271.38	0.98	0.18	5
	3	Null	-133.87	271.79	1.39	0.14	2
	4	dem + G.S.	-131.04	272.38	1.97	0.11	5
	5	rain	-133.20	272.52	2.12	0.10	3
	6	G.S.	-133.74	273.60	3.19	0.06	3
	7	rain + G.S.	-133.06	274.31	3.91	0.04	4
	8	rain * dem	-130.12	274.77	4.37	0.03	7
	9	G.S. * dem	-130.44	275.42	5.02	0.02	7
	10	dem * G.S. + rain	-129.78	276.25	5.85	0.02	8
	11	dem * rain + G.S.	-130.03	276.76	6.35	0.01	8
	12	G.S. * dem + rain * dem	-129.42	279.92	9.52	0	10
Random (1) vs periodic (0)	1	rain	-186.73	379.54	0	0.23	3
	2	rain + G.S.	-185.83	379.81	0.27	0.20	4
	3	dem * G.S. + rain	-182.17	380.88	1.34	0.12	8
	4	rain + dem	-185.35	380.92	1.38	0.11	5
	5	dem + G.S.	-185.76	381.74	2.20	0.08	5
	6	G.S.	-187.87	381.82	2.28	0.07	3
	7	Null	-189.06	382.16	2.62	0.06	2
	8	G.S. * dem	-184.04	382.49	2.95	0.05	7
	9	dem * rain + G.S.	-183.49	383.53	3.98	0.03	8
	10	dem	-187.83	383.80	4.26	0.03	4
	11	rain * dem	-185.17	384.76	5.21	0.02	7
	12	G.S. * dem + rain * dem	-182.05	384.93	5.39	0.02	10

Appendix 4.4. Model selection statistics for mixed effects linear models investigating lion movement parameters (net displacement, path length and speed). Explanatory variables consisted of (1) ‘dem’ – demographic category; (2) ‘G.S’ – number of individuals per group; (3) ‘rain’ – rainfall 60 days prior to the start of each window. In all models lion identity was entered as a random factor. Models were ranked according to Akaike weights (w_i). Included are log likelihood, AICc differences (Δ*i*) and number of parameters (K). We averaged parameter estimates across those models with AICc differences (Δ*i*<3; shown in bold) correcting for model weights.

Response variable	**Rank**	**Model**	**log likelihood**	**AICc**	**Δ*i***	**w_i**	**K**
	1	**G.S. * dem + rain * dem**	**-3027.130**	**6077.038**	**0**	**0.393**	**11**
Net displacement	2	**G.S. * dem**	**-3030.492**	**6077.405**	**0.366**	**0.327**	**8**
	3	**G.S. * dem + rain**	**-3029.597**	**6077.722**	**0.683**	**0.279**	**9**
	4	rain * dem	-3045.560	6107.541	30.502	0	8
	5	dem	-3049.002	6108.177	31.139	0	5
	6	rain + dem	-3048.464	6109.172	32.134	0	6
	7	dem * rain + G.S.	-3045.551	6109.631	32.592	0	9
	8	dem + G.S.	-3048.998	6110.240	33.202	0	6
	9	Null	-3058.698	6123.465	46.427	0	3
	10	rain	-3058.236	6124.587	47.548	0	4
	11	G.S.	-3058.569	6125.253	48.215	0	4
	12	rain + G.S.	-3058.064	6126.301	49.263	0	5
Path length	**1**	**G.S. * dem + rain * dem**	**-3143.599**	**6309.976**	**0**	**0.515**	**11**
	2	**G.S. * dem + rain**	**-3145.865**	**6310.258**	**0.282**	**0.447**	**9**
	3	G.S. * dem	-3149.386	6315.193	5.217	0.038	8
	4	dem * rain + G.S.	-3157.208	6332.944	22.968	0	9
	5	rain * dem	-3158.997	6334.416	24.440	0	8
	6	rain + dem	-3161.909	6336.062	26.087	0	6
	7	dem + G.S.	-3162.743	6337.730	27.754	0	6
	8	dem	-3164.389	6338.952	28.977	0	5
	9	rain + G.S.	-3166.907	6343.989	34.013	0	5
	10	rain	-3169.708	6347.532	37.556	0	4
	11	G.S.	-3169.779	6347.673	37.697	0	4
	12	Null	-3172.120	6350.310	40.334	0	3
Speed	**1**	**G.S. * dem + rain**	**-2246.051**	**4510.630**	**0**	**0.734**	**9**
	2	**G.S. * dem + rain * dem**	**-2244.988**	**4512.754**	**2.124**	**0.254**	**11**
	3	G.S. * dem	-2251.273	4518.966	8.336	0.011	8
	4	rain + dem	-2256.236	4524.716	14.086	0.001	6
	5	rain * dem	-2254.955	4526.330	15.700	0	8
	6	dem * rain + G.S.	-2254.453	4527.434	16.804	0	9
	7	dem	-2260.589	4531.351	20.721	0	5
	8	dem + G.S.	-2260.237	4532.718	22.088	0	6
	9	rain	-2265.342	4538.800	28.170	0	4
	10	rain + G.S.	-2264.460	4539.095	28.465	0	5
	11	Null	-2269.532	4545.133	34.503	0	3
	12	G.S.	-2268.952	4546.020	35.390	0	4

Chapter 5

The devil is in the dispersers: predictions of landscape connectivity change with demography

Resubmitted to *Journal of Applied Ecology* for final decision

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Statement of authorship: NE collected data, performed modelling work and analysed output data; SC assisted with modelling techniques; AL collected data; AL and DM oversaw this project; NE wrote the first draft of the manuscript and all authors contributed to revisions

Abstract

Concern about the effects of habitat fragmentation has led to increasing interest in dispersal and connectivity modelling. Most modern techniques for connectivity modelling have resistance surfaces as their foundation. However, resistance surfaces for animal movement are frequently estimated without considering dispersal, despite this being the principal natural mechanism by which organisms move between populations. We collected GPS data over ten years from 50 African lions (*Panthera leo*) (11 dispersing sub-adult males, 20 adult males and 19 adult females) and used a path level analysis to parameterise demographic-specific resistance surfaces for the entire Kavango Zambezi Transfrontier Conservation Area (KAZA) in Southern Africa. Lion path selection varied according to demographic grouping: Adult females were most averse to risky landscapes such as agro-pastoral lands, towns, areas of high human density and highways. Dispersers were the least risk averse suggesting they are potentially the most prone demographic to human-lion conflict. Adults of both sexes selected bushed grassland and shrubland habitats and avoided woodland. Dispersing males displayed the opposite trend suggesting con-specific avoidance and/or sub-optimal habitat use. We used the resistance surfaces to calculate factorial least-cost path networks for each demographic-specific resistance surface and present results that show substantial differences between predicted patterns of connectivity for dispersers, females and males. Resistance surfaces are widely used to create connectivity models, which are promoted for use by conservation managers. Our results suggest that the demographic category used to parameterise resistance surfaces may lead to radically different conclusions about connectivity. Failure to include dispersing individuals when parameterising resistance surfaces intended for connectivity modelling may lead to erroneous conclusions about levels of connectivity and potentially the application of unsound management strategies.

Introduction

As ecosystems become more fragmented the importance of dispersal is increasingly apparent since it is the principal mechanism by which organisms move within metapopulations and thereby maintain population viability and genetic diversity (Clobert *et al.* 2012). Thus there has been increasing interest in identifying corridors and maintaining connectivity between populations (for reviews see Sawyer *et al.* 2011, Zeller *et al.* 2012). Resistance surfaces that indicate the cost of movement as a function of landscape features are the foundation of most contemporary methods for mapping potential corridors and predicting connectivity (Zeller *et al.* 2012). In order to evaluate functional landscape connectivity, numerous techniques can be applied to the resistance surface, with least-cost modelling being the dominant tool (reviewed in Rudnick *et al.* 2012, Cushman *et al.* 2013). However, regardless of which connectivity metric is calculated, false assumptions pertaining to the underlying resistance surface may result in erroneous conclusions regarding connectivity (Janin *et al.* 2009). Since connectivity models are widely promoted as a conservation tool to address the effects of fragmentation, it is critical that the underlying resistance surfaces are reliable. To this end, recent research has investigated how the accuracy of resistance surfaces may be affected by the functional grain of environmental variables (Galpern and Manseau 2013), cost surface parameterisation (Koen *et al.* 2012) and the functions used to transform habitat suitability into resistance values (Trainor *et al.* 2013). However, as Zeller *et al.* (2012) noted in a review of papers relating to resistance surfaces, it is also crucial to compare the data types used and how these may alter the resultant resistance surface.

Expert opinion is the most common basis for parameterising resistance surfaces, followed by the use of genetic and detection data (Zeller *et al.* 2012). Recently, the use of telemetry data has increased (e.g. Trainor *et al.* 2013) and arguably provides the most direct and informative means for identifying landscape features that affect connectivity under current landscape conditions (Cushman *et al.* 2010). Studies that incorporate telemetry data typically use data obtained from settled adult individuals (e.g. Squires *et al.* 2013). For example, Cushman and Lewis (2010) created resistance surfaces based on telemetry data of 19 adult American black bears (*Ursus americanus*) of both sexes. This could give rise to two limitations: firstly, grouping males and females could mask important differences between sexes (e.g. Koehler and Pierce 2003); secondly, data collected on settled adults may give a biologically misleading impression of the factors that are important to dispersing individuals and therefore, connectivity. This is because data gleaned from the movement and resource selection of settled adults reflect choices to optimise fitness within home ranges, while habitats selected during dispersal need only provide those resources required by individuals moving through that patch (Soulé 1991). It is therefore striking that although dispersal is widely recognised as the primary means of population connectivity, few studies have used dispersal data to parameterise resistance surfaces (but see Richard and Armstrong 2010) and none has compared resistance surfaces derived from the behaviour of resident adults as opposed to dispersers.

In this paper we show that radically different conclusions about resistance surfaces and connectivity emerge when models are parameterised on the basis of the behaviour of different demographic categories. Specifically, we use telemetry data, spanning ten years, from 50 African lions (*Panthera leo*) in three demographic categories (11 dispersing males, 20 adult males and 19 adult females) to parameterise demographic-specific resistance surfaces based on 11 environmental variables.

Lion populations have become increasingly fragmented, with an estimated 75% range loss in the last 500 years (Riggio *et al.* 2013). A population genetics model predicted a minimum of 50-100 prides, with no limits to dispersal, are required to maintain long-term genetic diversity (Bjorklund 2003). Few remnant populations meet this criteria, raising the threat of diminished genetic diversity, shown to increase sperm abnormality and decrease reproductive performance (Packer *et al.* 1991). However, the degree to which remnant lion populations are functionally isolated and the factors that may facilitate gene flow between them through dispersal are largely unknown. Therefore, in parameterising resistance surfaces based on data from dispersers, adult males and adult females, we not only highlight the different results derived from each dataset but also lay the foundation for future work in connectivity modelling for this species.

Methods

Study extent

The study extent (≈1.4 million km^2) encompasses the entire Kavango Zambezi Transfrontier Conservation Area (KAZA-TFCA) and traverses sections of Angola, Botswana, Namibia, Zambia and Zimbabwe (Figure 5.1). Approximately 31% (≈446,000 km^2) of the study extent is managed for wildlife, including 26 national parks, 297 forest reserves and 117 wildlife management areas (WMA). This extensive area is of great conservation importance for lions as it contains 13 ‘Lion Conservation Units’ (IUCN 2006) and the Okavango-Hwange ecosystem is one of Africa’s 10 remaining lion ‘strongholds’ (Riggio *et al.* 2013).

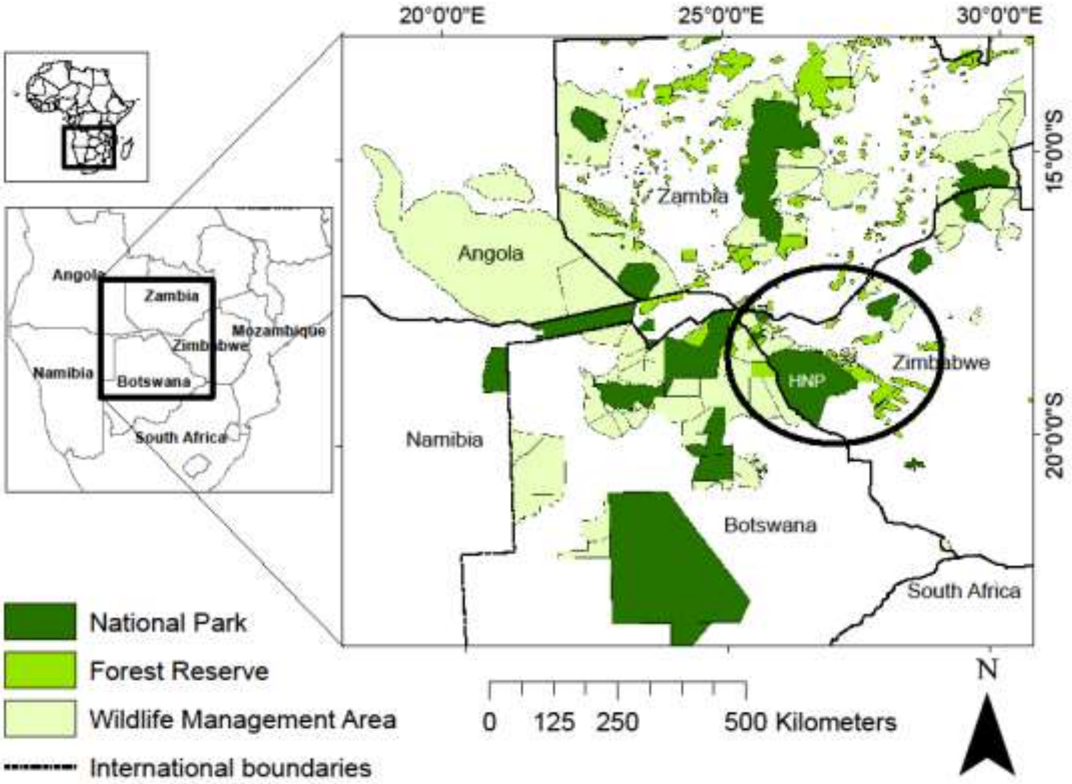


Figure 5.1: Study extent for evaluation of movement paths of African lions in Southern Africa. The black ellipse details the approximate extent of the GPS telemetry data obtained from collared lions in the study.

Environmental data

We proposed, *a priori*, three groups of variables (land use, habitat and anthropogenic) known to influence lion movement (e.g. Hopcraft *et al.* 2005, Valeix *et al.* 2012a, Loarie *et al.* 2013, Schuette *et al.* 2013). We used open-source geographic information system (GIS) layers or created our own. Layers that had a resolution <500m were retained in their original form. In order to maintain a consistent grain size, coarse-grained layers (>500m) were resampled to 500m using nearest neighbour (for categorical variables) or bilinear interpolation (for continuous variables) in ArcInfo Workstation (ESRI 2010).

1. ***Land use***: We obtained GIS layers depicting wildlife areas from the World Database on Protected Areas (IUCN and UNEP 2010) and reclassified them as:
   a. National parks: Gazetted by government (IUCN Category II). 'Game Reserves' in Botswana (IUCN Category IV) were also included as they have the same function.
   b. Forest reserves: Government-owned land primarily set aside for forest products, with a mandate for conservation.
   c. Wildlife management areas: State, private or community-owned land managed for wildlife. The focus is on trophy hunting with a few areas set aside for photographic tourism.
   d. Agro-pastoral lands: All land not included in the three categories above was converted into a layer of human habitation.
2. ***Habitat***: We used the European Space Agency (ESA) global land cover map, version 2.3 (ESA and UCLouvain 2010) consisting of 22 habitat classifications. Only nine categories occurred in our study extent and were retained for sampling. These were reclassified according to habitat structure and place into three broad groups: woodland, shrubland and bushed grassland (see Appendix 5.1). In addition, we used the Moderate Resolution Imaging Spectroradiometer (MODIS) Vegetation Continuous Fields dataset (Hansen *et al.* 2005), which quantifies percentage tree cover.
3. ***Anthropogenic***
   a. Human density: We used the Gridded Population of the World (GPWv3) dataset based on population data estimates from 2000 and projected (in 2004) to the year 2010 (CIESIN and CIAT 2005). Projections were based on growth rates from census data and United Nations statistics.

b. Towns: We digitised the extent of all towns in the study extent using DigiPoint3 (Zonum Solutions 2010) in Google Earth (Google Inc. 2011). To reflect the size of each town, and hence how these physical structures may impact lion movement, this was converted to a point density layer by converting the raster to a point coverage and calculating the focal point density on that surface within a 5,000m radius focal window (ESRI 2010).

c. Highways: All major roads were recorded using a handheld Global Positioning System (GPS) device (Garmin, Olathe, Kansas, USA) programmed to collect fixes at 100m intervals (accuracy ± 4m).

Lion telemetry data

Lion telemetry data were obtained from a source population in and around Hwange National Park (HNP), in North West Zimbabwe (19°00´S, 26°30´E). The population has been intensively monitored without interruption since 1999 (for a description of the study area and lion population see Loveridge *et al.* 2010). Between 2003 and 2012, location data were obtained from 50 lions in different social groups (11 dispersing males, 20 adult males and 19 adult females). Each lion was fitted with a GPS radio-collar (see Loveridge *et al.* 2007c for details), programmed to take hourly fixes when lions were active (1800-0700). All lions were collared within HNP and surrounding areas, but were not confined to this area. See Appendix 5.2 - 5.5 for representative data for each demographic category.

Data preparation

To ensure accuracy, we retained only those fixes with a Dilution of Precision <10 (Frair *et al.* 2010). To reduce the effects of non-stationarity (Cushman *et al.* 2005) the study period was split into sequential temporal windows of 30 day intervals. We created 229 temporal window periods, starting on 11 March 2003 and ending on 20 August 2012. The data for each individual lion were split according to these windows.

Lion demographic categories

Lions were classified as dispersing males, adult males or adult females, based on field observations:

Dispersing males: The transience phase was deemed to have commenced once the sub-adult had left its natal pride and did not return thereafter. A dispersing individual was deemed to have established a territory when it had been in a consistent home-range for a minimum period of two months and occupied a fixed home-range thereafter. The onset of establishment was back-dated to the time the lion entered the new home-range. Only data gathered during dispersal were retained (70 windows).

Adults: All adults used in this study were at least four years old, either in established territories or, in a few cases, temporarily nomadic for short periods after being displaced from their territory (adult males = 371 windows; adult females = 486 windows).

Path selection and scaling

To predict lion movement as a function of landscape features we converted the series of sequential locations for each utilised window into a path in ArcInfo Workstation (ESRI 2010). Path selection functions are a robust method for comparing the attributes of landscape features along an animal's utilised path with those that would be encountered in available paths (Cushman and Lewis 2010). This approach is arguably the most powerful selection function for creating resistance surfaces (Zeller *et al.* 2012), and avoids problems of autocorrelation associated with step selection functions (Cushman 2010).

Ecological processes, such as dispersal, may be driven by environmental factors across a range of spatial scales (Wiens 1989), making it important to measure a response variable at the correct scale (Sawyer *et al.* 2011). Failure to do so may result in erroneous evaluation of a relationship effect size or detection of a relationship altogether (Cushman and Landguth 2010). It is therefore recommended that one quantifies variables at multiple scales to determine scale dependency in the underlying process (Galpern and Manseau 2013). We used four scales to investigate relationships between lion movement paths and GIS variables detailed above. For each utilised path we created nine matched available paths of identical topology to the utilised path at each scale. The available paths were then shifted a random distance in x and y and randomly rotated between 0 and 360°. The four spatial scales correspond to random shifts of: (1) no shift and distances between (2) 0-12.5km, (3) 0-25km, (4) 0-50km. Thus, for each used path we had nine random paths at each scale resulting in a total of 36 available paths per used path. Issues of autocorrelation are avoided by converting the points to paths, retaining the topology of the used paths and randomly rotating and shifting those paths (Cushman 2010). In total our dataset comprised 927 utilised and 8343 available paths, each of 30 day duration.

Conditional logistic regression

Predictor variables were derived in ArcInfo Workstation (ESRI 2010) by calculating the mean value for each GIS variable of all pixels that fell along the utilised and available path trajectories. We used conditional logistic regression to match each utilised path with the nine available paths at each scale. Thus the results of the model are conditional upon each group of corresponding used and available paths and no intercept is estimated. With the present study design, conditional logistic regression is an appropriate modelling approach (Hegel *et al.* 2010) and is useful for radio-telemetry data, where there is a lack of independence (Fortin *et al.* 2005, Coulon *et al.* 2008), since it minimises issues of autocorrelation inherent in spatial data (Craiu *et al.* 2008). In addition, this approach is particularly powerful for studying fine-scale habitat selection (Compton *et al.* 2002) and provides a robust way to rank alternative hypotheses with Akaike’s Information Criterion (AIC; Burnham and Anderson 2002, Cushman and Lewis 2010). Consistent with Coulon *et al.* (2008), we used the Cox function and performed all statistical analysis in R 2.15.1 (R Core Team 2012). Lion ID was used as a random effect in all models.

We conducted the conditional logistic regression in two steps. First, we performed a univariate scaling analysis (e.g. Thompson and McGarigal 2002) for each variable to determine which scale had the strongest relationship with lion path selection. We used model selection to identify the most supported scale for each variable based on Akaike Information Criterion corrected for small sample size (AICc). The scale with the lowest AICc ranking was inferred to be the one at which lions selected their paths, and thus was retained for the next step.

Second, we created candidate models for each group of variables. Models were ranked using AICc and relative support was assessed using Akaike weights (w_i). When one model was superior (w_i>0.9) this was used, otherwise we averaged parameter estimates across the models correcting for model weights (Burnham and Anderson 2002).

Resistance surfaces

Using the results from the second step of analysis we produced resistance surfaces for each demographic category. For each group of models we took the coefficients from the dominant model or those produced by model averaging and used them to produce resistance surfaces. Resistance surfaces were created in ArcInfo Workstation (ESRI 2010) by calculating $z = \beta_1 v_1 + \beta_2 v_2 + \ldots + \beta_n v_n$, where β_i is the coefficient for variable v_i and rescaling such that resistance = (z * -1) / min(z * -1). To explore the similarity between the resistance surfaces for adult male, adult female and dispersing lions, we created Relative Difference Grids (RDGs) by calculating the difference between two surfaces as a proportion of the dispersal resistance surface. RDGs were created for males and females by calculating (dispersal resistance – adult male or female resistance) / dispersal resistance.

Factorial least-cost paths

We calculated factorial least-cost path (LCP) networks (e.g. Cushman, McKelvey & Schwartz 2009) to illustrate the changes in connectivity and their implications for management. Factorial LCPs have an advantage over tradition LCP analyses since they calculate LCPs among many pairs of source and destination cells (Cushman and Landguth 2012). We created a uniform grid of 223 source points, spaced at 25km and located within national parks (Figure 5.4a) and used UNICOR (Landguth *et al.* 2012) to calculate factorial LCPs with a 250,000 cost-distance threshold. This threshold roughly translates to 80km through the most costly land use, agro-pastoral land, and is well within the dispersal ability of lions (Appendix 5.3-5.5).

We used FRAGSTATS (McGarigal *et al.* 2012) to quantify the differences in demographic-specific corridor networks in two different ways. First, we calculated four landscape metrics to quantify the extent and fragmentation of each predicted corridor network (PLAND – percentage of the landscape covered by the predicted corridor network; NIP – number of isolated patches in the corridor network; Correlation Length – correlation length of predicted corridor network; Mean Shape Index – area-weighted shape index calculating the shape complexity of each patch in the corridor network). Second, we calculated the intersection of predicted corridors outside national parks between each demographic category with intensity greater than mean plus one standard deviation (SD) and mean plus two SD. These signify weak and intense corridors respectively and quantify the degree to which predicted corridor networks for each demographic group are accurate surrogates for the others.

Results

Univariate scaling

AICc rankings showed that land use and anthropogenic variables were most frequently selected or avoided at broad scales (0-25km), while habitat variables were either selected at small scales (0km) or large scales (0-50km; Appendix 5.6). There was strong and consistent selection of protected areas and avoidance of humans and agro-pastoral land by lions. National parks were selected by all demographic categories across all scales; in each instance the most supported scale was 0-25km. Agro-pastoral land and areas of high human density were avoided at all scales by all demographic categories, again 0-25km being the most supported scale. Towns and highways were generally only avoided at larger scales, while avoidance was not detected at small scales.

Multivariate analysis

Models and model comparison statistics for each demographic-specific group of analyses can be found in Appendix 5.7.

Land use

All three demographic categories avoided agro-pastoral lands, but the extent to which they did so varied, as evidenced by the coefficients (Appendix 5.8). Dispersing males showed the weakest avoidance of agro-pastoral lands, followed by adult males (twice that of dispersers). Adult females showed the strongest avoidance of agro-pastoral lands (seven times that of dispersers) and the strongest selection for national parks. Dispersing males had the weakest selection for national parks, followed by adult males. Forest reserves were selected by dispersers, with weak selection or avoidance by adult males and females of forest reserves and WMA’s.

Habitat

Bushed grassland and shrubland areas were selected by adult males and females (Appendix 5.9). Conversely, dispersing males avoided these habitat types and selected woodlands, which were avoided by adults of both sex. All three demographic categories avoided areas with higher percentages of tree cover.

Anthropogenic

Each of the anthropogenic parameters was avoided by all demographic categories, but to varying degrees (Appendix 5.10). Both highways and humans were least avoided by dispersing males, with adult males displaying intermediate avoidance and adult females the strongest avoidance. Adult females avoided highways to an 11-fold greater extent than did dispersers and adult males five times more than dispersers. Adult females most strongly avoided areas of human density (four times that of dispersers) with adult males having intermediate avoidance (twice that of dispersers). Towns were most strongly avoided by adult females, then dispersers, followed by adult males.

Resistance surfaces

Resistance surfaces produced from all 11 variables for each demographic category are displayed in Figure 5.2. Mean resistance for adult males was twice as high (mean ± SD = 61.096 ± 191.2) as that of dispersing males (mean ± SD = 29.8 ± 101.9), while adult females had the highest resistance (mean ± SD = 82.7 ± 448). The Relative Difference Grids illustrate these differences (Figure 5.3), with larger negative values indicating areas where the paired demographic category (either males or females) had higher resistance than did dispersers and positive values indicating areas where the paired demographic category had lower resistance than did dispersers.

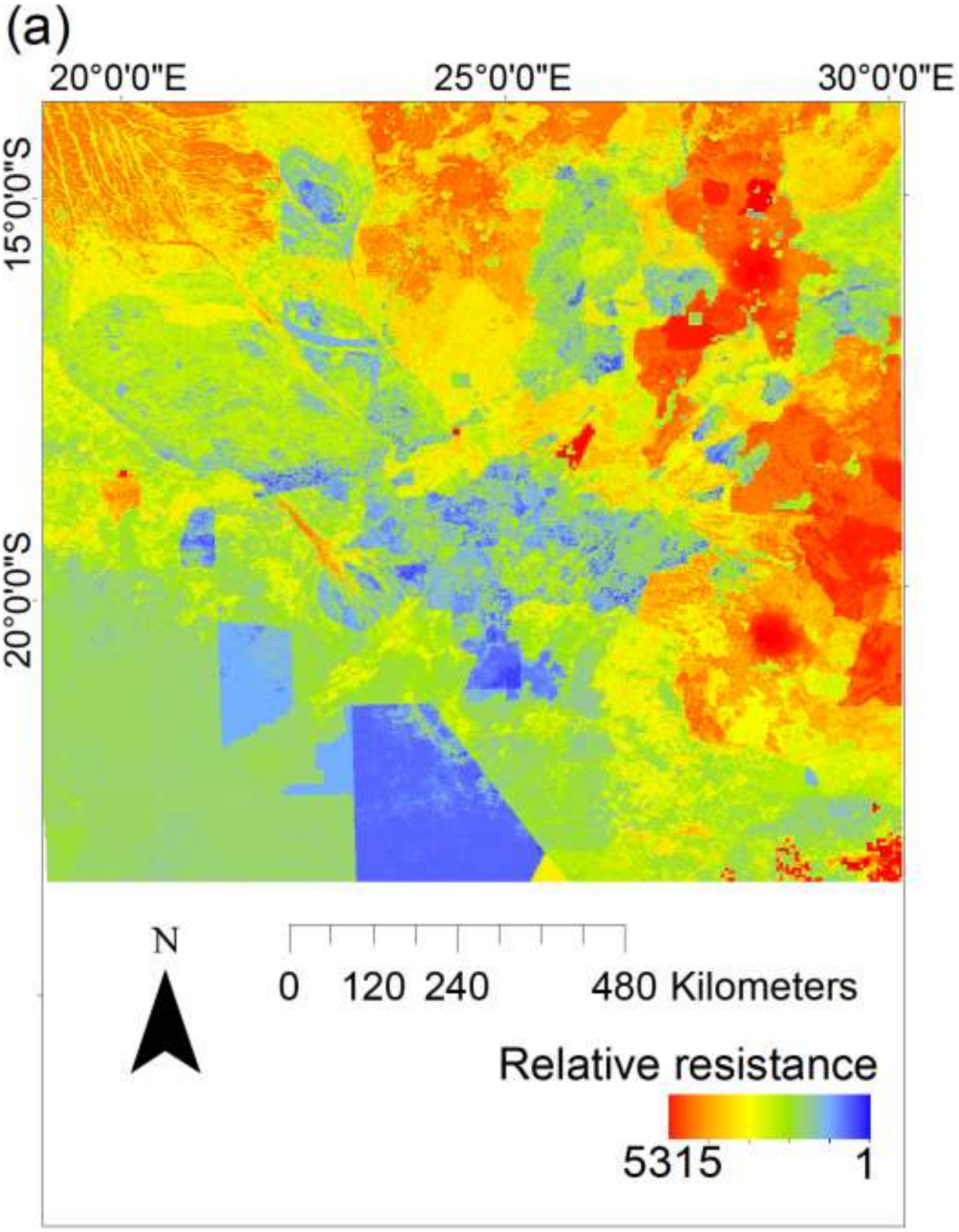
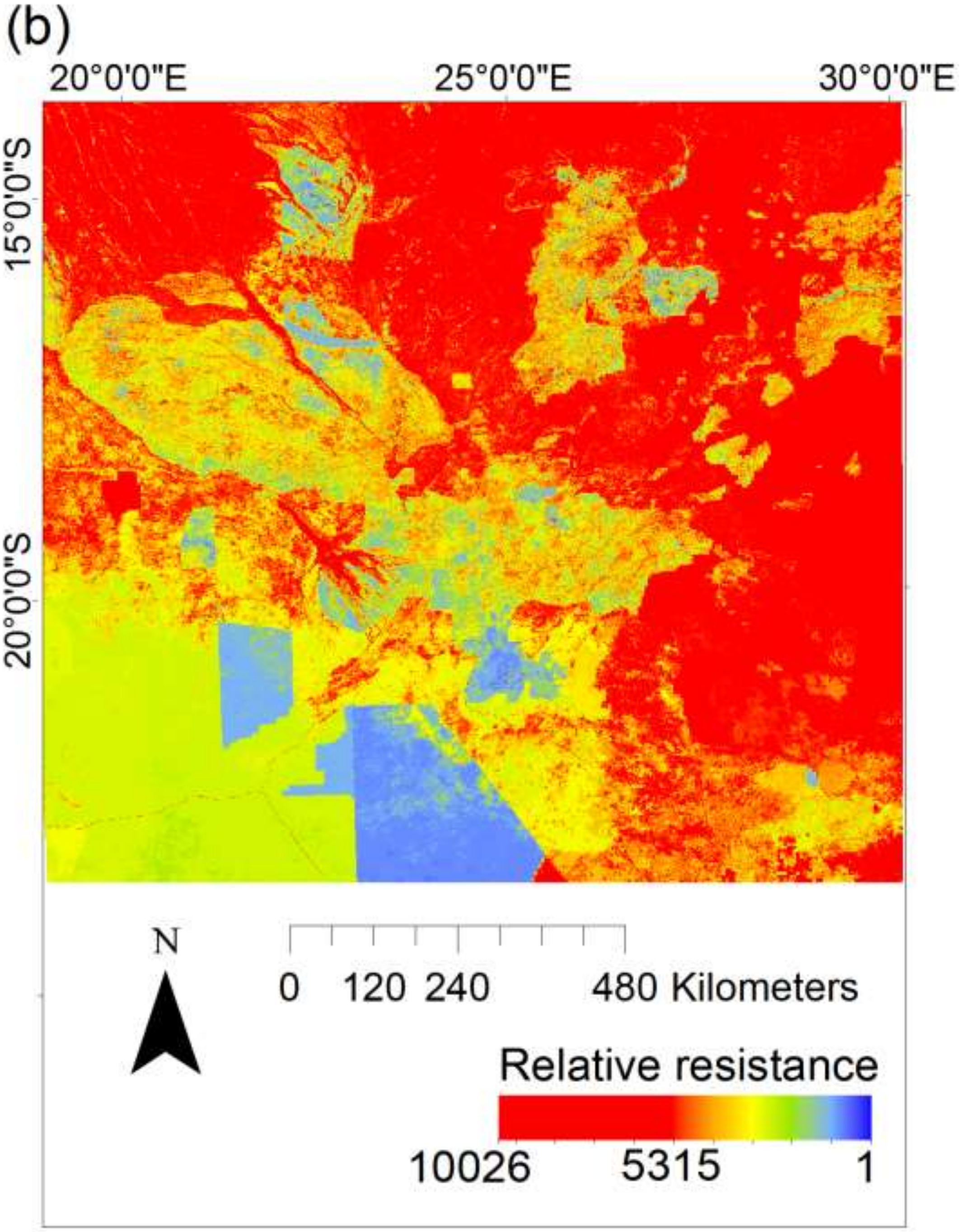
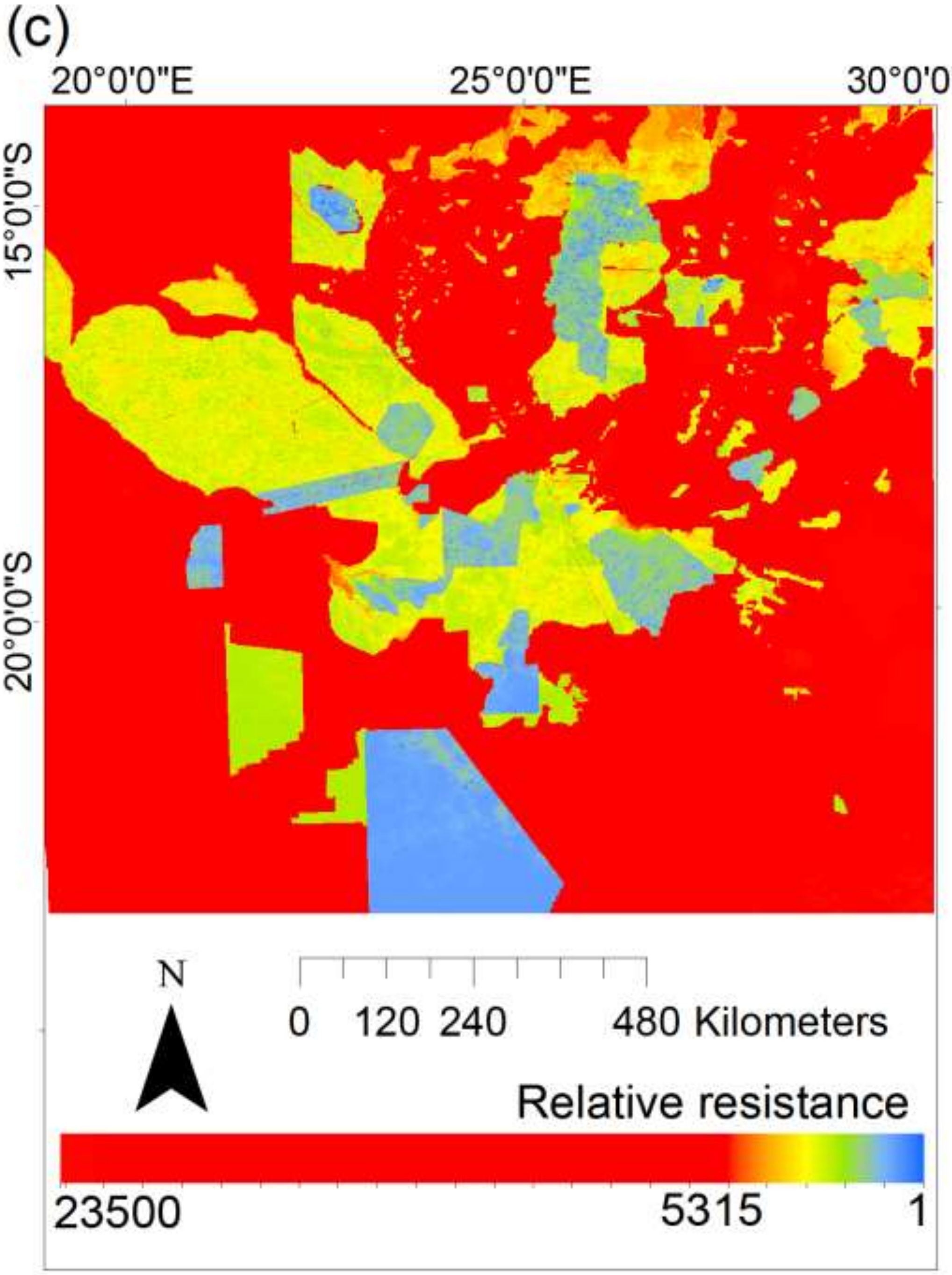


Figure 5.2: Resistance surfaces for a 1.4 million km^2 area in Southern Africa parameterised from GPS telemetry data obtained from (a) dispersing male lions, (b) adult male lions pg. 126 and (c) adult female lions pg. 127. Resistance surfaces were created by calculating $z = \beta_1 v_1 + \beta_2 v_2 + \ldots + \beta_n v_n$, where β_i is the coefficient for variable v_i and rescaling such that resistance = (z * -1) / min(z * -1). For display, we stretched the adult male and adult female surfaces to match the scale of the disperser resistance surface.


(b)
20°0'0"E
25°0'0"E
30°0'0"E
15°0'0"S
20°0'0"S
N
0
120
240
480 Kilometers
Relative resistance
10026
5315
1


(c)
20°0'0"E
25°0'0"E
30°0'0"E
15°0'0"S
20°0'0"S
N
0 120 240 480 Kilometers
Relative resistance
23500
5315
1

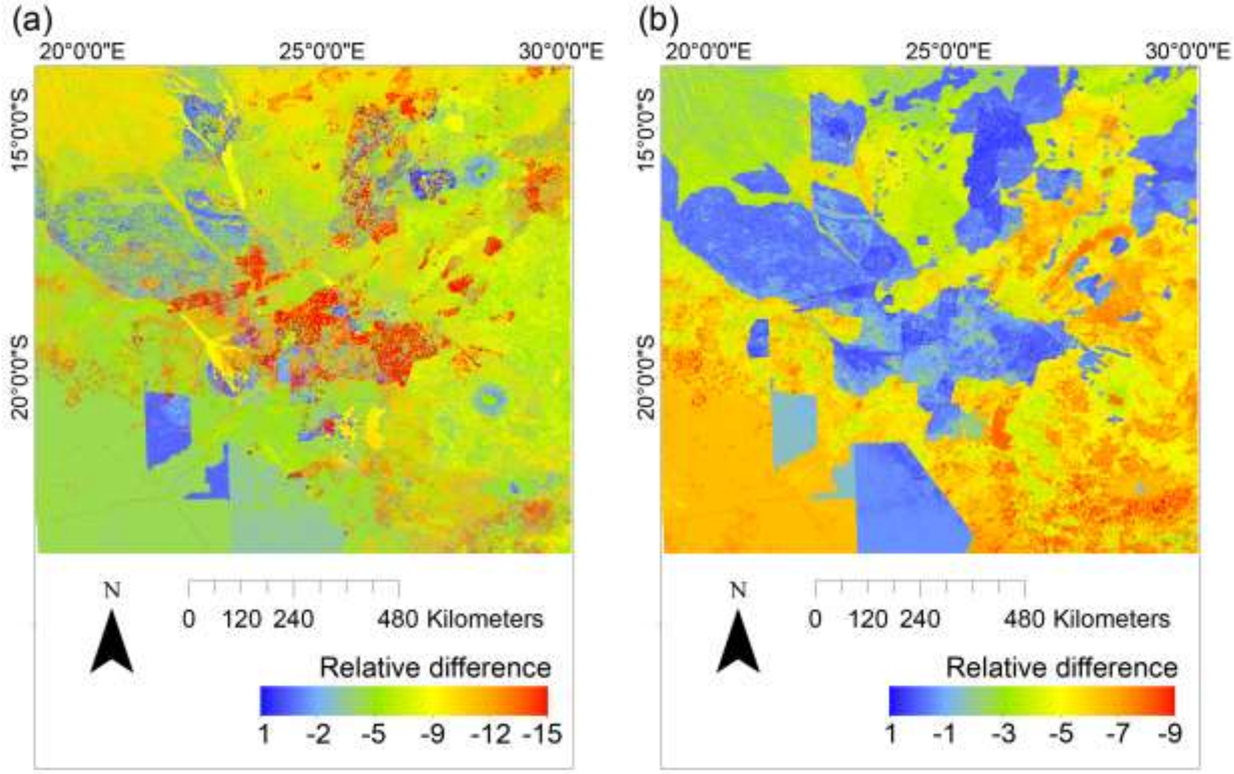


Figure 5.3: Relative Difference Grids for paired demographics of lions in Southern Africa and highlight differences between resistance surfaces derived from (a) dispersal data compared to adult male data and (b) dispersal data compared to adult female data. Negative values indicate areas where the paired demographic category (either males or females) had higher resistance than did dispersers and positive values indicating areas where the paired demographic category had lower resistance than did dispersers.

Factorial least-cost paths

The model indicated substantial differences between patterns of connectivity predicted for dispersers (Figure 5.4b), females (Figure 5.4c) and males (Figure 5.4d). For example, the extent of the landscape occupied by the corridor network for dispersers was 22.6% higher than for females and 37.7% higher than for males. Similarly, the total fragmentation of the network, as judged by number of isolated patches, was 233% higher for males and females than for dispersers (see Appendix 5.11 for full set of differences and explanations).

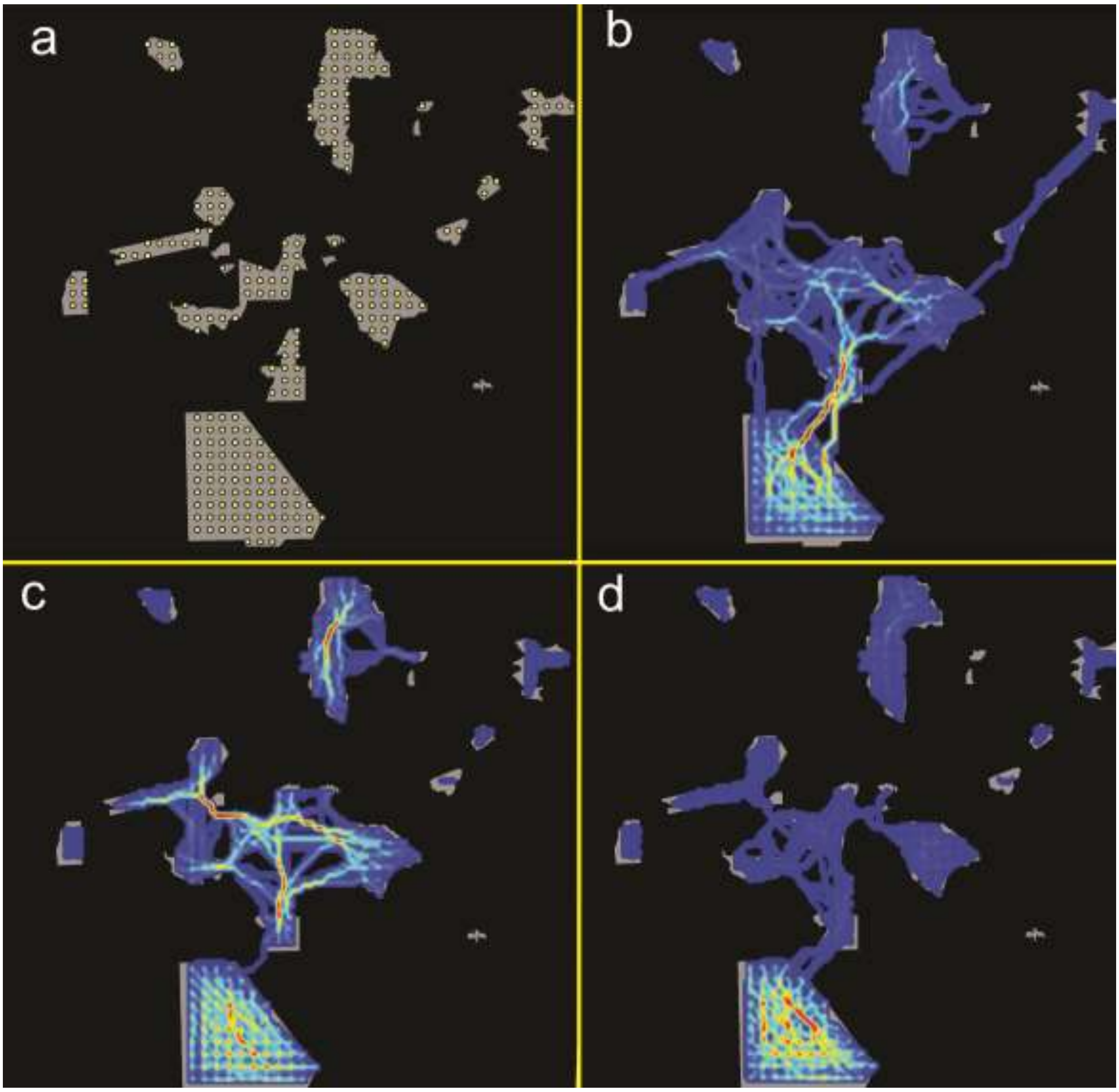


Figure 5.4: Illustration of the differences in predicted connectivity for resistance maps derived from different demographic categories of lions. Panel (a) shows national parks in grey and 223 source points in yellow. Panel (b) shows the predicted corridor network connecting source points within the cost distance threshold (250,000 cost units) for dispersing sub-adult male lions, (c) adult female lions, (d) adult male lions. The colour ramp indicates corridor intensity, as measured by the number of least-cost paths among combinations of source points passing through a given pixel, and ranges from 0 (black) to 197 (dark red).

The intersection analysis (Table 5.1) revealed that for both weak and intense corridors there is low intersection among demographic groups: For all combinations there is no case where the intersection amounts to 50% of the corridor network (Table 5.1 all values less than 0.5). In addition, the degree of intersection for all combinations of demographic group are smaller in the upper triangle (Table 5.1) than in the lower triangle, indicating that there is proportionally more overlap for weak corridors than for intense corridors. Finally, the intersection between the predicted corridor network for adult male lions and dispersers was higher than between females and males, or females and dispersers (especially for the most intense corridors – upper triangle) suggesting that resident males and dispersers have the most similar optimal corridor networks.

Table 5.1. Intersection of predicted corridors outside national parks between male, female, and dispersing African lions. Values in the upper triangle are for intersections of all corridors with intensity greater than $\bar{x}$ + 2 SD (‘intense corridors’). Values in the lower triangle are for intersections of corridors of intensity value greater than $\bar{x}$ + 1 SD (‘weak corridors’). The values in the table on the left correspond to the size of network intersections for the group listed in the column name as a proportion of the group listed in the row name. The table on the right is the group in the row name as a proportion of the group in the column name. For example, left table, column 1, row 2, the value is 0.190. This is interpreted as 19% of the extent of the female corridor network (at $\bar{x}$ + 1sd intensity level) intersects with the male corridor network.

	Adult males	Adult females	Dispersers
Adult males	X	0.069	0.411
Adult females	0.190	X	0.039
Dispersers	0.265	0.269	X

	Adult males	Adult females	Dispersers
Adult males	X	0.029	0.236
Adult females	0.135	X	0.029
Dispersers	0.485	0.349	X

Discussion

Our results show that strikingly different resistance surfaces and connectivity metrics can be predicted depending on whether data on the movements of dispersing, adult male or adult female lions are used to parameterise models. The differences arise primarily because dispersing male lions avoided what might be interpreted as risky conditions (agro-pastoral lands, highways and humans) to a lesser extent than did adults. The movements of adult females were only weakly affected by habitat type but, like adult males, they selected for bushed grasslands and shrubland habitats while avoiding woodland. Dispersers showed the opposite trend: selecting for woodland and avoiding bushed grassland and shrubland. We propose that such differences are likely to occur in other species since dispersal through a habitat patch may be driven by different factors to those affecting movements of adults (Wasserman *et al.* 2010).

In dimorphic and polygynous species males are more likely to take risks than females (Trivers 1985). Conversely, females, especially those with dependent young, may be more averse to raiding compared to males (e.g. Bunnefeld *et al.* 2006). Dispersal on the other hand, is inherently risky, particularly when travelling through novel environments and frequently results in mortality (Bonte *et al.* 2012). Dispersing sub-adult males are smaller than adult males and during transience pass through occupied territories, where they are not tolerated (Packer 2001). It is therefore unsurprising that dispersers, while searching vast areas for patches in which to settle, encounter anthropogenically risky environments more frequently than do territorial adults. Indeed, stock-raiding lions are frequently dispersing sub-adults (Stander 1990, Patterson *et al.* 2004) and our results highlight dispersers as the demographic group most prone to coming into contact with people and hence be involved in human-lion conflict. This has important management implications since complete protection of land may aid, but not be essential to effectively link lion populations, provided lions are tolerated (e.g. Schuette *et al.* 2013). As such, conflict mitigation should be part of connectivity planning for this species.

The univariate scaling analysis identified the functional scale at which lion path selection was most related to each environmental variable. Avoidance of towns and highways was only detected at larger scales, highlighting the importance of assessing variables at multiple scales, without which an erroneous conclusion that lions do not avoid towns and highways may have been made. Our multivariate analysis revealed the magnitude of the effect for each variable at the most appropriate scale. The overall approach and resultant resistance surfaces integrate landscape patterns and behavioural processes to lay the foundation for realistic and accurate connectivity modelling. Future work should build on the resistance layers of dispersers to investigate changes in landscape connectivity under a range of management scenarios. These could include the addition or removal of protected areas, an increase in human density or the use of fencing. This would be timely since a recent, widely publicised study suggested that fencing lions populations would benefit their conservation (Packer *et al.* 2013), while others argue that promoting connectivity would be more effective (Creel *et al.* 2013).

Once a paradigm largely restricted to the Western world (Beier and Noss 1998), connectivity conservation is now widely promoted and has engendered considerable political and popular support globally (Doerr *et al.* 2011). In Africa for example, an initiative by Peace Parks Foundation (PPF) has elevated the study of connectivity from an academic pursuit to a necessity. Throughout Africa, PPF have developed Transfrontier Conservation Areas (TFCA's) with government-signed MoU's and treaties for 10 TFCA's and plans for eight more (PPF 2013c). Tens of millions of dollars have been raised, in part to achieve one of their core objectives: connectivity. KAZA TFCA, which our study extent encompasses, is one such example and it is therefore critical that connectivity plans are created from realistic data.

Currently most TFCA connectivity strategies are based on expert opinion, which has demonstrated limitations and weaknesses (Sawyer *et al.* 2011). While use of empirical data is an improvement, our results indicate that connectivity models, which are not based on the most relevant demographic to connectivity, i.e. dispersers, may also lead to potentially unsound management decisions. The intersection analysis revealed that there was low overlap of predicted corridors among demographic groups. Similarly, we found that there was more overlap among weak predicted corridor networks than intense networks for the different demographic groups. This indicates that connectivity models developed from one demographic category are likely to be poor surrogates for other demographics, particularly for the most intense corridors, which are most likely to be prioritised by targeted conservation actions. In addition, the models of predicted connectivity for adult lions neglect that there may already be viable corridors between for instance HNP and Chizarira National Park and an intense corridor between Makgadikgadi and the Central Kalahari Game Reserve (Figure 5.4). Thus management decisions based on adult resistance surfaces might focus on areas that are not in line with existing dispersal routes.

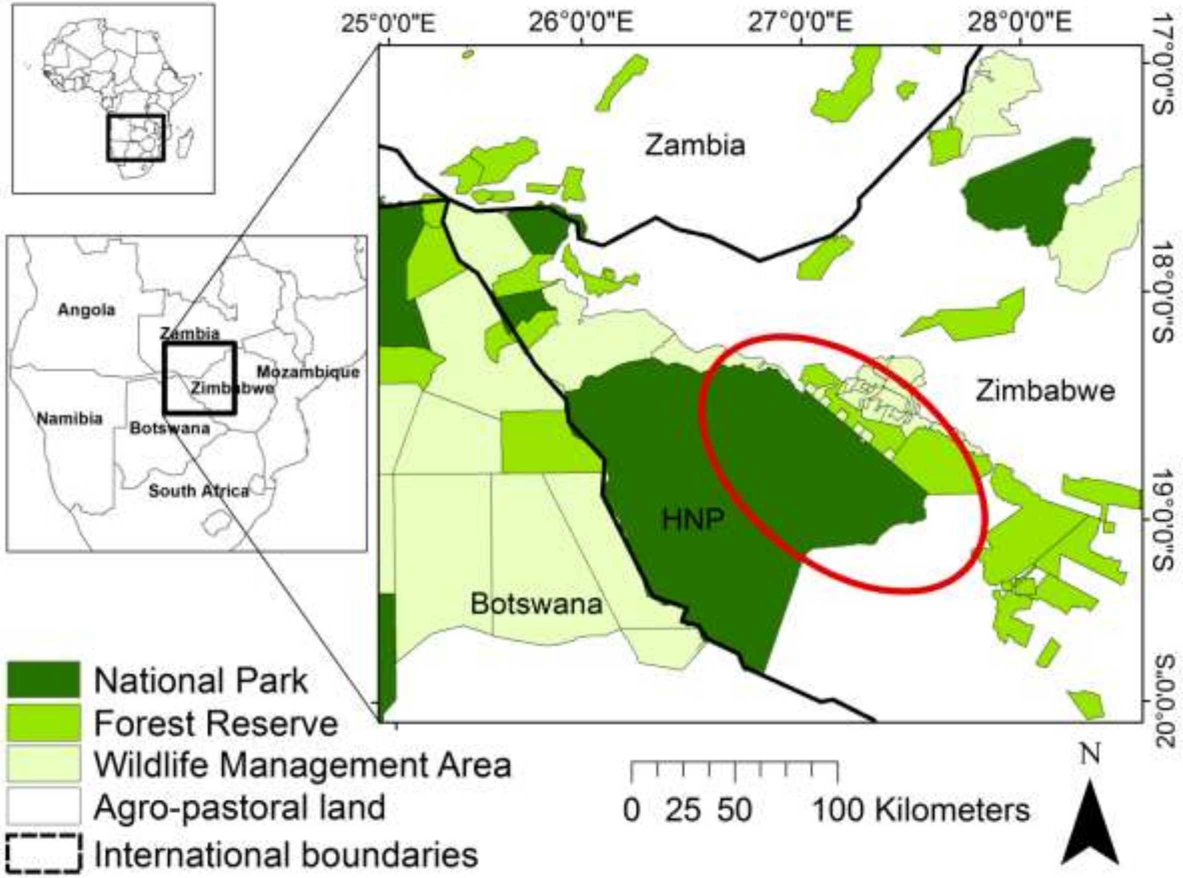
Protecting dispersal corridors has become a cornerstone of modern conservation (Chetkiewicz *et al.* 2006, Rudnick *et al.* 2012). Their effectiveness for facilitating movement has been demonstrated in a variety of taxa (Haddad *et al.* 2003), but can be counterproductive, especially when based on scant biological data (Chetkiewicz *et al.* 2006). As a result, some authors argue that the importance of connectivity is overstated, primarily due to uncertainty in models, regarding for instance how dispersers search for habitat (Hodgson *et al.* 2009). Meanwhile, others suggest that advances in knowledge and theory on dispersal behaviour limit such uncertainty (Doerr *et al.* 2011). We contend that both arguments are partly correct: there is uncertainty in many connectivity models and there is a rapidly increasing understanding of dispersal. The uncertainties arise however, largely because studies frequently do not incorporate empirical dispersal data and behaviour into connectivity models. Our results indicate that it is critical to do so.

Appendix

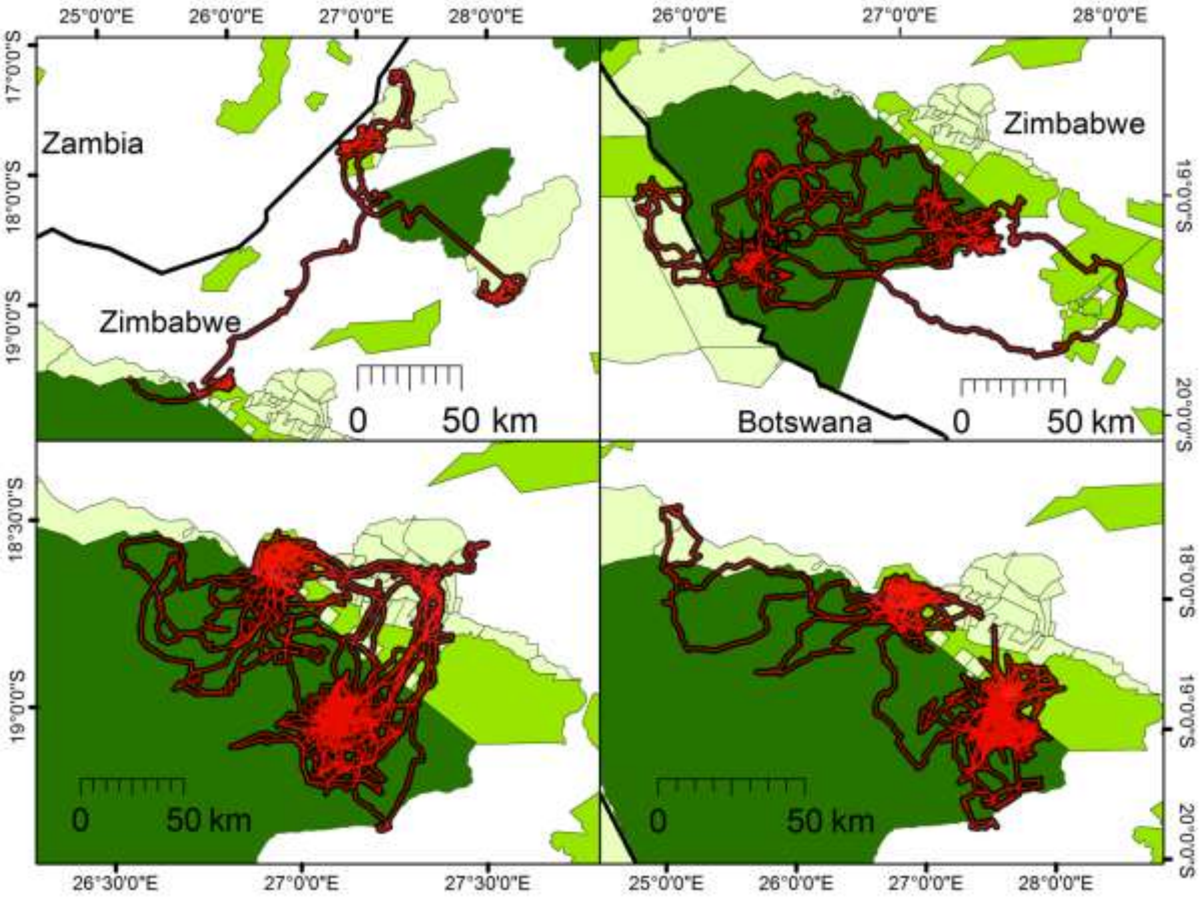
Appendix 5.1. Habitat reclassification table. The original grid code and description from the European Space Agency (ESA) global land cover map, version 2.3 was reclassified into seven groups. Of these, only three (reclassified as woodland, shrubland and bushed grassland) occurred in our study area and were retained for sampling.

Original Grid code	Original description	Reclassification	Reclassified description	Total area (km2)	% habitat type in study extent (km2)
30	Mosaic vegetation (grassland/shrubland/forest) (50-70%) / cropland (20-50%)	woodland	15 - >40% forest	276356	18.6
50	Closed (>40%) broadleaved deciduous forest (>5m)	woodland	15 - >40% forest	84984	5.7
60	Open (15-40%) broadleaved deciduous forest/woodland (>5m)	woodland	15 - >40% forest	114729	7.7
110	Mosaic forest or shrubland (50-70%) / grassland (20-50%)	shrubland	Forest and shrubland (50%) / grassland (50%)	63065	4.2
120	Mosaic grassland (50-70%) / forest or shrubland (20-50%)	shrubland	Forest and shrubland (50%) / grassland (50%)	54743	3.7
100	Closed to open (>15%) mixed broadleaved and needleleaved forest (>5m)	bushed grassland	Closed to open shrubland (+/-15%)	17536	1.2
130	Closed to open (>15%) (broadleaved or needleleaved, evergreen or deciduous) shrubland (<5m)	bushed grassland	Closed to open shrubland (+/-15%)	267815	18.0
140	Closed to open (>15%) herbaceous vegetation (grassland, savannahs or lichens/mosses)	bushed grassland	Closed to open shrubland (+/-15%)	606173	40.7
150	Sparse (<15%) vegetation	bushed grassland	Closed to open shrubland (+/-15%)	2942	0.2

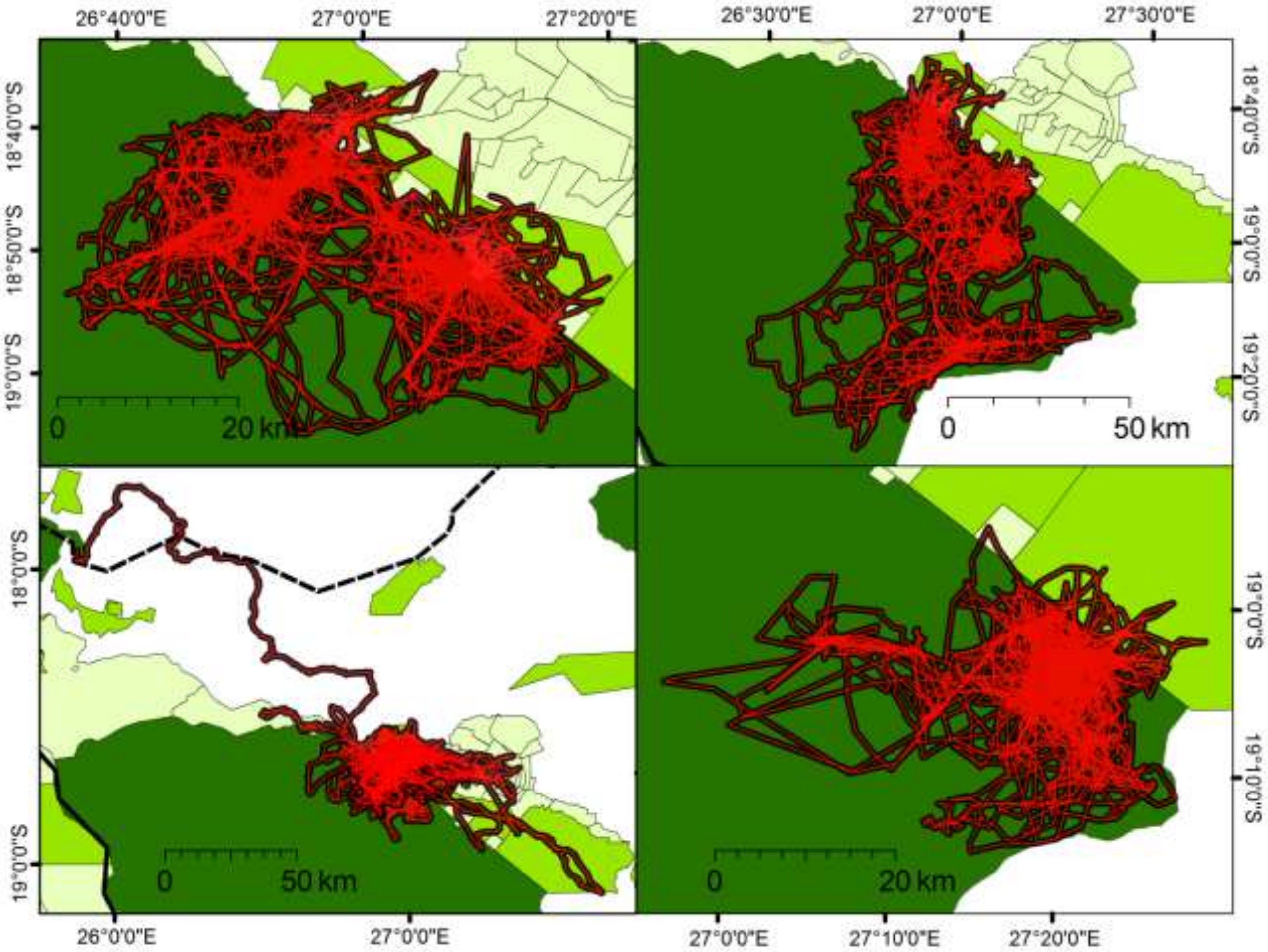
Appendix 5.2 – 5.5. The following figures are designed to display representative data used in this study. These example data were chosen as they aid in the visualisation of lion movement paths, home ranges and selection or avoidance of land use types. As such they display our entire datasets for four individuals from each demographic group. These data were overlaid on various environmental variables in order to perform a path level analysis and parameterise demographic-specific resistance surfaces. The data displayed below are particularly informative in interpreting our results pertaining to the varying degrees to which each demographic group avoided agro-pastoral lands.



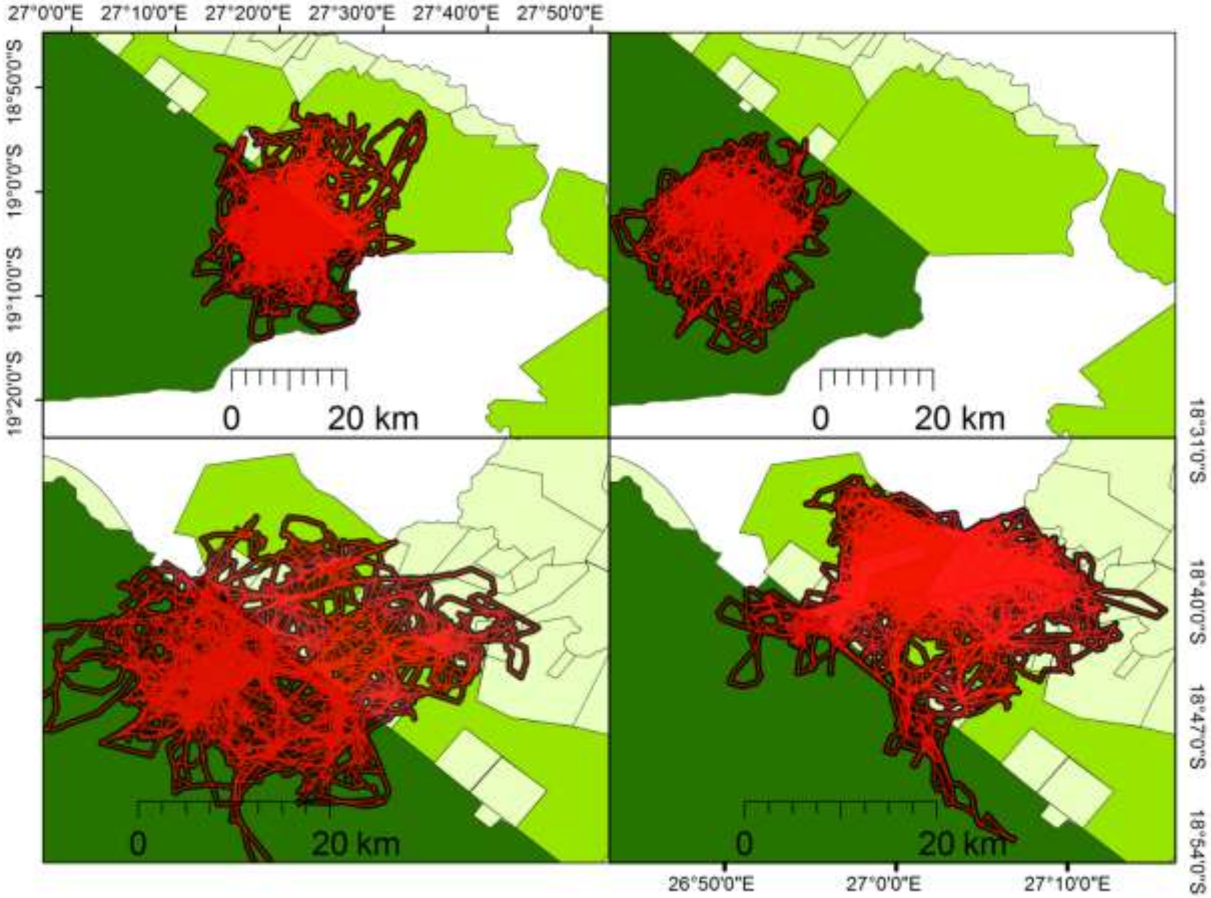
Appendix 5.2. The red ellipse indicates the core study area, which has been intensively monitored since 1999. All lions radio-collared during this study were captured in Hwange National Park and the surrounding wildlife management areas and forest reserves. Two of the major focuses of this research project include monitoring the effects of trophy hunting and investigating human-lion conflict. As such, we aimed to collar lions situated in close proximity to the boundaries of protected areas. As a result, lions of all demographic categories had equal chance of leaving the protected areas.



Appendix 5.3. Dispersal movement paths. Panels (a) and (b) are representative of dispersing males that left the protected area for considerable lengths of time. While panels (c) and (d) are representative of dispersing males that spent the majority of transience within the confines of HNP and the surrounding protected areas. More specifically, (a) illustrates the movement path of a dispersing male who left HNP and walked over 100km through agro-pastoral lands where he was recorded killing considerable amounts of livestock. At the time of writing, it appears that he has settled in the Chizarira/Chirisa complex in the north east; (b) illustrates the path of a young male that also spent considerable time in agro-pastoral lands and crossed into Botswana. This male was transient for 848 days and travelled some 4,223 kilometres during the 16 months he was radio collared. He was finally shot for raiding livestock. Note that despite traversing a huge area his start and end points are very close together highlighting the value of radio-telemetry data since start and end points only would provide a misleading interpretation of this lion's transience phase; (c) and (d) were two dispersing males in two separate groups despite going to similar areas. Both (c) and (d) represent 690 days. Both lions were recorded to kill livestock, particularly the individual displayed in (c) who spent vast amounts of time in the north east of the map and killed substantial quantities of livestock. Both lions survived dispersal and established territories within HNP.



Appendix 5.4. Adult males. Panels (a) and (b) display data over 1,740 days and 1,200 days respectively. Notice how for both males the territory shifts over this time frame as they were ousted from one area and gained residence in another. Of particular interest in panel (b) is the time spent on the southern boundary of HNP where despite being in the area for one and a half years, this lion never crossed the boundary despite many patrols along it. Panel (c) is an exceptional example of an adult male who was originally in a coalition of four. One by one these males were either trophy hunted or poached, resulting in this male becoming a singleton and unable to hold his territory. When he was eventually ousted he first travelled south east, reached the end of the protected area and turned back. He then travelled north west through agro-pastoral lands (approximately 100km in a straight line) and crossed the Zambezi river in Zambia. He was subsequently captured outside Livingston after becoming an habitual livestock raider. Panel (d) is illustrative of an adult male, whose territory was in close proximity to agro-pastoral land. This data represents 570 days during which time he never left the protected areas.



Appendix 5.5. Adult females. The first difference to note is the small size of adult female territories in comparison to adult males. Panel (a) represents 1,920 days of GPS data, during which time this female only left the protected area on one occasion, despite being situated on the boundary. Panel (b) represents 1,470 days and a female which never left the protected area. Panel (c) illustrates 1,170 days. This female left the protected area on a number of occasions. Panel (d) represent 1,860 days. This female was the most prolific livestock-killer we have recorded and was subsequently shot as a problem animal.

Appendix 5.6. Summary of the univariate scaling analysis. We performed a univariate scaling analysis using conditional logistic regression for each variable to determine the scale that had the strongest relationship with lion path selection in southern Africa. We used model selection to identify the most supported scale for each variable based on Akaike Information Criterion corrected for small sample size (AICc). For each variable we retained only the scale with the lowest AICc score for the multivariate analysis. In all models lion identity was entered as a random factor. Included are the log likelihood (LL), the AICc values, the AICc differences (Δi) and the Akaike weights (wi), in addition to the regression coefficients (β) and their associated standard errors (SE(β)).

Dispersing sub-adult male lions. See pg. 141 for full explanation of table.

Variable	Shift (km)	log likelihood	AICc	Δ*i*	w_i	β	SE(β)
National Park	25	-110.16	224.5	0	1	4.32	0.58
	50	-148.81	301.8	77.31	0	1.88	0.57
	0	-156.09	316.4	91.86	0	4.64	1.52
	12.5	-158.79	321.8	97.27	0	1.47	0.69
Forest reserve	50	-157.98	320.1	0	0.46	1.39	1.13
	25	-158.64	321.5	1.32	0.24	-1.18	1.53
	0	-158.84	321.9	1.73	0.19	-3.60	4.56
	12.5	-159.39	323	2.83	0.11	-0.14	1.59
WMA	25	-159.64	323.5	0	0.35	-1.34	0.88
	0	-159.76	323.7	0.24	0.31	3.10	1.83
	50	-160.01	324.2	0.73	0.24	-1.03	1.03
	12.5	-160.90	326	2.51	0.10	0.84	1.10
Agro-pastoral lands	25	-106.65	217.5	0	1	-12.07	4.35
	50	-133.28	270.7	53.25	0	-5.80	1.52
	0	-149.47	303.1	85.63	0	-11.37	3.64
	12.5	-151.48	307.1	89.65	0	-5.42	1.90
Bushed grassland	25	-159.52	323.2	0	0.45	-1.53	1.86
	12.5	-160.12	324.4	1.18	0.25	1.69	2.07
	0	-160.43	325	1.82	0.18	0.88	3.47
	50	-160.93	326	2.8	0.11	-0.15	1.64
Shrubland	0	-159.11	322.4	0	0.48	-6.54	5.79
	12.5	-159.70	323.6	1.19	0.27	-3.39	4.25
	50	-160.26	324.7	2.3	0.15	-2.04	3.57
	25	-160.66	325.5	3.11	0.10	-2.62	3.16
Woodland	25	-159.43	323	0	0.47	1.72	1.50
	0	-159.71	323.6	0.56	0.35	3.43	2.03
	12.5	-161.05	326.3	3.23	0.09	0.75	1.44
	50	-161.10	326.4	3.34	0.09	0.43	1.29
% tree cover	0	-135.16	274.5	0	1	-0.64	0.32
	12.5	-148.68	301.5	27.04	0	-0.29	0.14
	50	-155.05	314.3	39.79	0	-0.04	0.06
	25	-160.16	324.5	50.01	0	-0.16	0.08
Human density	25	-111.57	227.3	0	1	-0.88	0.32
	50	-138.62	281.4	54.1	0	-0.42	0.13
	12.5	-153.91	312	84.68	0	-0.40	0.17
	0	-156.31	316.8	89.48	0	-0.53	0.25
Towns	50	-155.83	315.8	0	0.67	-39.03	18.47
	25	-156.72	317.6	1.77	0.28	-38.08	17.92
	12.5	-158.95	322.1	6.23	0.03	-72.22	39.33
	0	-159.24	322.7	6.81	0.02	-106.84	69.76
Highways	25	-153.51	311.2	0	0.91	-27.73	14.03
	0	-156.08	316.3	5.15	0.07	8.17	14.51
	50	-157.47	319.1	7.92	0.02	-16.79	9.98
	12.5	-159.46	323.1	11.9	0.00	7.17	4.43

Adult male lions. See pg. 141 for full explanation of table.

Variable	**Shift (km)**	**log likelihood**	**AICc**	**Δ*i***	**w_i**	**β**	**SE(β)**
National Park	25	-466.41	936.9	0	1	4.98	0.68
	50	-686.69	1377.4	440.57	0	3.49	0.86
	0	-803.93	1611.9	675.04	0	10.53	2.85
	12.5	-807.69	1619.4	682.56	0	3.15	0.95
Forest reserve	25	-781.67	1567.4	0	1	-4.78	1.58
	0	-806.98	1618	50.63	0	-12.63	3.83
	12.5	-809.49	1623	55.65	0	-3.95	1.52
	50	-811.97	1628	60.62	0	-2.20	1.30
WMA	25	-804.35	1612.7	0	1	-5.96	2.36
	50	-815.00	1634	21.29	0	-3.57	1.51
	12.5	-849.87	1703.8	91.03	0	-0.13	1.01
	0	-852.61	1709.3	96.52	0	1.93	1.07
Agro-pastoral lands	25	-487.06	978.2	0	1	-37.18	7.99
	50	-665.73	1335.5	357.34	0	-31.26	8.03
	12.5	-798.34	1600.7	622.56	0	-19.35	4.29
	0	-803.66	1611.4	633.19	0	-31.13	8.78
Bushed grassland	0	-735.22	1474.5	0	1	10.06	3.77
	50	-782.29	1568.6	94.14	0	2.79	2.38
	25	-787.86	1579.7	105.28	0	0.47	2.08
	12.5	-790.77	1585.6	111.1	0	5.09	2.19
Shrubland	0	-829.29	1662.6	0	1	-0.24	5.85
	12.5	-840.66	1685.4	22.73	0	-2.06	3.09
	50	-848.60	1701.2	38.61	0	0.43	1.79
	25	-850.18	1704.4	41.78	0	-1.37	1.39
Woodland	50	-779.62	1563.3	0	1.00	-2.87	2.06
	0	-785.56	1575.2	11.88	0.00	-9.93	2.49
	25	-792.59	1589.2	25.93	0	-0.43	1.81
	12.5	-811.17	1626.4	63.1	0	-4.19	1.62
% tree cover	0	-524.07	1052.2	0	1	-1.55	0.24
	12.5	-602.34	1208.7	156.55	0	-0.64	0.13
	50	-685.49	1375	322.84	0	-0.27	0.12
	25	-794.30	1592.6	540.48	0	-0.04	0.07
Human density	25	-509.49	1023	0	1	-3.81	1.02
	50	-682.55	1369.1	346.13	0	-3.00	0.87
	12.5	-818.39	1640.8	617.79	0	-2.31	0.76
	0	-824.17	1652.4	629.35	0	-2.26	0.77
Towns	25	-835.61	1675.2	0	0.78	-29.66	15.65
	50	-836.84	1677.7	2.47	0.23	-31.51	9.24
	0	-844.69	1693.4	18.17	0	-129.84	204.76
	12.5	-853.43	1710.9	35.64	0	-37.50	27.25
Highways	25	-743.27	1490.6	0	1	-61.59	13.11
	50	-789.23	1582.5	91.92	0	-60.75	18.62
	0	-848.56	1701.2	210.59	0	-16.54	5.44
	12.5	-850.51	1705	214.48	0	-7.82	3.60

Adult female lions. See pg. 141 for full explanation of table.

Variable	**Shift (km)**	**log likelihood**	**AICc**	**Δ*i***	**w*i***	**β**	**SE(β)**
National Park	25	-620.38	1244.8	0	1	6.23	1.17
	50	-854.50	1713	468.24	0	7.32	2.12
	12.5	-1042.31	2088.7	843.87	0	6.69	2.33
	0	-1071.50	2147	902.25	0	12.48	3.76
Forest reserve	25	-992.17	1988.4	0	1	-11.76	4.02
	50	-1042.57	2089.2	100.8	0	-5.67	2.20
	12.5	-1062.01	2128	139.67	0	-6.95	2.94
	0	-1107.75	2219.5	231.16	0	-6.53	2.64
WMA	25	-1007.02	2018.1	0	1	-10.60	2.96
	50	-1019.46	2042.9	24.88	0	-9.29	2.73
	12.5	-1108.53	2221.1	203.02	0	-7.07	3.19
	0	-1116.64	2237.3	219.23	0	0.70	1.74
Agro-pastoral lands	25	-624.75	1253.5	0	1	-76.81	21.64
	50	-857.77	1719.6	466.04	0	-51.61	14.60
	12.5	-1024.45	2052.9	799.4	0	-38.74	11.42
	0	-1046.91	2097.8	844.32	0	-55.58	13.54
Bushed grassland	50	-1005.91	2015.8	0	1.00	0.33	1.94
	25	-1011.78	2027.6	11.75	0.00	-0.67	1.99
	0	-1053.93	2111.9	96.03	0	4.61	2.54
	12.5	-1070.94	2145.9	130.05	0	1.04	1.85
Shrubland	12.5	-1064.83	2133.7	0	1	0.80	3.82
	50	-1078.48	2161	27.29	0	-2.63	2.55
	25	-1088.88	2181.8	48.1	0	-2.97	2.27
	0	-1104.74	2213.5	79.81	0	4.50	3.82
Woodland	50	-982.69	1969.4	0	1	-0.64	1.97
	25	-994.16	1992.4	22.96	0	0.32	2.00
	0	-1066.78	2137.6	168.19	0	-5.81	2.08
	12.5	-1080.01	2164	194.65	0	-1.66	1.52
% tree cover	50	-881.57	1767.2	0	1	-0.24	0.10
	0	-954.97	1914	146.81	0	-0.81	0.11
	12.5	-980.21	1964.4	197.28	0	-0.41	0.08
	25	-995.31	1994.6	227.49	0	-0.07	0.07
Human density	25	-636.20	1276.4	0	1	-5.44	1.49
	50	-871.83	1747.7	471.27	0	-3.86	1.13
	12.5	-1045.10	2094.2	817.8	0	-2.97	0.96
	0	-1071.66	2147.3	870.92	0	-4.20	1.51
Towns	50	-1094.05	2192.1	0	0.99	-39.53	10.69
	25	-1098.38	2200.8	8.65	0.01	-57.76	33.36
	0	-1103.82	2211.7	19.54	0	-434.53	476.50
	12.5	-1115.10	2234.2	42.09	0	-56.49	36.11
Highways	25	-999.48	2003	0	1	-73.22	16.80
	50	-1044.14	2092.3	89.31	0	-57.76	16.90
	12.5	-1113.83	2231.7	228.69	0	-12.56	7.33
	0	-1116.37	2236.8	233.78	0	-16.65	10.42

Appendix 5.7. Summary of model selection statistics for path selection of lions in southern Africa as a function of landscape features. We created candidate models for each group of variables (land use, N=15; vegetation, N=15 and anthropogenic, N=7). Models were ranked using AICc and relative support for each model was assessed using Akaike weights (denoted w_i). When one model was superior (w_i>0.9) this was used, otherwise we averaged parameter estimates across the models correcting for model weights. We compared used lion paths (1) with nine matched available paths (0) using mixed effects conditional logistic regression. Models were ranked according to Akaike weights (w_i) based on the Akaike Information Criterion for small sample size (AICc). In all models the identity of individual lions was entered as a random factor. When one model was clearly superior (w_i>0.9) this was used, otherwise model averaging was performed. Included are the log likelihood and the AICc differences (Δi). The tables below specify the lion demographic category at the top, and the subsequent tables are in the order, Land use, habitat type, anthropogenic variables. Land use types used in the models were forest reserves (FR), national parks (NP), wildlife management areas (WMA) and rural lands (RL). Vegetation types used in the models were grassland (grass), savannah (sav), woodland (wood) and percentage tree cover (treeP). Anthropogenic variables used in the models were large towns (towns), major highways (hway) and human density (human). Descriptions of these variables can be found in the *Methods* section of the main text.

Dispersing sub-adult male lions as a function of land use, habitat type and anthropogenic variables. See pg. 145 for full explanation of table

Rank	**Model**	**log likelihood**	**AICc**	**Δ*i***	**w$_i$**	**d.f.**
1	FR + NP + RL	-93.581	200.5	0	0.795	6
2	FR + NP + WMA + RL	-93.374	205.1	4.61	0.079	8
3	NP + RL	-98.461	205.5	5.04	0.064	4
4	FR + WMA + RL	-96.807	206.9	6.45	0.032	6
5	WMA + RL	-99.904	208.4	7.93	0.015	4
6	NP + WMA + RL	-97.7	208.7	8.24	0.013	6
7	FR + NP	-102.903	214.4	13.92	0.001	4
8	FR + NP + WMA	-100.631	214.6	14.1	0.001	6
9	RL	-106.652	217.5	16.99	0	2
10	FR + RL	-104.769	218.2	17.66	0	4
11	NP	-110.158	224.5	24	0	2
12	NP + WMA	-108.313	225.2	24.75	0	4
13	FR	-157.978	320.1	119.64	0	2
14	FR + WMA	-156.215	321	120.55	0	4
15	WMA	-159.641	323.5	122.96	0	2

Rank	**Model**	**log likelihood**	**AICc**	**Δ*i***	**w$_i$**	**d.f.**
1	treeP	-135.16	274.5	0	0.453	2
2	treeP + wood	-133.639	275.9	1.39	0.226	4
3	sav + treeP	-134.291	277.2	2.7	0.118	4
4	grass + treeP	-134.614	277.8	3.34	0.085	4
5	sav + wood + treeP	-132.516	278.4	3.87	0.066	6
6	grass + wood + treeP	-133.458	280.3	5.75	0.026	6
7	grass + sav + treeP	-133.698	280.7	6.23	0.02	6
8	grass + sav + wood + treeP	-132.251	282.9	8.36	0.007	8
9	sav	-159.108	322.4	47.9	0	2
10	wood	-159.433	323	48.55	0	2
11	grass	-159.523	323.2	48.73	0	2
12	sav + wood	-157.469	323.6	49.05	0	4
13	grass _ sav	-157.732	324.1	49.58	0	4
14	grass + wood	-158.63	325.9	51.38	0	4
15	grass + sav + wood	-156.837	327	52.51	0	6

Rank	**Model**	**log likelihood**	**AICc**	**Δ*i***	**w$_i$**	**d.f.**
1	towns + hway + human	-104.107	221.5	0	0.686	6
2	towns + human	-107.58	223.8	2.23	0.225	4
3	hway + human	-109.059	226.7	5.19	0.051	4
4	human	-111.572	227.3	5.78	0.038	2
5	towns _ hway	-146.87	302.4	80.81	0	4
6	hway	-153.507	311.2	89.65	0	2
7	towns	-155.834	315.8	94.3	0	2

Adult male lions as a function of land use, habitat type and anthropogenic variables. See pg. 145 for full explanation of table

Rank	**Model**	**log likelihood**	**AICc**	**Δ*i***	**w$_i$**	**d.f.**
1	NP + RL	-390.823	789.8	0	0.516	4
2	FR + NP + RL	-389.07	790.4	0.61	0.379	6
3	NP + WMA + RL	-390.557	793.3	3.59	0.086	6
4	FR + WMA + RL	-392.065	796.4	6.61	0.019	6
5	FR + NP + WMA	-395.8	803.8	14.07	0	6
6	FR + RL	-409.128	826.4	36.61	0	4
7	NP + WMA	-436.227	880.6	90.81	0	4
8	FR + NP	-446.731	901.6	111.82	0	4
9	WMA + RL	-453.644	915.4	125.64	0	4
10	NP	-466.411	936.9	147.1	0	2
11	RL	-487.063	978.2	188.4	0	2
12	FR + WMA	-742.183	1492.5	702.72	0	4
13	FR	-781.666	1567.4	777.61	0	2
14	WMA	-804.352	1612.7	822.98	0	2

Rank	**Model**	**log likelihood**	**AICc**	**Δ*i***	**w$_i$**	**d.f.**
1	grass + sav + wood + treeP	-455.169	926.7	0	1	8
2	grass + wood + treeP	-467.616	947.5	20.73	0	6
3	grass + sav + treeP	-479.033	970.3	43.56	0	6
4	sav + wood + treeP	-484.176	980.6	53.85	0	6
5	grass + treeP	-491.679	991.5	64.73	0	4
6	wood + treeP	-493.741	995.6	68.86	0	4
7	sav + treeP	-514.513	1037.1	110.4	0	4
8	treeP	-524.067	1052.2	125.43	0	2
9	grass + sav + wood	-673.033	1358.3	431.56	0	6
10	grass + wood	-682.826	1373.8	447.03	0	4
11	grass + sav	-725.901	1459.9	533.18	0	4
12	grass	-735.217	1474.5	547.73	0	2
13	sav + wood	-758.692	1525.5	598.76	0	4
14	wood	-779.618	1563.3	636.53	0	2
15	sav	-829.292	1662.6	735.88	0	2

Rank	**Model**	**log likelihood**	**AICc**	**Δ*i***	**w$_i$**	**d.f.**
1	towns + hway + human	-456.553	925.3	0	0.922	6
2	hway + human	-461.077	930.3	4.93	0.078	4
3	towns + human	-504.69	1017.5	92.15	0	4
4	human	-509.49	1023	97.68	0	2
5	hway	-743.267	1490.6	565.23	0	2
6	towns + hway	-751.602	1511.3	585.98	0	4
7	towns	-835.607	1675.2	749.91	0	2

Adult female lions as a function of land use, habitat type and anthropogenic variables. See pg. 145 for full explanation of table

Rank	Model	log likelihood	AICc	Δ*i*	w_i	d.f.
1	NP + WMA + RL	-442.553	897.3	0	0.677	6
2	FR + NP + RL	-443.547	899.3	1.99	0.251	6
3	NP + RL	-447.053	902.2	4.91	0.058	4
4	FR + WMA + RL	-446.389	905	7.67	0.015	6
5	FR + NP + WMA	-461.245	934.7	37.38	0	6
6	FR + RL	-501.802	1011.7	114.41	0	4
7	WMA + RL	-533.338	1074.8	177.48	0	4
8	FR + NP	-557.662	1123.4	226.13	0	4
9	NP + WMA	-574.649	1157.4	260.1	0	4
10	NP	-620.378	1244.8	347.5	0	2
11	RL	-624.751	1253.5	356.25	0	2
12	FR + WMA	-882.606	1773.3	876.01	0	4
13	FR	-992.172	1988.4	1091.09	0	2
14	WMA	-1007.02	2018.1	1120.79	0	2

Rank	Model	log likelihood	AICc	Δ*i*	w_i	d.f.
1	grass + sav + wood + treeP	-754.246	1524.8	0	0.873	8
2	sav + wood + treeP	-758.237	1528.7	3.86	0.127	6
3	grass + wood + treeP	-784.952	1582.1	57.29	0	6
4	grass + sav + treeP	-787.207	1586.6	61.8	0	6
5	wood + treeP	-794.152	1596.4	71.59	0	4
6	grass + treeP	-820.791	1649.7	124.87	0	4
7	sav + treeP	-843.845	1695.8	170.98	0	4
8	TreeP	-881.567	1767.2	242.37	0	2
9	grass + sav + wood	-925.833	1863.8	339.05	0	6
10	sav + wood	-933.412	1874.9	350.11	0	4
11	grass + sav	-960.465	1929	404.22	0	4
12	grass + wood	-968.455	1945	420.2	0	4
13	wood	-982.687	1969.4	444.61	0	2
14	grass	-1005.91	2015.8	491.05	0	2
15	sav	-1064.83	2133.7	608.9	0	2

Rank	Model	log likelihood	AICc	Δ*i*	w_i	d.f.
1	towns + hway + human	-554.874	1121.9	0	1	6
2	hway + human	-580.356	1168.8	46.87	0	4
3	towns + human	-610.643	1229.4	107.45	0	4
4	human	-636.197	1276.4	154.49	0	2
5	towns + hway	-970.152	1948.4	826.46	0	4
6	hway	-999.484	2003	881.07	0	2
7	towns	-1094.05	2192.1	1070.2	0	2

Appendix 5.8. Model averaged parameter estimates of conditional logistic regression models investigating demographic-specific lion movement path selection in relation to different land use types in Southern Africa

Demographic	**Variable**	**Coefficient**	**S.E.**	***Z*-value**
dispersing males	national park	2.762	0.738	3.746
	rural lands	-7.111	3.114	2.284
	forest reserve	3.181	1.305	2.437
	WMA	-1.258	1.386	0.907
adult males	national park	3.090	0.935	3.305
	rural lands	-15.095	3.626	4.163
	forest reserve	-1.265	1.035	1.222
	WMA	0.614	0.727	0.844
adult females	national park	5.873	2.587	2.271
	rural lands	-48.185	20.166	2.389
	forest reserve	0.337	1.079	0.313
	WMA	-2.063	1.482	1.392

Appendix 5.9. Model averaged parameter estimates of conditional logistic regression models investigating the effect of different habitat types on demographic-specific lion movement path selection

Demographic	**Variable**	**Coefficient**	**S.E.**	***Z*-value**
dispersing males	grassland	-1.512	1.473	1.026
	savannah	-4.646	6.883	0.675
	woodland	2.167	1.238	1.751
	% tree cover	-0.639	0.321	1.991
§adult males	grassland	8.094	3.394	2.380
	savannah	15.159	4.396	3.450
	woodland	-1.085	1.873	-0.580
	% tree cover	-1.485	0.252	-5.900
adult females	grassland	0.130	1.637	0.079
	savannah	4.311	3.462	1.245
	woodland	-0.256	2.326	0.110
	% tree cover	-0.226	0.100	2.259

§ For adult males, the all-inclusive model was clearly superior ($w_i > 0.9$; Appendix 5.7) and therefore estimates presented here were obtained from that model alone.

Appendix 5.10. Model averaged parameter estimates of conditional logistic regression models investigating demographic-specific lion movement path selection depending on anthropogenic variables

Demographic	**Variable**	**Coefficient**	**S.E.**	***Z*-value**
dispersing males	towns	-42.614	20.506	2.078
	major highways	-20.129	13.313	1.512
	human density	-0.791	0.310	2.553
[§]adult males	towns	-28.003	22.095	-1.27
	major highways	-90.803	32.477	-2.8
	human density	-1.491	0.356	-4.19
[§]adult females	towns	-72.527	21.608	-3.36
	major highways	-213.405	99.019	-2.16
	human density	-3.508	1.039	-3.38

[§] For adult males and females, the all-inclusive model was clearly superior ($w_i > 0.9$; Appendix 5.7) and therefore estimates presented here were obtained from that model alone.

Appendix 5.11. FRAGSTATS metrics calculating the extent and fragmentation of the predicted corridor network for dispersing male, adult male and adult female lions. The landscape metrics include: PLAND – proportion of the study area occupied by predicted corridors; NIP – the number of isolated patches in the corridor network; Correlation length – correlation length of the corridor network; Mean shape index – area weighted mean shape index calculating the shape complexity of the corridor network.

	¥PLAND	#NIP	ΔCorrelation length	§Mean shape index
Dispersers	14.6	3	216856	4.54
Females	11.9	7	179012	3.21
Males	10.6	7	182740	3.37

Interpretations:

¥ The extent of the landscape occupied by the corridor network was 22.6% higher for dispersers than females and 37.7% higher for dispersers than males

The total fragmentation of the network, as judged by number of isolated patches in the network, was 233% higher for males and females than for dispersers

Δ The correlation length of the corridor network, which measures total network extent (McGarigal 2002), was 21.1% higher for dispersers than females, and 18.7% higher for dispersers than males

§ The shape complexity of dispersing corridor networks was 41.3% higher than for females and 34.7% higher than for males

Chapter 6

General discussion

Key findings

Chapter 2: '*In the name of the father: dispersal mortality reveals a delayed infanticide in African lions*'

- There was a wide distribution of dispersal ages (mean = 31.5 months, range = 18-45 months)
- Male lions that disperse before 31 months of age have a high probability of mortality during transience
- Sub-adults dispersed soon after immigrant adult males replaced the natal pride males
- Dispersal occurred primarily in the wet season, but was more likely to be in the dry season when incoming males were not a factor

Synthesis: In ecosystems characterised by high off-take of territorial males, this may induce a previously undescribed, 'delayed infanticide', as sub-adults are forced to disperse regardless of age or condition

Chapter 3: '*Differences in rest site selection by dispersers and adults: The case of the African lion*'

- Adult males rest in areas of high visibility, close to roads, close to water and in bushed grassland habitats
- Dispersing males selected rest sites at random in terms of visibility and proximity to roads and water, but did select sites in bushed grassland
- Rest sites of dispersers were further from territorial males than expected by chance

Synthesis: Dispersing males appear to be aware of the risks associated with territorial males and thus spatially avoid them

Chapter 4: '*Movements vary according to dispersal status, group size and rainfall: the case of the African lion*'

- Transient lions had higher net displacement and moved further and faster per night than during either pre- or post-dispersal
- Transient lions were more likely to engage in directional rather than random or periodic movement compared to pre- or post-dispersal
- Transient lions were more likely to engage in directional rather than random or periodic movement compared to territorial males or females
- Transient males moved faster and further in smaller groups than those in bigger groups while adult males had the opposite trend

Synthesis: Movement behaviour reflects a transition from directional movement during transience to random or periodic use of a fixed territory after settlement. In addition group size appears to affect the search and settlement strategies of dispersers

Chapter 5: '*The devil is in the dispersers: predictions of landscape connectivity change with demography*'

- Transient males showed the weakest avoidance of agro-pastoral lands, followed by adult males (twice that of dispersers), then adult females (seven times that of dispersers)
- Highways and humans were least avoided by transient males, with adult males displaying intermediate avoidance and adult females the strongest avoidance
- Adult males and females selected bushed grassland and savannah habitats, avoiding woodland, while transient males habitat use was the direct opposite

Synthesis: Resistance surfaces, and therefore predicted corridors, are dramatically different depending on which demographic category is used to parameterise the models

Changes throughout ontogeny

Dispersal is best conceptualised and most efficiently studied as a process involving three distinct stages: departure, transience and settlement (Ims and Yoccoz 1997, Clobert *et al.* 2001, Bonte *et al.* 2012). However, this is frequently ignored in empirical studies and a fine-scale investigation into the whole process has probably never been carried out on any one species (Bowler and Benton 2005). Lions are one of the most studied carnivores, and are thus an ideal species to accumulate information on and build up an understanding of a single species throughout its ontogeny. The vast literature on lions generally focuses on adulthood, particularly territorial adults, with little known on lion dispersal. I differentiate between settlement and adulthood since settlement is the process of selecting a settlement site, rather than long term residence within it. Figure 6.1 incorporates the findings from this study into a schematic of the dispersal process in male lions and the feedback loop between dispersal stages and territorial adults. Below I discuss the findings of my study in the context of previous lion and dispersal literature. The study of dispersal in lions is advantageous in that the rich array of literature during adulthood allows for a comprehensive overview of the shifting processes throughout life history.

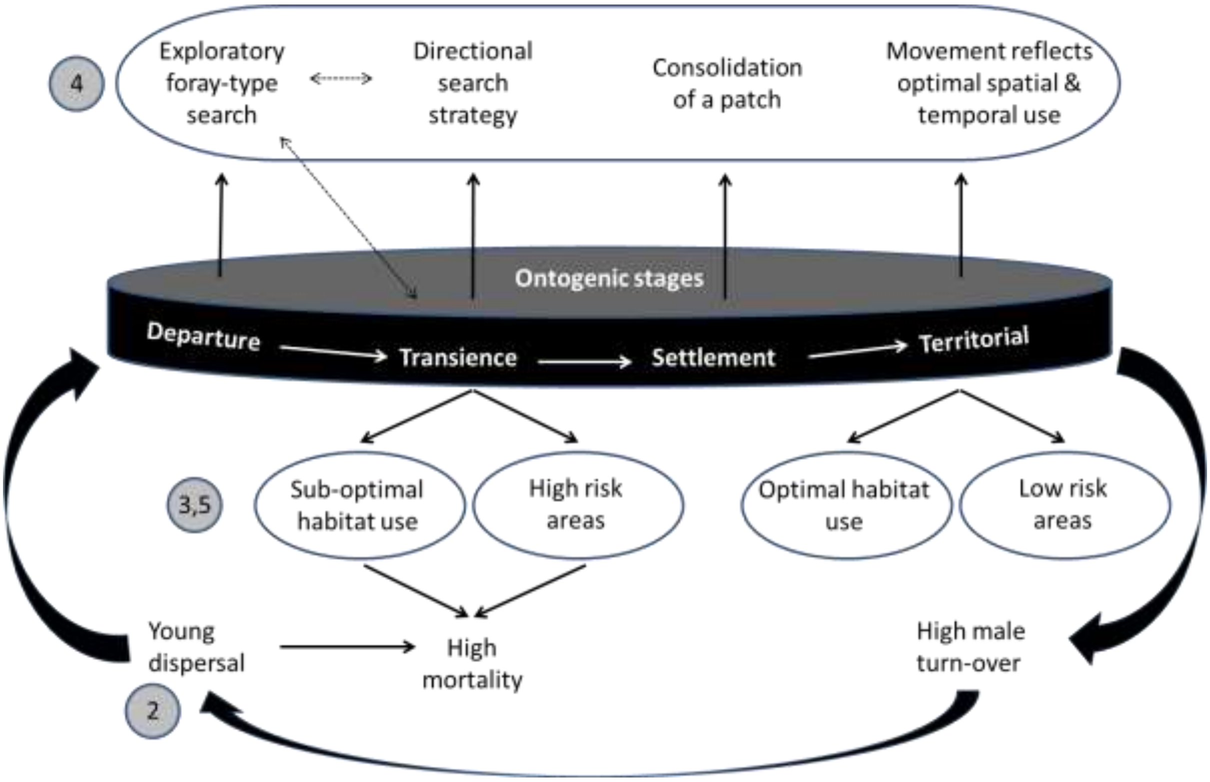


Figure 6.1: A schematic framework of the dispersal process in lions incorporating the findings from this thesis. The numbers in the grey circles refer to the chapter number and broadly indicate for each dispersal stage (4) the movement and search strategies, (3, 5) space and habitat use and (2) the feedback between territorial male turn-over, leading to young dispersal and subsequent high mortality during transience. The dotted arrows indicate how information gained in one dispersal stage can flow to another stage.

Departure

Of the three dispersal phases, the departure stage has received the most attention in lions (Hanby and Bygott 1987, Pusey and Packer 1987, Packer and Pusey 1993, VanderWaal *et al.* 2009). This research largely focused on the evolution of dispersal and examined the reasons and costs of philopatry versus dispersal in female lions. I therefore did not aim to replicate these studies by exploring the decision to disperse, but rather to add to them with a more fine-scale approach. As such, I have contributed to our knowledge on the departure stage in two ways: Firstly, Chapter 2 examines the determinants of the age at which lions disperse, with the expectation that variation in dispersal age could result costs during transience. Secondly, the movement data presented and analysed in Chapter 4 provides a unique insight into pre-dispersal movements and how they shift as transience ensues.

In Chapter 2, I hypothesised that the age at which lions disperse would impact upon their survival since age is directly linked to body mass in lions (Smuts *et al.* 1980) and smaller lions would be at a competitive disadvantage. It was noted in the General Introduction (pages 10-11) that there are conflicting reports pertaining to body mass and its influence on dispersal timing in a variety of taxa (e.g. Holekamp 1984, Stamps 2006). On the one hand the silver spoon hypothesis suggests that individuals in good condition have a competitive advantage and may force subordinates to disperse first (Stamps 2006). For instance, dispersing red-cockaded woodpeckers (*Picoides borealis*) were lighter than their philopatric siblings indicating that social dominance may trigger dispersal (Pasinelli and Walters 2002). On the other hand dispersal may be initiated only once a critical mass has been obtained, as reported for European roe deer (*Capreolus capreolus*), which appear to have a threshold of 14kg, under which no dispersal occurs (Debeffe *et al.* 2012). Therefore increased body size may hasten or delay dispersal.

In many taxa, dispersal occurs at a specific age and may be related to behavioural independence, seasonal constraints, hormones or condition (Nunes and Holekamp 1996, Nunes *et al.* 1998, Matthysen 2012). Thus an optimal dispersal time may reflect dispersal ability and fitness benefits may be enhanced if an individual disperses when it is most suited to doing so (Bowler and Benton 2005). In lions, body mass has a strong linear relationship with age up until 36 months of age (Smuts *et al.* 1980). For instance, a sub-adult male of 30 months is likely to weigh around 140kg whereas one that is 20 months may weigh as little as 80kg (Smuts *et al.* 1980). Therefore, if dispersal were condition-dependent it would be expected to occur after 36 months of age since this is the time that body mass starts to approach that of adult males. In addition, as Hanby and Bygott (1987) noted, if dispersal were to have a developmental trigger, or be age-dependent, dispersal would be expected between 25-36 months of age, around the onset of sexual maturity. However the wide distribution of dispersal ages found in both the Serengeti study (20-65 months; Hanby and Bygott 1987)) and the present one (18-45 months), confound the hypotheses that dispersal in lions is either condition-dependent or age-dependent.

An alternative, but often co-occurring process is density-dependent dispersal, which can either be positive (when increased competition induces dispersal) or negative (when crowding impedes movement; reviewed in Matthysen 2005). Since lion home range size is strongly correlated to prey biomass (Loveridge *et al.* 2009b) one might expect that dispersal in lions is positively density-dependent as a home range may only support a certain amount of lions. If that were the case, dispersal would be expected to occur once pride biomass reaches a critical point, or the number of sub-adults within the natal pride exceeds a certain limit, or new cubs are born. In the present study I found little evidence that dispersal timing was related to any of these variables, leading to the conclusion that in HNP lion dispersal is not density-dependent. Rather, I found that the arrival of new males into the natal pride was highly related to the timing of dispersal. HNP is an ecosystem characterised by a high turn-over of territorial males as a consequence of trophy hunting and other anthropogenic mortality causes on the periphery of this protected area (Loveridge *et al.* 2007c, Loveridge *et al.* 2010). Due to this high off-take of territorial males and their subsequent replacement by despotic immigrants, dispersal may frequently be occurring before individuals have reached a suitable condition for successful dispersal. This in turn, results in the high mortality of sub-adult males that dispersed prior to the age of 31 months. I contend then, that optimal dispersal age in lions would be at least 30 months and ideally in the dry season in HNP, which was frequently the case in the absence of incoming males. Dispersal during the dry season would be advantageous in HNP since prey are concentrated in high densities around scarce waterholes and are frequently weakened and many expire in times of drought (Loveridge *et al.* 2006, Valeix *et al.* 2012b).

However, I do not discount the possibility that density-dependent dispersal in lions may occur in populations where the turn-over of territorial males is less severe than it is in HNP. Indeed, while the present study did not find strong evidence of density-dependent dispersal, two previous studies have shown it may be important: Hanby and Bygott (1987) found that larger groups of sub-adults dispersed later than smaller groups and suggested that larger groups may be better able to resist eviction from pride females. A second study reported that female dispersal was more likely once pride size had exceeded the habitat-specific optimum (VanderWaal *et al.* 2009). Thus dispersal in lions may be density-dependent, particularly in ecosystems such as the Serengeti with a relatively low anthropogenically caused male mortality, and induced by competition (specifically incoming males). Finally, both these processes may drive dispersal in tandem, in other words dispersal may be multi-causal (Matthysen 2012).

Movement and search strategies

In Chapter 4, I quantified the movement of sub-adult males in a six month window prior to dispersal. This time frame was selected due to observations of both collared and uncollared sub-adults conducting exploratory trips, sometimes for several weeks, before re-joining the natal pride prior to eventual departure. Interestingly, these trips often involved sub-adult females even when they eventually remained philopatric and on occasion began up to nine months prior to final departure. For example, the ‘Balla Balla’ pride originally consisted of two adult females, four sub-adult females and two sub-adult males. The two sub-adult males eventually dispersed in April 2011, while the females remained in the natal area, but all six sub-adults conducted exploratory trips outside the home range as early as August 2010. In those nine months before dispersal the sub-adults made 11 exploratory trips away from their mother, mostly within the natal range, and never moving more than 20km away from it. Finally, on 08 April 2011 the two males and one of their sisters left the natal area and travelled approximately 55km away in three days. They then returned to the natal area, where the female remained, the two males leaving immediately thereafter, never to return.

A similar pattern of exploratory trips was observed in all sub-adult groups prior to dispersal. This type of movement is comparable to foray search where an individual searches its surroundings in loops, returning to a favourable habitat (Conradt *et al.* 2003). Indeed during departure I found that sub-adult males predominately displayed what I defined as ‘periodic’ movement indicating that they were returning to one or several loci. Similar pre-dispersal exploratory behaviour has previously been reported in other mammal species such as juvenile flying squirrels (*Pteromys volans*), and in North American red squirrels (*Tamiasciurus hudsonicus*; Selonen and Hanski 2006). Exploratory behaviour may lower the costs associated with the transience phase since information gathered through exploration can help locate or reject suitable settlement sites while spending the majority of time in the natal home range (Stamps and Krishnan 1999, Clobert *et al.* 2009). Consequently it has been found that exploration of juvenile North American red squirrels is a strong correlate of subsequent settlement sites (Haughland and Larsen 2004).

The movement parameters of sub-adult male lions in the departure stage were in between that of adult males and adult females. For instance, the mean nightly net displacement for sub-adults, adult females and adult males was 3.2km, 2.8km and 5.2km respectively (Chapter 4). Since sub-adults in the departure stage are still spending the majority of time with their mothers, their movement more closely resembles that of adult females, but with slightly higher net displacement, speed and path length, indicative of the exploratory trips. However, I did not have sufficient data during exploratory trips to properly quantify and describe the movement parameters and search strategies utilised. Additional data collected during departure, with a focus on exploratory trips, would help to fill this gap and shed light on how they affect search strategies during transience and site selection during settlement.

Sex-biased dispersal

The primary focus of this thesis was on dispersal in sub-adult males as opposed to females. Since I aimed to assess the ecology of all three dispersal stages in lions primarily through the use of GPS radio collars, the acquisition and deployment of which is expensive and labour intensive, I chose to concentrate on sub-adult males since they were guaranteed to disperse should they survive to do so. This approach was based on the following previous studies, which indicated that female dispersal was less common or predictable.

Early studies of lions suggested that sub-adult males will always leave their pride while sub-adult females may disperse or remain philopatric (Schaller 1972, Bertram 1975). Over a decade later two studies investigated the ultimate causes and evolution of dispersal in lions, examining the factors leading to philopatry or dispersal (Hanby and Bygott 1987, Pusey and Packer 1987). Both studies confirmed the assumptions of Schaller (1972) and Bertram (1975) and concluded that lions display sex-biased dispersal as all males disperse while most females (two-thirds) are philopatric. Following on from this research, VanderWaal *et al.* (2009) studied female dispersal decisions and dispersal costs. While all five of the above studies were conducted in the Serengeti National Park and the Ngorongoro Crater, Spong and Creel (2001) reached similar conclusions relating to female dispersal in the Selous Game Reserve, reporting that around 80% of females are philopatric. As a result of these studies, the dispersal of lions is frequently described as sex-biased (e.g. Funston *et al.* 2003, Dubach *et al.* 2005).

Due to these studies I decided that sub-adult males should be the focus group. However, during the course of data collection, I obtained data on female sub-adults where possible, which revealed some surprising trends. In total 53 sub-adult females were recorded to either disperse or remain and breed within their natal pride. While my study of lion dispersal in HNP confirms the assertion that all males disperse, a far greater proportion of females dispersed (62%, N=33) in HNP as opposed to approximately 30% and 20% in the Serengeti and Selous respectively (Pusey and Packer 1987, Spong and Creel 2001). Since I did not collect behavioural data on these prides it is difficult to draw conclusions as to the factors relating to reduced philopatry of female lions in HNP. However, the high turn-over of adult males in this study area (Loveridge *et al.* 2007c, Loveridge *et al.* 2010) could have contributed since incoming males evict all female sub-adults too young to breed (Chapter 2, Hanby and Bygott 1987). It is possible then, that pride structure and the dispersal patterns of females may by affected in populations that experience a high turn-over of males. Increased rates of female dispersal could lead to increased costs which may have important social and reproductive implications for lion populations. These costs are likely to be deferred until the settlement stage (Pusey and Packer 1987) and are discussed in full below under the heading ‘Settlement, pg. 168’. It is important therefore to study these dispersal costs and decisions and future work should focus on understanding the mechanisms of female dispersal and philopatry in populations experiencing high levels of anthropogenic perturbation.

Transience

The transience phase has traditionally been the most difficult to study due to the challenges associated with tracking organisms as they move, often over large distances and through inhospitable environments (reviewed in Nathan *et al.* 2003, Jacobson and Peres-Neto 2010). As a result there is a paucity of data during this stage for many taxa, which has led most population models to assume that individuals move at random in heterogeneous environments (for a review see Patterson *et al.* 2008). The present study was able to quantify and describe the movement and search strategies of lions, the costs that are paid in transience but inherited from departure, and the habitat use and site selection of lions in the transience phase.

Male lions that dispersed while young had a high probability of mortality during dispersal (Chapter 2). While I maintain that the primary factor responsible for this mortality is due to young dispersal, triggered by despotic immigrant males and exacerbated by high anthropogenic disturbance in the study area, it is useful to discuss the processes contributing to the observed mortalities.

As noted above, lion body mass has a strong linear relationship with age (Smuts *et al.* 1980). The youngest male to disperse in this study was 20 months and, weighing approximately 80kg, it can be reasonably assumed would be at a competitive disadvantage when challenging for a territory with adult males that have a mean mass (± SD) of 199 ± 10kg in this study area (Loveridge *et al.* 2009b). This may increase the amount of time spent, and therefore the costs, of living as a vulnerable transient, since a young disperser may need a couple of years before being large enough to challenge for territory. The data on sub-adult males that survived dispersal (N=17) show a tendency of support for this hypothesis as males which dispersed when older were often transient for less months compared to those which dispersed younger (Table 6.1). Another contributing factor to the time length of the transience phase is group size. While we found no evidence that larger groups of sub-adults either accelerated or delayed dispersal, it is possible that larger groups were able to attain residence sooner than smaller groups. Of the sub-adult males that survived to establish a territory those in groups of one and two individuals were transient on average for 16 months while those in groups of three and four individuals were transient on average 10 months (Table 6.1). The movement data presented in Chapter 4 indicate support for this hypothesis: bigger groups of dispersers were shown to move slower and less far than smaller groups. I suggest then that larger groups constitute the ‘bold’ individuals described by Baguette and Van Dyck (2007) as larger groups may have less to fear from detection by resident adults and may challenge for territory sooner than smaller groups. More data on dispersal distances and time-length is needed to confirm whether group size and age of dispersal may influence the length of the transience phase and thereby constitute both time and energetic costs (Bonte *et al.* 2012).

Table 6.1. Composition and dispersal characteristics for the 17 sub-adult males that dispersed and survived to establish a territory in Hwange National Park, Zimbabwe.

Dispersal group size	Dispersal age	Age at establishment	Months nomadic
4	32	51	19
3	35	44	9
3	36	37	0.4
1	31	57	26
1	38	68	30
2	42	48	6
1	40	55	15
2	42	47	5

Another factor that may contribute to mortality during transience in general and in lions in particular, is risk taking. The transience phase is inherently risky and has many associated costs (reviewed in Bonte *et al.* 2012). Numerous studies on dispersal in various taxa have reported increased mortality costs during dispersal, and note that they are frequently anthropogenic: vehicle collisions (Massemin *et al.* 1998, Klar *et al.* 2009); collision with wind turbines (Smallwood *et al.* 2009); collision with power lines (Real and

Mañosa 2001); human persecution (Stander 1990, Kenward *et al.* 1999, Real and Mañosa 2001).

Lions in the transient stage moved slower than their territorial counterparts, but displayed high levels of directional movement (Chapter 4). Both these strategies may reduce the risks associated with dispersal: An individual moving at slower speeds can perform more effective anti-predator behaviour (Zollner and Lima 2005) and by adopting directional movement an individual reduces the number of steps it will take to reach a suitable patch and thereby reduces the mortality risk associated with transience (Zollner and Lima 1999). At the same time, directional movement may reflect a risky environment: Barton *et al.* (2009) suggested that in an inherently risky matrix, where suitable settlement patches are sparse or occupied, a strategy of directional movement may evolve as unsuitable patches are quickly rejected and individuals identify a destination moving directly towards it. On the other hand, when suitable patches are clumped, search strategies with a lower degree of correlation may evolve (Heinz and Strand 2006). It is possible, that in an ecosystem such as HNP, where hard edges border the protected area, that directional movement, or ‘sequential search strategies’ (Stamps *et al.* 2005) are more likely to bring lions into contact with agro-pastoralist land (Chapter 5). As Macdonald and Johnson (2001) noted, long journeys in modern fragmented landscapes are very likely to involve encounters with human development. A possible scenario emerges where transient lions traverse the protected area in a directional manner, rejecting or being expelled from occupied patches, before reaching agro-pastoral land, which is unoccupied by territorial lions and has plentiful prey in the form of livestock. They thus escape the known threat of territorial males, only to be confronted with the hitherto unknown risk posed by people. Indeed of the fourteen transient lions whose cause of death was determined, thirteen were anthropogenically induced (Chapter 2).

Although transient lions seem relatively less averse of risky anthropogenic habitats (Chapter 5), they do appear to be aware of, and react to, the risks associated with territorial males (Chapters 5). The habitats used during dispersal are the exact opposite of territorial male habitat use. Dispersers select for woodlands and avoid the two habitat types selected for by territorial males and females: bushed grassland and shrubland. Previous research in this ecosystem demonstrated that prey abundance was higher in bushed grassland than any other habitat but that lions were more likely to kill in thickets (Davidson *et al.* 2012). In contrast woodland areas had considerably lower prey biomass. Transient lions then face a trade-off between prey-rich habitats that have a high probably of encountering territorial lions, or utilising prey-poor habitats with a low encounter probability, and select for the latter (Chapter 5). This supports the assertion by Selonen and Hanski (2006) that adult habitat use is not a good predictor of dispersal habitat use and accords with findings of suboptimal habitat use by dispersing lynx *Lynx pardinus* and tigers *Panthera tigris* (Smith 1993, Palomares *et al.* 2000). Further evidence of the reaction of transient males to territorial males was found when investigating the rest sites of each demographic (Chapter 3). While territorial males selected sites of high visibility, close to prey-rich waterholes and near to roads, transient males appeared to have no selection for these areas. Instead, I found that the most important determinant of rest site selection in transient males was the proximity of territorial males. Therefore, in their bid to remain far from territorial males, transient males may forego optimal habitats. Thus the findings from Chapters 3 and 5 therefore add support to the scenario proposed above since transient males appear to be averse of territorial males but perhaps naïve to anthropogenic risks.

Settlement

During the settlement phase sub-adult males moved slower and less far per night than they did during transience. In addition, while directional movement was prominent in the transience phase, this was replaced by periodic and random movements (Chapter 4). It appears then that during the first six months of settlement, sub-adult males consolidate a territory, perhaps around a focal point such as a waterhole. Their movements now more closely resemble that of territorial males, but are more conservative. This is in line with field observations: For instance, a coalition of two males entered a recently vacated territory at the end of July 2011 and remained within the vicinity of two waterholes for the next couple of months while the older of the two males began mating with the resident females. They later began to explore more widely. Interestingly the norm during this study appeared to be the filling of vacant territories rather than pride take-overs. In seven instances I was able to confirm whether settlement of males occurred in a vacant territory or an occupied one. On six occasions the settlement site was unoccupied by resident males and in the seventh it was occupied by the sub-adults father who permitted them to join him in the new territory. In the case of female sub-adults three groups settled in a portion of their natal territory but did not associate with their natal pride or fathers, and two groups settled in adjacent territories. The observed settlement in unoccupied territories is a product of the high turn-over of males in this study area (Loveridge *et al.* 2007c, Loveridge *et al.* 2010).

The present study did not attempt to quantify the costs during settlement. However, a study by Pusey and Packer (1987) reported that philopatric females in the Serengeti gave birth to surviving cubs earlier than those that dispersed (opportunity costs), and that philopatric females in the Ngorongoro Crater were more likely to survive beyond eight years than those that dispersed (risk and opportunity costs). In addition, the authors reported that larger coalitions of transient males became resident younger and spent fewer transient months (time costs) than those in smaller coalitions (Pusey and Packer 1987, Bonte *et al.* 2012). As noted above, my data tends to support this last finding (Table 6.1) but more data is needed to confirm this.

If we take the results of Hanby and Bygott (1987) in conjunction with those of Pusey and Packer (1987) and the present study, a scenario emerges whereby larger groups of sub-adult males are more able to resist eviction, thereby delaying dispersal. When they do finally disperse, their age, body size and group size combine to reduce the transience period and enable rapid settlement. However, if an unfamiliar male enters the pride, dispersal occurs despite group size or age. In their eagerness to avoid territorial males, transient lions frequently leave the protected area and turn to stock-raiding (Elliot pers obs, Stander 1990, Patterson *et al.* 2003, Patterson *et al.* 2004). This in turn translates to increased mortality costs during transience. Where settlement is achieved, it is frequently in patches unoccupied by territorial males (in this study area at least) but where female adults are in residence and the immigrant males evict all sub-adults, repeating the cycle.

Territorial males and females

While this study focused on dispersal, I frequently compared sub-adult males to adult males and females in order to determine their differences. Thus, although the literature is replete with studies of adult lions, I was able to provide new insights into their behaviour and strategies. For instance, Chapter 4 details the movement patterns of adult male and female lions and how this varies according to group size and rainfall. Their movements are predominately periodic as they rotate between waterholes, which are known focal points for lion hunting behaviour (Valeix *et al.* 2010, Davidson *et al.* 2013). Resident lions have a more complete spatial and temporal knowledge of their surroundings compared to transients and so their movements reflect their ability to maximise their space use and respond to temporal shifts in prey as a result of rainfall. My results on habitat use in Chapters 3 and 5 confirm the findings of previous studies regarding habitat selection by adult lions (Hopcraft *et al.* 2005, Valeix *et al.* 2010, Davidson *et al.* 2013). For instance, in Chapter 5, I demonstrated territorial male and female preference for bushed grassland and shrubland, a finding which also reflects the night time rest sites of territorial males (Chapter 3). Rest sites of territorial males were also typically close to waterholes, which are rich in prey, and roads which provide direct routes between waterholes. It is likely that these sites, with high visibility, are used as vantage points to detect prey which are then killed in thicker habitats (Davidson *et al.* 2012, Loarie *et al.* 2013). A major contribution to the literature on territorial lions is the strength of their avoidance of anthropogenic landscapes (Chapter 5). Adult females were particularly averse to agro-pastoral lands while adult males were less so. This finding, along with others presented in this thesis, has important applications not only for the management of lions, but also other felids and carnivores in general, as well providing new insights into the dispersal process that are applicable to a wide range of organisms.

Applied conservation

The number of free ranging African lions is declining. It is likely that in the last thirty years the total population has halved and a maximum of 35,000 lions remain (Ferreras and Cousins 1996, Riggio *et al.* 2013). As with most carnivores, the responsibility for their decline rests almost solely with humans. Preventative and retaliatory killings of lions in response to attacks on livestock and people (Packer *et al.* 2005b, Woodroffe and Frank 2005), the loss and fragmentation of their habitat and subsequent depletion of prey (Cole Burton *et al.* 2011, Bauer *et al.* 2012, Riggio *et al.* 2013) and unsustainable trophy hunting (Whitman *et al.* 2004, Loveridge *et al.* 2007c) are widely acknowledged as being the primary reasons for the decline of the lion. As a result there has been a proliferation of lion-related research pertaining to anthropogenic perturbations and specifically regarding human-lion conflict (for examples see Woodroffe and Ginsberg 1998, O'Connell-Rodwell *et al.* 2000, Packer *et al.* 2005b, Romañach *et al.* 2007, Kissui 2008, Gusset *et al.* 2009, Hazzah *et al.* 2009, Hemson *et al.* 2009, Maclennan *et al.* 2009, Packer *et al.* 2009, Bauer *et al.* 2010, Loveridge *et al.* 2010, Mogensen *et al.* 2011, Funston *et al.* 2013, Hazzah *et al.* 2013, Lindsey *et al.* 2013, Riggio *et al.* 2013, Tumenta *et al.* 2013, Winterbach *et al.* 2013). It is somewhat surprising then, that despite the urgency and subsequent interest, the research listed above focuses on human-lion conflict from the perspective of humans. Perhaps this is because humans are perceived to be easier to understand and manage. However, in order to fully understand human-lion conflict, indeed human-carnivore conflict, and effectively mitigate against it, there is a need to understand under what circumstances lions turn to conflict and which lions are most prone to doing so. This will allow for more effective wildlife management. To this end, a few studies have provided vital clues (Kerbis Peterhans and Gnoske 2001, Patterson *et al.* 2004, Valeix *et al.* 2012a, Schuette *et al.* 2013, Trinkel 2013). For instance, Kerbis Peterhans and Gnoske (2001) reported that adult males were more likely to attack livestock than adult females, while Patterson *et al.* (2003) reported that in Tsavo, Kenya, most ‘problem lions’ were young males that were dispersing and, too young to challenge for territory, turned to livestock killing. In Namibia a similar pattern emerged, as sub-adult males were the most prominent livestock raiders, followed by adult males and then adult females (Stander 1990). In Hluhluwe-Umfolozi, South Africa, twice as many males as females were destroyed outside the protected area (Anderson 1981). Valeix *et al.* (2012a) demonstrated that adult lions in the Makgadikgadi, Botswana, may have some perception of the risk posed by humans since they not only avoided temporal overlap but travelled at high speed when in close proximity to settlements. These studies and many of the results presented in this thesis, provide vital information for conservation managers.

In Chapter 5, I demonstrate that dispersing males are the least risk averse demographic in terms of avoiding anthropogenic landscapes. Territorial males had intermediate avoidance while territorial females had the strongest avoidance. I have heretofore discussed the underlying mechanisms surrounding transience and conflict with humans. In the case of HNP, and indeed many African ecosystems, a hard edge occurs with protected land on one side and agro-pastoral land on the other. Where stock-raiding is committed by adult lions they are typically territorial lions living on the edge of the protected area. Woodroffe and Ginsberg (1998) proposed that species which range widely are most exposed to threats on the boundaries of protected areas and that carnivores with larger home ranges are more prone to conflict with people. Dispersing lions range the most widely and male lions typically have larger territories than females (Loveridge *et al.* 2009b, Davidson *et al.* 2011).

Wildlife managers generally have three choices when faced with livestock raiding lions: (1) employ community-based initiatives such as increased protection of livestock or fortification of bomas; (2) destroy the ‘problem’ lions; (3) capture and relocate them. Considering territorial females are severely risk averse, if they are the offending animal, perhaps increasing protection surrounding livestock and people would be effective. If it is territorial males, the situation may be more complex. Destroying them or relocating them will have the same effect on the pride: their removal will create a vacuum (Loveridge *et al.* 2010), filled by incoming males, and resulting in social disruption and infanticide (Bertram 1975, Packer and Pusey 1984). It will also result in the eviction of sub-adults, which are likely to cause the conflict that managers were trying to prevent, and if still young, will likely suffer high mortality (Chapter 2). Therefore, neither relocation nor the managed killing of these animals is desirable. Perhaps then, it is better to mitigate this conflict through community-based initiatives, which have been shown to be effective (e.g. Hazzah *et al.* 2009, Schuette *et al.* 2013). When the offending lion is a transient male, management decisions should be context-specific. For instance, if population connectivity is a key objective, tolerance for wildlife will need to be enhanced, the depletion of wild prey halted and measures put in place to facilitate desirable dispersal. Another management tool that has recently been promoted and received much attention, is fencing.

Packer *et al.* (2013) reported that lions in fenced reserves are closer to their carrying capacities and cost less to manage than populations in unfenced reserves. The authors argue that their "analysis suggests that human-wildlife co-existence should only be considered in areas where large-scale megafaunal (and pastoralist) migration precludes any form of fencing" (Packer *et al.* 2013). By extension, this statement is effectively arguing the case for the fencing of almost all protected areas in Africa, except those such as the Serengeti ecosystem where large-scale wildebeest (*Connochaetes taurinus*) migration occurs (Boone *et al.* 2006). However, fencing protected areas in an effort to mitigate human-lion conflict will interrupt natural patterns of dispersal and gene flow, not only of lions, but all large mammals. According to a population genetics model, a minimum of 50-100 prides are needed to maintain long term genetic diversity (Bjorklund 2003). It is important to note that 50-100 prides translates to a conservative estimate of 150-300 adult female lions (saying nothing of adult males and cubs) if you consider an average pride size of three. Take for example the study extent presented in Chapter 5. Despite containing ≈446,000 km^2 of land managed for wildlife, this area is characterised by small protected areas that hold under 50 lions (including all demographic groups, Figure 6.2). The detrimental effects of inbreeding in lions was best illustrated in the Ngorongoro Crater where a population bottleneck resulted in increased sperm abnormality and decreased reproductive performance (Packer *et al.* 1991).

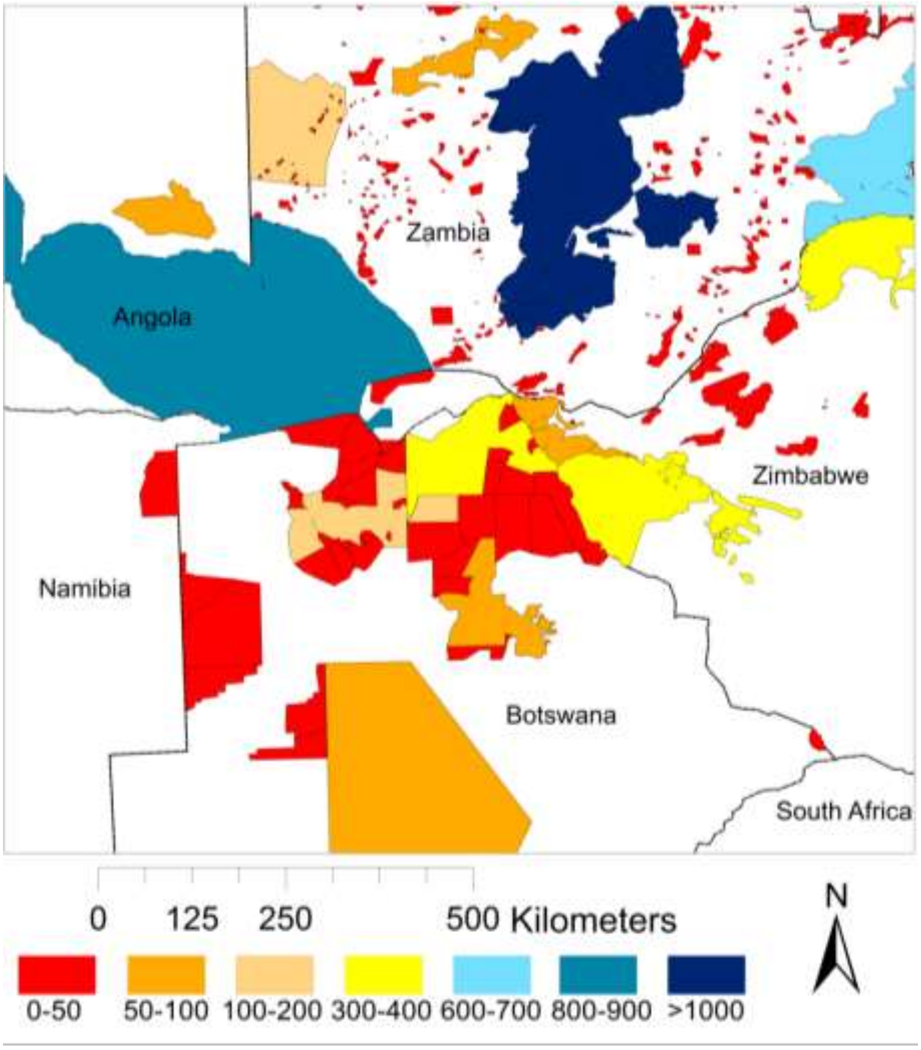


Figure 6.2: Map of the same study extent depicted in Chapter 5. Here I detail the number of African lions predicted per protected area based on the predictions of a GIS meta-analysis modelling the distribution of lions (Loveridge *et al.* 2007a).

Thus, complete fencing of all protected areas would effectively isolate lion populations and result in a loss of genetic diversity. In addition, the management of fenced populations would require extensive genetic management and relocation of animals which would not only be expensive, but also further disrupt lion society. Finally, past efforts at fencing have shown that the wire is often used for snare poaching (e.g. Becker *et al.* 2013) and may be ineffective: in Hluhluwe-Umfolozi, South Africa, despite a 2m high fence that was buried 0.5m underground, and a further measure of shooting at any lion that came within 400m of the fence, the number of cattle killed by lions continued to rise (Anderson

1981). An alternative method to complete fencing is partial fencing or the use of ‘funnel fences’ (Hargrove *et al.* 2005).

Using the resistance surfaces produced in Chapter 5, future work could assess the factorial least cost paths across the landscape and how these may be altered by for example funnelling fences (Figure 6.3a). One could imagine a range of scenarios that could be tested and other questions that could be asked of this model, such as: What would happen if all forest reserves and wildlife management areas were to disappear? Would connectivity be increased by the protection of certain land in order to create wildlife corridors (Figure 6.3b)? What would happen if all national parks were effectively fenced? What impact would a doubling of the human population have on connectivity? Once the factorial least cost paths have been created and a range of scenarios tested, future work could run a population genetics model such as CDPOP (Landguth and Cushman 2010) in order to assess how genetic diversity would be affected by the potential scenarios proposed above. The results of these simulations would allow for landscape planners to make effective management decisions that reflect the habitat use of the biologically relevant demographic: dispersing lions.

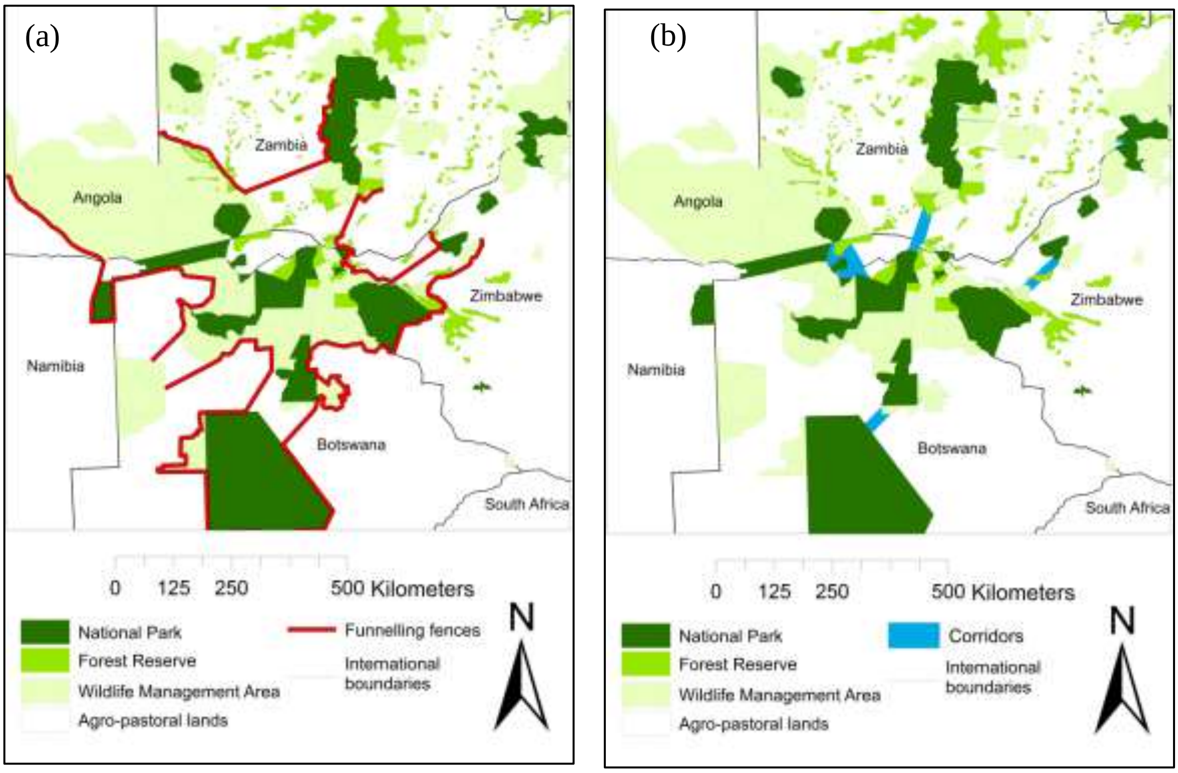


Figure 6.3: Proposed future work building on the resistance surfaces derived from dispersal data and presented in Chapter 5. A range of scenarios could be tested to determine changes in connectivity and gene flow in a landscape where (a) funnelling fences are used to direct dispersers to certain areas and while deterring them from others and (b) the protection of land to for corridors connecting current protected areas.

In recent years there has been a surge of interest in identifying corridors and maintaining connectivity between populations (for reviews see Sawyer *et al.* 2011, Zeller *et al.* 2012, Cushman *et al.* 2013). Indeed, particularly in North America, corridors have become a cornerstone of modern conservation (Noss 2003, Chetkiewicz *et al.* 2006). In Africa too, connecting landscapes has become a major drive and transboundary conservation has elevated corridors beyond being an ecological tool and into the realm of politics. Take for example, the Kavango Zambezi (KAZA) Transfrontier Conservation Area (TFCA), of which Hwange National Park is a part. The TFCA covers approximately 520,000 km^2 and in 2006 a memorandum of understanding was signed by the governments of Angola, Botswana, Namibia, Zambia and Zimbabwe, making this the largest conservation area in Africa and the world's largest TFCA. The initiation of transfrontier conservation areas in Africa is largely facilitated by Peace Parks Foundation (PPF 2013c). One of the major goals in the creation of these TFCAs is "to promote and facilitate the development of a complementary network of protected areas within the KAZA TFCA through corridors" (PPF 2013b). The formation of this TFCA and the funding that is going into it ensure that the pursuit of connectivity in this area is no longer merely an academic pursuit but one which will have consequences for wildlife and people. Indeed their efforts have received considerable funding: on the 8th of March 2013 PPF reported (PPF 2013a) that they had received €15.5 million from the German Federal Ministry for Economic Cooperation and Development (BMZ). In June 2010 BMZ announced that KfW Development bank would provide €20 million towards the development of KAZA stating that the money would be invested in, among others, wildlife corridors (PPF 2013b). With this in mind, it is critical that any management policies should be based on accurate and reliable data. In so doing, money and effort can be used to effectively protect existing dispersal routes and facilitate the creation of new wildlife corridors that are directly applicable to the species of most concern. When they are based on limited biological data, the use of corridors can be costly and counterproductive (Chetkiewicz *et al.* 2006). The results presented in Chapter 5 illustrate how different conclusions may be drawn based on the data used. However, in the same chapter I discuss how naively promoting connectivity may lead to increased levels of human-lion conflict. This will result in the loss of livestock to agro-pastoralist communities, retaliatory killings of lions, infanticide committed by incoming males and induced dispersal, resulting in more conflict and increased mortality of dispersing lions. Therefore, any attempts at promoting connectivity should have a strong community-based initiative to promote tolerance of wildlife and facilitate their coexistence.

In summary, I suggest that the results of this thesis, and particularly Chapter 2, point towards the stability of lion society as being critical, not just for persistence of lion populations, but also for the reduction of human-lion conflict. Traditional methods of conflict mitigation such as relocation and destroying of problem animals may serve only to exacerbate the problems they were designed to prevent. In addition, excessive trophy hunting quotas may lead not only to infanticide but also to high levels of mortality among sub-adult males, i.e. a delayed infanticide. A stable lion population, with minimal anthropogenic induced mortality may result in sub-adults dispersing later and being able to challenge for territory sooner, reducing the transience period when lions are most likely to turn to stock-raiding. Dispersers that survive to establishment may enhance connectivity between protected areas, and provided they are based on robust biological data, can be effective. Indeed, recent research has shown that lions can exist at stable densities with minimal human conflict in areas that maintain connectivity for wildlife (Schuette *et al.* 2013). At the beginning of this thesis I stated that dispersal is probably the most important life-history trait involved in species persistence (Clobert *et al.* 2001) and that in the context of increased habitat fragmentation, dispersal is a crucial process as it is the principal mechanism by which organisms move within metapopulations and thereby maintain population viability and genetic diversity (Clobert *et al.* 2012). The findings of this thesis show that in lions, dispersal may be the most critical life-history trait and that the study of this process in lions, and probably other carnivores, may be vital to their conservation.

References

Andersen, N. M. 1993. The evolution of wing polymorphism in water striders (*Gerridae*): a phylogenetic approach. Oikos **67**:433-443.

Andersen, N. M. 2000. The evolution of dispersal dimporphism and other life history traits in water striders (*hemiptera gerridae*). Entomological Science **3**:187-199.

Anderson, J. L. 1981. The re-establishment and management of a lion *Panthera leo* population in Zululand, South Africa. Biological Conservation **19**:107-117.

Aragón, P., S. Meylan, and J. Clobert. 2006. Dispersal status-dependent response to the social environment in the Common Lizard, *Lacerta vivipara*. Functional Ecology **20**:900-907.

Baguette, M., S. Blanchet, D. Legrand, V. M. Stevens, and C. Turlure. 2013. Individual dispersal, landscape connectivity and ecological networks. Biological Reviews **88**:310-326.

Baguette, M. and H. Van Dyck. 2007. Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. Landscape Ecology **22**:1117-1129.

Barbraud, C., A. R. Johnson, and G. Bertault. 2003. Phenotypic correlates of post-fledging dispersal in a population of greater flamingos: the importance of body condition. Journal of Animal Ecology **72**:246-257.

Barros, Á., D. Álvarez, and A. Velando. 2013. Climate influences fledgling sex ratio and sex-specific dispersal in a seabird. PLoS ONE **8**:e71358.

Barton, K. A., B. L. Phillips, J. M. Morales, and J. M. J. Travis. 2009. The evolution of an 'intelligent' dispersal strategy: biased, correlated random walks in patchy landscapes. Oikos **118**:309-319.

Barton, N. H. 2001. The evolutionary consequences of gene flow and local adaptation: future approaches. Pages 329-340 *in* J. Clobert, E. Danchin, A. Dhondt, and J. D. Nichols, editors. Dispersal. Oxford University Press, Oxford.

Bates, D., M. Maechler, and B. M. Bolker. 2012. lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-0. http://CRAN.R-project.org/package=lme4. http://cran.r-project.org/web/packages/lme4/index.html

Bauer, H., H. de Iongh, and E. Sogbohossou. 2010. Assessment and mitigation of human-lion conflict in West and Central Africa. Mammalia **74**:363-367.

Bauer, H., K. Nowell, and C. Packer. 2012. *Panthera leo.* IUCN Red List of Threatened Species. www.iucnredlist.org. 26 July 2013

Becker, M., R. McRobb, F. Watson, E. Droge, B. Kanyembo, J. Murdoch, and C. Kakumbi. 2013. Evaluating wire-snare poaching trends and the impacts of by-catch on elephants and large carnivores. Biological Conservation **158**:26-36.

Begon, M., C. R. Townsend, and J. L. Harper. 2006. Dispersal, dormancy and metapopulations. Pages 163-185 Ecology: from individuals to ecosystems Blackwell Publishing Ltd. .

Beier, P. 1995. Dispersal of juvenile cougars in fragmented habitat. Journal of Wildlife Management **59**:228-237.

Beier, P. and R. F. Noss. 1998. Do habitat corridors provide connectivity? Conservation Biology **12**:1241-1252.

Bélichon, S., J. Clobert, and M. Massot. 1996. Are there differences in fitness components between philopatric and dispersing individuals? Acta Oecologica **17**:503-517.

Benard, M. F. and S. J. McCauley. 2008. Integrating across life-history stages: consequences of natal habitat effects on dispersal. American Naturalist **171**:553-567.

Berg, M. P., E. T. Kiers, G. Driessen, M. Van Der Heijden, B. W. Kooi, F. Kuenen, M. Liefting, H. A. Verhoef, and J. Ellers. 2010. Adapt or disperse: understanding species persistence in a changing world. Global Change Biology **16**:587-598.

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

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

Bollinger, E. K., S. J. Harper, and G. W. Barrett. 1993. Inbreeding avoidance increases dispersal movements of the meadow vole. Ecology **74**:1153-1156.

Bonte, D. and E. de la Pena. 2009. Evolution of body condition-dependent dispersal in metapopulations. Journal of Evolutionary Biology **22**:1242-1251.

Bonte, D., H. Van Dyck, J. M. Bullock, A. Coulon, M. Delgado, M. Gibbs, V. Lehouck, E. Matthysen, K. Mustin, M. Saastamoinen, N. Schtickzelle, V. M. Stevens, S. Vandewoestijne, M. Baguette, K. Barton, T. G. Benton, A. Chaput-Bardy, J. Clobert, C. Dytham, T. Hovestadt, C. M. Meier, S. C. F. Palmer, C. Turlure, and J. M. J. Travis. 2012. Costs of dispersal. Biological Reviews **87**:290-312.

Boone, R. B., S. J. Thirgood, and J. G. C. Hopcraft. 2006. Serengeti wildebeest migratory patterns modeled from rainfall and new vegetation growth. Ecology **87**:1987-1994.

Bowler, D. E. and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological Reviews **80**:205-225.

Boydston, E. E., K. M. Kapheim, M. Szykman, and K. E. Holekamp. 2003. Individual variation in space use by female spotted hyenas. Journal of Mammalogy **84**:1006-1018.

Broekhuis, F., G. Cozzi, M. Valeix, J. W. McNutt, and D. W. Macdonald. 2013. Risk avoidance in sympatric large carnivores: reactive or predictive? Journal of Animal Ecology **82**:1098-1105.

Bullock, J. M., R. Kenward, and R. Hails. 2002. Dispersal ecology : the 42nd Symposium of the British Ecological Society held at the University of Reading 2-5 April 2001. Blackwell Publishing, Oxford.

Bunnefeld, N., J. D. C. Linnell, J. Odden, M. A. J. Van Duijn, and R. Andersen. 2006. Risk taking by Eurasian lynx (*Lynx lynx*) in a human-dominated landscape: effects of sex and reproductive status. Journal of Zoology **270**:31-39.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer Verlag, New York.

Byers, J. A. 2001. Correlated random walk equations of animal dispersal resolved by simulation Ecology **82**:1680–1690.

Bygott, J. D., B. C. R. Bertram, and J. P. Hanby. 1979. Male lions in large coalitions gain reproductive advantages. Nature **282**:839-841.

Camp, M. J., J. L. Rachlow, B. A. Woods, T. R. Johnson, and L. A. Shipley. 2012. When to run and when to hide: the influence of concealment, visibility, and proximity to refugia on perceptions of risk. Ethology **118**:1010-1017.

Campioni, L., M. D. M. Delgado, and V. Penteriani. 2010. Social status influences microhabitat selection: breeder and floater Eagle Owls *Bubo bubo* use different post sites. Ibis **152**:569-579.

Campioni, L., R. Lourenço, M. Delgado, and V. Penteriani. 2012. Breeders and floaters use different habitat cover: should habitat use be a social status-dependent strategy? Journal of Ornithology **153**:1215-1223.

Castillo-Chavez, C. and A.-A. Yakubu. 2001. Dispersal, disease and life-history evolution. Mathematical Biosciences **173**:35-53.

Chaianunporn, T. and T. Hovestadt. 2012. Evolution of dispersal in metacommunities of interacting species. Journal of Evolutionary Biology **25**:2511-2525.

Chaine, A. S., S. Legendre, and J. Clobert. 2013. The co-evolution of multiply-informed dispersal: information transfer across landscapes from neighbors and immigrants. PeerJ **1**:e44.

Chamaillé-Jammes, S., M. Valeix, M. Bourgarel, F. Murindagomo, and H. Fritz. 2009. Seasonal density estimates of common large herbivores in Hwange National Park, Zimbabwe. African Journal of Ecology **47**:804-808.

Chardonnet, P. 2002. Conservation of the African Lion: Contribution to a status survey. International Foundation for the Conservation of Wildlife, France & Conservation Force, USA.

Charlesworth, D. and B. Charlesworth. 1987. Inbreeding depression and its evolutionary consequences. Annual Review of Ecology and Systematics **18**:237-268

Chetkiewicz, C.-L. B., C. C. St. Clair, and M. S. Boyce. 2006. Corridors for conservation: Integrating pattern and process. Annual Review of Ecology, Evolution, and Systematics **37**:317-342.

CIESIN and CIAT. 2005. Gridded Population of the World, Version 3 (GPWv3): Population Density Grid, Future Estimates.*in* NASA Socioeconomic Data and Applications Center (SEDAC), editor., New York.

Clobert, J., M. Baguette, T. G. Benton, and J. M. Bullock. 2012. Dispersal ecology and evolution. Oxford University Press, Oxford.

Clobert, J., E. Danchin, A. Dhondt, and J. Nichols. 2001. Dispersal. Oxford University Press, Oxford.

Clobert, J., R. A. Ims, and F. Rousset. 2004. Causes, mechanisms and consequences of dispersal. Pages 307-335 *in* H. Ilkka and E. G. Oscar, editors. Ecology, Genetics and Evolution of Metapopulations. Academic Press, Burlington.

Clobert, J., J. F. Le Galliard, J. Cote, S. Meylan, and M. Massot. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecology Letters **12**:197-209.

Clobert, J., M. Massot, J. Lecomte, G. Sorci, M. Fraipont, and R. Barbault. 1994. Determinants of dispersal behavior: the common lizard as a case study.*in* L. J. Vitt and E. R. Pianka, editors. Lizard ecology: historical and experimental perspectives. Princeton University Press, Princeton, New Jersey.

Clutton-Brock, T. 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. Science **296**:69-72.

Clutton-Brock, T. H. 1989. Female transfer and inbreeding avoidance in social mammals. Nature **337**:70-72.

Clutton-Brock, T. H. and G. R. Iason. 1986. Sex ratio variation in mammals. The Quarterly Review of Biology **61**:339-374.

Clutton-Brock, T. H., G. R. Iason, and F. E. Guinness. 1987. Sexual segregation and density-related changes in habitat use in male and female Red deer (*Cerrus elaphus*). Journal of Zoology **211**:275-289.

Colas, B., I. Olivieri, and M. Riba. 1997. *Centaurea corymbosa,* a cliff-dwelling species tottering on the brink of extinction: A demographic and genetic study. Proceedings of the National Academy of Sciences **94**:3471-3476.

Cole Burton, A., E. B. Buedi, C. Balangtaa, D. G. Kpelle, M. K. Sam, and J. S. Brashares. 2011. The decline of lions in Ghana's Mole National Park. African Journal of Ecology **49**:122-126.

Compton, B. W., J. M. Rhymer, and M. McCollough. 2002. Habitat selection by wood turtles (*Clemmys insculpta*): An application of paired logistic regression. Ecology **83**:833-843.

Conradt, L., P. A. Zollner, T. J. Roper, K. Frank, and C. D. Thomas. 2003. Foray search: an effective systematic dispersal strategy in fragmented landscapes. American Naturalist **161**:905-915.

Conradt, L. and T. J. Roper. 2006. Nonrandom movement behavior at habitat boundaries in two butterfly species: implications for dispersal. Ecology **87**:125-132.

Costello, C. M., S. R. Creel, S. T. Kalinowski, N. V. Vu, and H. B. Quigley. 2008. Sex-biased natal dispersal and inbreeding avoidance in American black bears as revealed by spatial genetic analyses. Molecular Ecology **17**:4713-4723.

Coulon, A., N. Morellet, M. Goulard, B. Cargnelutti, J.-M. Angibault, and A. Hewison. 2008. Inferring the effects of landscape structure on roe deer (*Capreolus capreolus*) movements using a step selection function. Landscape Ecology **23**:603-614.

Craiu, R. V., T. Duchesne, and D. Fortin. 2008. Inference methods for the conditional logistic regression model with longitudinal data. Biometrical Journal **50**:97-109.

Creel, S., M. S. Becker, S. M. Durant, J. M'Soka, W. Matandiko, A. J. Dickman, D. Christianson, E. Dröge, T. Mweetwa, N. Pettorelli, E. Rosenblatt, P. Schuette, R. Woodroffe, S. Bashir, R. C. Beudels-Jamar, S. Blake, M. Borner, C. Breitenmoser, F. Broekhuis, G. Cozzi, T. R. B. Davenport, J. Deutsch, L. Dollar, S. Dolrenry, I. Douglas-Hamilton, E. Fitzherbert, C. Foley, L. Hazzah, P. Henschel, R. Hilborn, J. G. C. Hopcraft, D. Ikanda, A. Jacobson, B. Joubert, D. Joubert, M. S. Kelly, L. Lichtenfeld, G. M. Mace, J. Milanzi, N. Mitchell, M. Msuha, R. Muir, J. Nyahongo, S. Pimm, G. Purchase, C. Schenck, C. Sillero-Zubiri, A. R. E. Sinclair, A. N. Songorwa, M. Stanley-Price, C. A. Tehou, C. Trout, J. Wall, G. Wittemyer, and A. Zimmermann. 2013. Conserving large populations of lions – the argument for fences has holes. Ecology Letters **DOI: 10.1111/ele.12145**.

Cremer, S. and J. Heinze. 2003. Stress grows wings: environmental induction of winged dispersal males in *Cardiocondyla* ants. Current Biology **13**:219-223.

Cushman, S. and E. Landguth. 2010. Scale dependent inference in landscape genetics. Landscape Ecology **25**:967-979.

Cushman, S. and J. Lewis. 2010. Movement behavior explains genetic differentiation in American black bears. Landscape Ecology **25**:1613-1625.

Cushman, S. A. 2010. Animal movement data: GPS telemetry, autocorrelation and the need for path-level analysis. Pages 131-149 *in* S. A. Cushman and F. Huettmann, editors. Spatial Complexity, Informatics, and Wildlife Conservation. Springer, New York.

Cushman, S. A., M. Chase, and C. Griffin. 2005. Elephants in space and time. Oikos **109**:331-341.

Cushman, S. A., M. Chase, and C. Griffin. 2010. Mapping landscape resistance to identify corridors and barriers for elephant movement in southern Africa. Pages 349-367 *in* S. A. Cushman and F. Huettmann, editors. Spatial Complexity, Informatics, and Wildlife Conservation. Springer, New York.

Cushman, S. A. and E. L. Landguth. 2012. Multi-taxa population connectivity in the Northern Rocky Mountains. Ecological Modelling **231**:101-112.

Cushman, S. A., B. McRae, F. Adriaensen, P. Beier, M. Shirley, and K. Zeller. 2013. Biological corridors and connectivity. Pages 384-404 *in* D. W. Macdonald and K. J. Willis, editors. Key Topics in Conservation Biology 2. John Wiley & Sons, Oxford.

Davidson, Z. 2009. Lion ecology and socio-spatial impacts of trophy hunting in Zimbabwe. DPhil. University of Oxford, Oxford.

Davidson, Z., M. Valeix, A. J. Loveridge, J. E. Hunt, P. J. Johnson, H. Madzikanda, and D. W. Macdonald. 2012. Environmental determinants of habitat and kill site selection in a large carnivore: scale matters. Journal of Mammalogy **93**:677-685.

Davidson, Z., M. Valeix, A. J. Loveridge, H. Madzikanda, and D. W. Macdonald. 2011. Socio-spatial behaviour of an African lion population following perturbation by sport hunting. Biological Conservation **144**:114-121.

Davidson, Z., M. Valeix, F. Van Kesteren, A. J. Loveridge, J. E. Hunt, F. Murindagomo, and D. W. Macdonald. 2013. Seasonal diet and prey preference of the African Lion in a waterhole-driven semi-arid savanna. PLoS ONE **8**:e55182.

Davis, J. M. and J. A. Stamps. 2004. The effect of natal experience on habitat preferences. Trends in Ecology and Evolution **19**:411-416.

Debeffe, L., N. Morellet, B. Cargnelutti, B. Lourtet, R. Bon, J.-M. Gaillard, and M. A. J. Hewison. 2012. Condition-dependent natal dispersal in a large herbivore: heavier animals show a greater propensity to disperse and travel further. Journal of Animal Ecology **81**:1365-2656.

Delgado, M. M. and V. Penteriani. 2008. Behavioral states help translate dispersal movements into spatial distribution patterns of floaters. American Naturalist **172**:475-485.

Delgado, M. M., V. Penteriani, V. Nams, and L. Campioni. 2009. Changes of movement patterns from early dispersal to settlement. Behavioral Ecology and Sociobiology **64**:35-43.

Delgado, M. M., V. Penteriani, E. Revilla, and V. O. Nams. 2010. The effect of phenotypic traits and external cues on natal dispersal movements. Journal of Animal Ecology **79**:620-632.

Dingle, H. 1996. Migration: the biology of life on the move. Oxford University Press, New York.

Dobson, F. S. and W. T. Jones. 1985. Multiple causes of dispersal. American Naturalist **126**:855-858.

Doerr, V. A. J., T. Barrett, and E. D. Doerr. 2011. Connectivity, dispersal behaviour and conservation under climate change: a response to Hodgson et al. Journal of Applied Ecology **48**:143-147.

Doerr, V. A. J. and E. D. Doerr. 2004. Fractal analysis can explain individual variation in dispersal search paths. Ecology **85**:1428–1438.

Dubach, J., B. D. Patterson, M. B. Briggs, K. Venzke, J. Flamand, P. Stander, L. Scheepers, and R. W. Kays. 2005. Molecular genetic variation across the southern and eastern geographic ranges of the African lion, *Panthera leo*. Conservation Genetics **6**:15–24.

Dufty, A. M. and J. R. Belthoff. 2001. Proximate mechanisms of natal dispersal: the role of body condition and hormones. Pages 217-229 *in* J. Clobert, E. Danchin, A. Dhondt, and J. Nichols, editors. Dispersal. Oxford University Press, Oxford.

Ebenhard, T. 1987. High activity in bank voles in relation to colonization ability. Oikos **49**:297-302.

Ekman, J. 2006. Family living among birds. Journal of Avian Biology **37**:289-298.

Ekman, J., A. Bylin, and H. Tegelstrom. 1999. Increased lifetime reproductive success for Siberian jay (*Perisoreus infaustus*) males with delayed dispersal. Proceedings of the Royal Society B: Biological Sciences **266**:911-915.

Ekman, J. and M. Griesser. 2002. Why offspring delay dispersal: experimental evidence for a role of parental tolerance. Proceedings of the Royal Society B: Biological Sciences **269**:1709-1713.

Ekman, J. B. and C. E. H. Askenmo. 1984. Social rank and habitat use in willow tit groups. Animal Behaviour **32**:508-514.

ESA and UCLouvain. 2010. The GlobCover 2009 Project. http://dup.esrin.esa.it/globcover/.

ESRI. 2010. ArcInfo Workstation.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics **34**:487-515.

Ferrer, M. 1993. Wind-influenced juvenile dispersal of Spanish imperial eagles. Ornis Scandinavica **24**:330-333.

Ferreras, P. and S. Cousins. 1996. The use of a Delphi technique with GIS for estimating the global abundance of top predators: The lion in Africa. Unpublished report, International Eco Technology Research Centre, Cranfield University, UK.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behaviour shapes a trophic cascade in Yellowstone National Park. Ecology **86**:1320-1330.

Frair, J. L., J. Fieberg, M. Hebblewhite, F. Cagnacci, N. J. DeCesare, and L. Pedrotti. 2010. Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. Philosophical Transactions of the Royal Society B: Biological Sciences **365**:2187-2200.

Fraser, D. F., J. F. Gilliam, M. J. Daley, A. N. Le, and G. T. Skalski. 2001. Explaining leptokurtic movement distributions: Intrapopulation variation in boldness and exploration. American Naturalist **158**:124-135.

Funston, P. J. 2011. Population Characteristics of Lions (*Panthera leo*) in the Kgalagadi Transfrontier Park. South African Journal of Wildlife Research **41**:1-10.

Funston, P. J., R. J. Groom, and P. A. Lindsey. 2013. Insights into the management of large carnivores for profitable wildlife-based land uses in African savannas. PLoS ONE **8**:e59044.

Funston, P. J., M. G. L. Mills, and H. C. Biggs. 2001. Factors affecting hunting success of male and female lions in the Kruger National park. Journal of Zoology **253**:419 - 431.

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

Galpern, P. and M. Manseau. 2013. Finding the functional grain: comparing methods for scaling resistance surfaces. Landscape Ecology:1-13.

Gandon, S. and Y. Michalakis. 2001. Multiple causes of the evolution of dispersal. Pages 155-167 *in* C. J., D. E., D. A.A., and N. J.D., editors. Dispersal. Oxford: Oxford University Press, Oxford.

Gautestad, A. O., L. E. Loe, and A. Mysterud. 2013. Inferring spatial memory and spatiotemporal scaling from GPS data: comparing red deer *Cervus elaphus* movements with simulation models. Journal of Animal Ecology **82**:572-586.

Gese, E., M. 1998. Howling by coyotes (*Canis latrans*) : variation among social classes, seasons, and pack sizes. Canadian Journal Of Zoology **76**:1037-1043.

Gese, E. M. and R. L. Ruff. 1997. Scent-marking by coyotes,*Canis latrans*: the influence of social and ecological factors. Animal Behaviour **54**:1155-1166.

Gillis, E. A. and C. J. Krebs. 2000. Survival of dispersing versus philopatric juvenile snowshoe hares: do dispersers die? Oikos **90**:343-346.

Girman, D. J., M. G. L. Mills, E. Geffen, and R. K. Wayne. 1997. A molecular genetic analysis of social structure, dispersal, and interpack relationships of the African wild dog (*Lycaon pictus*). Behavioral Ecology and Sociobiology **40**:187-198.

Google Inc. 2011. Google Earth http://www.google.co.uk/intl/en_uk/earth/index.html

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour **28**:1140-1162.

Grinnell, J. and K. McComb. 1996. Maternal grouping as a defense against infanticide by males: evidence from field playback experiments on African lions. Behavioral Ecology **7**:55-59.

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

Gusset, M., M. J. Swarner, L. Mponwane, K. Keletile, and J. W. McNutt. 2009. Human-wildlife conflict in northern Botswana: livestock predation by Endangered African wild dog *Lycaon pictus* and other carnivores. Oryx **43**:67-72.

Gyllenberg, M., É. Kisdi, and M. Utz. 2008. Evolution of condition-dependent dispersal under kin competition. Journal of Mathematical Biology **57**:285-307.

Gyllenberg, M., K. Parvinen, and U. Dieckmann. 2002. Evolutionary suicide and evolution of dispersal in structured metapopulations. Journal of Mathematical Biology **45**:79-105.

Haddad, N. M., D. R. Bowne, A. Cunningham, B. J. Danielson, D. J. Levey, S. Sargent, and T. Spira. 2003. Corridor use by diverse taxa. Ecology **84**:609-615.

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

Hansen, M., R. DeFries, J. R. Townshend, M. Carroll, C. Dimiceli, and R. Sohlberg. 2005. Percent Tree Cover.*in* University of Maryland, editor., College Park, Maryland.

Hanski, I., A. Peltonen, and L. Kaski. 1991. Natal dispersal and social dominance in the common shrew (*Sorex araneus*). Oikos **62**:48-58.

Hansson, L. 1991. Dispersal and connectivity in metapopulations. Biological Journal of the Linnean Society **42**:89-103.

Hargrove, W. W., F. M. Hoffman, and R. A. Efroymson. 2005. A practical map-analysis tool for detecting potential dispersal corridors. Landscape Ecology **20**:361-373.

Harris, S. and W. J. Trewhella. 1988. An analysis of some of the factors affecting dispersal in an urban fox (*Vulpes vulpes*) population. Journal of Applied Ecology **25**:409-422.

Haughland, D. L. and K. W. Larsen. 2004. Exploration correlates with settlement: red squirrel dispersal in contrasting habitats. Journal of Animal Ecology **73**:1024-1034.

Haynes, G. 1996. Quaternary climates and environmental changes in Hwange National Park, Zimbabwe. University of Zimbabwe Publications, Harare.

Hazzah, L., S. Dolrenry, D. Kaplan, and L. Frank. 2013. The influence of park access during drought on attitudes toward wildlife and lion killing behaviour in Maasailand, Kenya. Environmental Conservation **40**:266-276.

Hazzah, L., M. B. Mulder, and L. Frank. 2009. Lions and Warriors: Social factors underlying declining African lion populations and the effect of incentive-based management in Kenya. Biological Conservation **142**:2428-2437.

Hegel, T. M., S. A. Cushman, J. Evans, and F. Huettmann. 2010. Current state of the art for statistical modeling of species distributions. Pages 273-311 *in* S. A. Cushman and F. Huettmann, editors. Spatial Complexity, Informatics, and Wildlife Conservation. Springer, New York.

Heinz, S. and E. Strand. 2006. Adaptive patch searching strategies in fragmented landscapes. Evolutionary Ecology **20**:113-130.

Hemson, G., P. Johnson, A. South, R. Kenward, R. Ripley, and D. W. Macdonald. 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.

Hemson, G., S. Maclennan, G. Mills, P. Johnson, and D. Macdonald. 2009. Community, lions, livestock and money: A spatial and social analysis of attitudes to wildlife and the conservation value of tourism in a human-carnivore conflict in Botswana. Biological Conservation **142**:2718-2725.

Hickling, R., D. B. Roy, J. K. Hill, and C. D. Thomas. 2005. A northward shift of range margins in British Odonata. Global Change Biology **11**:502-506.

Hill, G. E., R. R. Sargent, and M. B. Sargent. 1998. Recent change in the winter distribution of rufous hummingbirds. Auk **115**:240-245.

Hodgson, J. A., C. D. Thomas, B. A. Wintle, and A. Moilanen. 2009. Climate change, connectivity and conservation decision making: back to basics. Journal of Applied Ecology **46**:964-969.

Holdo, R. 2003. Woody plant damage by African elephants in relation to leaf nutrients in western Zimbabwe. Journal of Tropical Ecology **19**:189 - 196.

Holekamp, K. 1984. Natal dispersal in Belding's ground squirrels (*Spermophilus beldingi*). Behavioral Ecology and Sociobiology **16**:21-30.

Holekamp, K. E. 1986. Proximal causes of natal dispersal in Belding's ground squirrels (*Spermophilus beldingi*). Ecological Monographs **56**:365-391.

Holyoak, M., R. Casagrandi, R. Nathan, E. Revilla, and O. Spiegel. 2008. Trends and missing parts in the study of movement ecology. Proceedings of the National Academy of Sciences **105**:19060-19065.

Hopcraft, J. G. C., A. R. E. Sinclair, and C. Packer. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. Journal of Animal Ecology **74**:559-566.

Horváth, G., B. Bernáth, and G. Molnár. 1998. Dragonflies find crude oil visually more attractive than water: multiple-choice experiments on dragonfly *Polarotaxis*. Naturwissenschaften **85**:292-297.

Imbach, P. A., B. Locatelli, L. G. Molina, P. Ciais, and P. W. Leadley. 2013. Climate change and plant dispersal along corridors in fragmented landscapes of Mesoamerica. Ecology and Evolution **3**:2917–2932.

Immelmann, K. 1975. Ecological significance of imprinting and early learning. Annual Review of Ecology and Systematics **6**:15-37.

Ims, R. A. and D. Hjermann. 2001. Condition-dependent dispersal. Pages 203-216 *in* J. Clobert, E. Danchin, A. Dhondt, and J. Nichols, editors. Dispersal. Oxford University Press, Oxford.

Ims, R. A. and N. G. Yoccoz. 1997. The study of tranfer processes in metapopulations: emigration, dispersal and colonization. Pages 247–265 *in* I. A. Hanski and M. E. Gilpin, editors. Metapopulation dynamics: ecology, genetics and colonization. Academic Press, San Diego.

Innocent, T. M., J. Abe, S. A. West, and S. E. Reece. 2010. Competition between relatives and the evolution of dispersal in a parasitoid wasp. Journal of Evolutionary Biology **23**:1374-1385.

IUCN. 2006. Regional conservation strategy for the lion (*Panthera leo*) in eastern and southern Africa. International Union for the Conservation of Nature, Yaounde.

IUCN and UNEP. 2010. The World Database on Protected Areas (WDPA). www.protectedplanet.net.

Jacobson, B. and P. Peres-Neto. 2010. Quantifying and disentangling dispersal in metacommunities: how close have we come? How far is there to go? Landscape Ecology **25**:495-507.

Janin, A., J.-P. Léna, N. Ray, C. Delacourt, P. Allemand, and P. Joly. 2009. Assessing landscape connectivity with calibrated cost-distance modelling: predicting common toad distribution in a context of spreading agriculture. Journal of Applied Ecology **46**:833-841.

Johnson, C. A., J. M. Fryxell, I. D. Thompson, and J. A. Baker. 2009. Mortality risk increases with natal dispersal distance in American martens. Proceedings of the Royal Society B: Biological Sciences **276**:3361-3367.

Johnson, M. L. and M. S. Gaines. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Annual Review of Ecology and Systematics **21**:449-480.

Kareiva, P. M. and N. Shigesada. 1983. Analysing insect movement as a correlated random walk. Oceologia **56**:234-238.

Kenward, R. E., V. Marcström, and M. Karlbom. 1999. Demographic estimates from radio-tagging: models of age-specific survival and breeding in the goshawk. Journal of Animal Ecology **68**:1020-1033.

Kerbis Peterhans, J. C. and T. P. Gnoske. 2001. The science of 'man-eating' among lions *Panthera leo* with a reconstruction of the natural history of the 'man-eaters of Tsavo'. Journal of East African natural history **90**:1-40.

Kissui, B. M. 2008. Livestock predation by lions, leopards, spotted hyenas, and their vulnerability to retaliatory killing in the Maasai steppe, Tanzania. Animal Conservation **11**:422-432.

Klar, N., M. Herrmann, and S. Kramer-Schadt. 2009. Effects and mitigation of road impacts on individual movement behavior of wildcats. Journal of Wildlife Management **73**:631-638.

Koehler, G. M. and D. J. Pierce. 2003. Black bear home-range sizes in Washington: climatic, vegetative, and social influences. Journal of Mammalogy **84**:81-91.

Koen, E. L., J. Bowman, and A. A. Walpole. 2012. The effect of cost surface parameterization on landscape resistance estimates. Molecular Ecology Resources **12**:686-696.

Kokko, H. and A. López-Sepulcre. 2006. From individual dispersal to species ranges: perspectives for a changing world. Science **313**:789-791.

Kruuk, H. and D. W. Macdonald. 1985. Group territories of carnivores: empires and enclaves. Pages 521 - 536 *in* R. M. Silby, editor. Behavioural ecology: ecological consequences of adaptive behaviour. Blackwell Scientific Press.

Kuijper, B. and R. A. Johnstone. 2012. How dispersal influences parent–offspring conflict over investment. Behavioral Ecology.

Kullman, L. 2001. 20th century climate warming and tree-limit rise in the southern Scandes of Sweden. Ambio **30**:72-80.

Lam, K. Y. and Y. Lou. 2013. Evolution of conditional dispersal: evolutionarily stable strategies in spatial models. Journal of Mathematical Biology **15**:15.

Lambin, X., J. Aars, and S. B. Piertney. 2001. Dispersal, intraspecific competition, kin competition and kin facilitation: a review of the emperical evidence.*in* J. Clobert, E. Danchin, A. Dhondt, and J. Nichols, editors. Dispersal. Oxford University Press, Oxford.

Landguth, E. L. and S. A. Cushman. 2010. cdpop: A spatially explicit cost distance population genetics program. Molecular Ecology Resources **10**:156-161.

Landguth, E. L., B. K. Hand, J. Glassy, S. A. Cushman, and M. A. Sawaya. 2012. UNICOR: a species connectivity and corridor network simulator. Ecography **35**:9-14.

Lawson Handley, L. J. and N. Perrin. 2007. Advances in our understanding of mammalian sex-biased dispersal. Molecular Ecology **16**:1559-1578.

Lebigre, C., R. V. Alatalo, and H. Siitari. 2010. Female-biased dispersal alone can reduce the occurrence of inbreeding in black grouse (*Tetrao tetrix*). Molecular Ecology **19**:1929-1939.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology **74**:1659-1673.

Legendre, P. and M.-J. Fortin. 1989. Spatial pattern and ecological analysis. Vegetatio **80**:107-138.

Léna, J.-P., J. Clobert, M. de Fraipont, J. Lecomte, and G. Guyot. 1998. The relative influence of density and kinship on dispersal in the common lizard. Behavioral Ecology **9**:500-507.

Levin, S. A., H. C. Muller-Landau, R. Nathan, and J. Chave. 2003. The ecology and evolution of seed dispersal: a theoretical perspective. Annual Review of Ecology, Evolution, and Systematics **34**:575-604.

Lewis, M. A., P. K. Maini, and S. V. Petrovskii. 2013. Dispersal, individual movement and spatial ecology: a mathematical perspective. Springer Berlin Heidelberg, Berlin, Heidelberg.

Lima, S. L. and P. A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology & Evolution **11**:131-135.

Lindsey, P. A., C. P. Havemann, R. Lines, L. Palazy, A. E. Price, T. A. Retief, T. Rhebergen, and C. Van der Waal. 2013. Determinants of persistence and tolerance of carnivores on Namibian ranches: implications for conservation on Southern African private lands. PLoS ONE **8**:e52458.

Lloyd, H. G. 1980. The red fox. Batsford, London.

Loarie, S. R., C. J. Tambling, and G. P. Asner. 2013. Lion hunting behaviour and vegetation structure in an African savanna. Animal Behaviour **85**:899-906.

Long, E. S., D. R. Diefenbach, C. S. Rosenberry, and B. D. Wallingford. 2008. Multiple proximate and ultimate causes of natal dispersal in white-tailed deer. Behavioral Ecology **19**:1235-1242.

Loveridge, A. J., S. Canney, G. Hemson, and C. Sillero-Zubiri. 2007a. Modelling the distribution of African lion population using a GIS meta-analysis. Page 68 Felid Biology and Conservation Conference. 17–20 September 2007: Programmes and Abstracts. Wildife Conservation Research Unit, Oxford.

Loveridge, A. J., G. Hemson, Z. Davidson, and D. W. Macdonald. 2010. African lions on the edge: reserve boundaries as ‘attractive sinks’. Pages 283-304 *in* D. W. Macdonald and A. J. Loveridge, editors. The Biology and Conservation of Wild Felids. Oxford University Press, Oxford.

Loveridge, A. J., J. E. Hunt, F. Murindagomo, and D. W. Macdonald. 2006. The influence of drought on predation of elephant calves by lions in an African wooded savannah. Journal of Zoology **270**:253-530.

Loveridge, A. J., C. Packer, and A. Dutton. 2009a. Science and the recreational hunting of lions. Pages 108-124 Recreational Hunting, Conservation and Rural Livelihoods. Wiley-Blackwell.

Loveridge, A. J., J. C. Reynolds, and E. J. Milner-Gulland. 2007b. Does sport hunting benefit conservation? Pages 222 - 238 *in* D. W. Macdonald and K. Service, editors. Key Topics in Conservation Biology. Blackwell Publishing, Oxford.

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

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

Mabry, K. E. and J. A. Stamps. 2008. Dispersing brush mice prefer habitat like home. Proceedings of the Royal Society B: Biological Sciences **275**:543-548.

Macdonald, D. M. and D. D. P. Johnson. 2001. Dispersal in theory and practice: consequences for conservation biology. Pages 358-373 *in* J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. Dispersal. Oxford University Press, Oxford.

Macdonald, D. W., C. Newman, C. D. Buesching, and P. J. Johnson. 2008. Male-biased movement in a high-density population of the Eurasian Badger (*Meles meles*). Journal of Mammalogy **89**:1077-1086.

Macdonald, D. W. and S. Rushton. 2003. Modelling space use and dispersal of mammals in real landscapes: a tool for conservation. Journal of Biogeography, **30**:607–620.

Mackie, I. J. and P. A. Racey. 2007. Habitat use varies with reproductive state in noctule bats (*Nyctalus noctula*): Implications for conservation. Biological Conservation **140**:70-77.

Maclennan, S. D., R. J. Groom, D. W. Macdonald, and L. G. Frank. 2009. Evaluation of a compensation scheme to bring about pastoralist tolerance of lions. Biological Conservation **142**:2419-2427.

Maguire, B., Jr. 1963. The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. Ecological Monographs **33**:161-185.

Manel, S., M. K. Schwartz, G. Luikart, and P. Taberlet. 2003. Landscape genetics: combining landscape ecology and population genetics. Trends in Ecology and Evolution **18**:189-197.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Research **27**:209-220.

Massemin, S., Y. L. Maho, and Y. Handrich. 1998. Seasonal pattern in age, sex and body condition of Barn Owls *Tyto alba* killed on motorways. Ibis **140**:70-75.

Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. Ecography **28**:403-416.

Matthysen, E. 2012. Multicausality of dispersal: a review.*in* J. Clobert, M. Baguette, T. G. Benton, and J. M. Bullock, editors. Dispersal Ecology and Evolution. Oxford University Press, Oxford.

Mazerolle, M. J. 2013. Model selection and multimodel inference based on (Q)AIC(c). The R Project for Statistical Computing. http://cran.r-project.org/web/packages/AICcmodavg/index.html

McCallum, H. and A. Dobson. 2002. Disease, habitat fragmentation and conservation. Proceedings of the Royal Society of London. Series B: Biological Sciences **269**:2041-2049.

McComb, K. E. and C. Packer. 1994. Roaring and numerical assessment in contests between groups of female lions (*Panthera leo*). Animal Behaviour **47**:379 - 387.

McGarigal, K., S. A. Cushman, and E. Ene. 2012. FRAGSTATS v4: Spatial pattern analysis program for categorical and continuous maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: http://www.umass.edu/landeco/research/fragstats/fragstats.html.

McLoughlin, P., R. Case, R. Gau, D. Cluff, R. Mulders, and F. Messier. 2002. Hierarchical habitat selection by barren-ground grizzly bears in the central Canadian Arctic. Oecologia **132**:102-108.

Miller, G. S., R. J. Small, and E. C. Meslow. 1997. Habitat selection by spotted owls during natal dispersal in western Oregon. Journal of Wildlife Management **61**:140-150.

Moerkens, R., H. Leirs, G. Peusens, and B. Gobin. 2010. Dispersal of single- and double-brood populations of the European earwig, *Forficula auricularia*: a mark-recapture experiment. Entomologia Experimentalis et Applicata **137**:19-27.

Mogensen, N. L., J. O. Ogutu, and T. Dabelsteen. 2011. The effects of pastoralism and protection on lion behaviour, demography and space use in the Mara region of Kenya. African Zoology **46**:78-87.

Moore, J. and R. Ali. 1984. Are dispersal and inbreeding avoidance related? Animal Behaviour **32**:94-112.

Morris, D. 2003. Toward an ecological synthesis: a case for habitat selection. Oecologia **136**:1-13.

Mosser, A., J. M. Fryxell, L. Eberly, and C. Packer. 2009. Serengeti real estate: density vs. fitness-based indicators of lion habitat quality. Ecology Letters **12**:1050-1060.

Murren, C. J., R. Julliard, C. D. Schlichting, and J. Clobert. 2001. Dispersal individual phenotype, and phenotypic plasticity. Pages 261-272 *in* J. Clobert, E. Danchin, A. Dhondt, and J. Nichols, editors. Dispersal. Oxford University Press, New York.

Nathan, R. 2006. Long-distance dispersal of plants. Science **313**:786-788.

Nathan, R., G. Perry, J. T. Cronin, A. E. Strand, and M. L. Cain. 2003. Methods for estimating long-distance dispersal. Oikos **103**:261-273.

Norrdahl, K. and E. Korpimäki. 1998. Does mobility or sex of voles affect risk of predation by mammalian predators? Ecology **79**:226-232.

Noss, R. F. 2003. A Checklist for Wildlands Network Designs. Conservation Biology **17**:1270-1275.

Nunes, S., C.-D. T. Ha, P. J. Garrett, E.-M. Mueke, L. Smale, and K. E. Holekamp. 1998. Body fat and time of year interact to mediate dispersal behaviour in ground squirrels. Animal Behaviour **55**:605-614.

Nunes, S. and K. E. Holekamp. 1996. Mass and fat influence the timing of natal dispersal in Belding's ground squirrels. Journal of Mammalogy **77**:807-817.

O'Connell-Rodwell, C. E., T. Rodwell, M. Rice, and L. A. Hart. 2000. Living with the modern conservation paradigm: can agricultural communities co-exist with elephants? A five-year case study in East Caprivi, Namibia. Biological Conservation **93**:381-391.

O'Riain, M. J., J. U. M. Jarvis, and C. G. Faulkes. 1996. A dispersive morph in the naked mole-rat. Nature **380**:619-621.

Oden, N. L. and R. R. Sokal. 1986. Directional autocorrelation: an extension of spatial correlograms to two dimensions. Systematic Zoology **35**:608-617.

Packer, C. 1979. Inter-troop transfer and inbreeding avoidance in *Papio anubis*. Animal Behaviour **27**:1-36.

Packer, C. 2001. Infanticide is no fallacy. American Anthropologist **102**:829 - 857.

Packer, C., L. Herbst, A. E. Pusey, J. D. Bygott, J. P. Hanby, S. J. Cairns, and M. Borgerhoff-Mulder. 1988. Reproductive success in lions. Pages 363 - 383 *in* T. H. Clutton-Brock, editor. Reproductive Success: Studies of individual variation in crossbreeding systems. University of Chicago Press, Chicago.

Packer, C., R. Hilborn, A. Mosser, B. Kissui, M. Boner, G. Hopcraft, J. Wilmshurst, S. Mduma, and A. R. E. Sinclair. 2005a. Ecological change, group territoriality, and population dynamics in Serengeti lions. Science **307**:390 - 393

Packer, C., D. Ikanda, B. Kissui, and H. Kushnir. 2005b. Conservation biology: lion attacks on humans in Tanzania. Nature **436**:927-928.

Packer, C., M. Kosmala, H. S. Cooley, H. Brink, L. Pintea, D. Garshelis, G. Purchase, M. Strauss, A. Swanson, G. Balme, L. Hunter, and K. Nowell. 2009. Sport hunting, predator control and conservation of large carnivores. PLoS ONE **4**:e5941.

Packer, C., A. Loveridge, S. Canney, T. Caro, S. T. Garnett, M. Pfeifer, K. K. Zander, A. Swanson, D. MacNulty, G. Balme, H. Bauer, C. M. Begg, K. S. Begg, S. Bhalla, C. Bissett, T. Bodasing, H. Brink, A. Burger, A. C. Burton, B. Clegg, S. Dell, A. Delsink, T. Dickerson, S. M. Dloniak, D. Druce, L. Frank, P. Funston, N. Gichohi, R. Groom, C. Hanekom, B. Heath, L. Hunter, H. H. DeIongh, C. J. Joubert, S. M. Kasiki, B. Kissui, W. Knocker, B. Leathem, P. A. Lindsey, S. D. Maclennan, J. W. McNutt, S. M. Miller, S. Naylor, P. Nel, C. Ng'weno, K. Nicholls, J. O. Ogutu, E. Okot-Omoya, B. D. Patterson, A. Plumptre, J. Salerno, K. Skinner, R. Slotow, E. A. Sogbohossou, K. J. Stratford, C. Winterbach, H. Winterbach, and S. Polasky. 2013. Conserving large carnivores: dollars and fence. Ecology Letters **16**:635-641.

Packer, C. and A. E. Pusey. 1984. Infanticide in Carnivores. Aldine, New York.

Packer, C. and A. E. Pusey. 1993. Dispersal, kinship and inbreeding in lions. Pages 375 - 391 *in* N. Thornhill, editor. Natural history of inbreeding and outbreeding: Empirical and theoretical perspectives. University of Chicago Press.

Packer, C., A. E. Pusey, H. Rowley, D. A. Gilbert, J. Martenson, and S. J. O'Brien. 1991. Case study of a population bottleneck: lions of the Ngorongoro Crater. Conservation Biology **5**:219-230.

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

Packer, C., K. Whitman, A. Loveridge, J. Jackson, and P. Funston. 2006. Impacts of trophy hunting on lions in East and Southern Africa: Recent offtake and future recommendations. Eastern and Southern Africal Lion Conservation Workshop. WCS and IUCN, Johannesburg, South Africa.

Palomares, F., M. Delibes, P. Ferreras, J. M. Fedriani, J. Calzada, and E. Revilla. 2000. Iberian Lynx in a fragmented landscape: predispersal, dispersal and post-dispersal habitats. Conservation Biology **14**:809-818.

Panthera. 2013. Lion Maps. http://www.panthera.org/landscape-analysis-lab/maps/Lion. 20 July 2013

Pasinelli, G. and J. Walters. 2002. Social and environmental factors affect natal dispersal and philopatry of male red-cockaded woodpeckers. Ecology **83**:2229-2239.

Patterson, B. D., S. Kasiki, M, E. Selempo, and R. W. Kays. 2004. Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighboring Tsavo National Parks, Kenya. Biological Conservation **119**:507-516.

Patterson, B. D., E. J. Neiburger, and S. M. Kasiki. 2003. Tooth breakage and dental disease as causes of carnivore-human conflicts. Journal of Mammalogy **84**:190–196.

Patterson, T. A., L. Thomas, C. Wilcox, O. Ovaskainen, and J. Matthiopoulos. 2008. State-space models of individual animal movement. Trends in Ecology and Evolution **23**:87-94.

Pennycuick, C. J. and J. Rudnai. 1970. A method of identifying individual lions (*Panthera leo*), with an analysis of reliability of identification. Journal of Zoology **160**:497-508.

Penteriani, V., M. Ferrer, and M. M. Delgado. 2011. Floater strategies and dynamics in birds, and their importance in conservation biology: towards an understanding of nonbreeders in avian populations. Animal Conservation **14**:233-241.

Perrin, N. and J. Goudet. 2001. Inbreeding, kinship, and the evolution of natal dispersal.*in* J. Clobert, E. Danchin, A. Dhondt, and J. D. Nichols, editors. Dispersal. Oxford University Press, Oxford.

Pettorelli, N., A. Hilborn, F. Broekhuis, and S. M. Durant. 2009. Exploring habitat use by cheetahs using ecological niche factor analysis. Journal of Zoology **277**:141-148.

Phillips, B. L., G. P. Brown, J. K. Webb, and R. Shine. 2006. Invasion and the evolution of speed in toads. Nature **439**:803-803.

Pinheiro, J. C., D. Bates, S. DebRoy, D. Sarkar, and the R Development Core Team. 2012. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-104. http://cran.r-project.org/web/packages/nlme/index.html

Potts, F. C., H. Goodwin, and M. J. Walpole. 1996. People, wildlife and tourism in and around Hwange National Park, Zimbabwe. John Wiley and Sons.

PPF. 2013a. Another €15.5 million for Kavango Zambezi (KAZA) TFCA. http://www.peaceparks.org/news.php?pid=1264&mid=1302&lid=1008. 26 August 2013

PPF. 2013b. Kavango Zambezi Park Development. http://www.peaceparks.org/story.php?pid=1008&mid=1075. 26 August 2013

PPF. 2013c. Peace Parks Foundation. http://www.peaceparks.org. 20 July 2013

Precht, W. F. and R. B. Aronson. 2004. Climate flickers and range shifts of reef corals. Frontiers in Ecology and the Environment **2**:307-314.

Pusey, A. E. and C. Packer. 1987. The evolution of sex-biased dispersal in lions. Behaviour **101**:75 - 310.

Quantum GIS Development Team. 2012. Quantum GIS Geographic Information System.

R Core Team. 2012. R: A language and environment for statistical computing.

Real, J. and S. Mañosa. 2001. Dispersal of juvenile and immature Bonelli's eagles in Northeastern Spain. Journal of Raptor Research **35**:9-14.

Richard, Y. and D. P. Armstrong. 2010. Cost distance modelling of landscape connectivity and gap-crossing ability using radio-tracking data. Journal of Applied Ecology **47**:603-610.

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

Rodway, M. S., H. M. Regehr, and F. Cooke. 2003. Sex and age differences in distribution, abundance, and habitat preferences of wintering Harlequin ducks: implications for conservation and estimating recruitment rates. Canadian Journal Of Zoology **81**:492-503.

Rogers, C. M. L. 1993. A woody vegetation survey of Hwange National Park. Departmental report.

Romañach, S. S., P. A. Lindsey, and R. Woodroffe. 2007. Determinants of attitudes towards predators in central Kenya and suggestions for increasing tolerance in livestock dominated landscapes. Oryx **41**:185-195.

Ronce, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. Annual Review of Ecology, Evolution, and Systematics **38**:231-253.

Ronce, O., I. Olivieri, J. Clobert, and E. Danchin. 2001. Persepctives on the study of dispersal evolution. Pages 341-358 *in* J. Clobert, E. Danchin, A. Dhondt, and J. Nichols, editors. Dispersal. Oxford University Press, Oxford.

Rudnick, D., S. Ryan, P. Beier, S. Cushman, F. Dieffenbach, C. Epps, L. Gerber, J. Hartter, J. Jenness, J. Kintsch, A. Merenlender, R. Perkl, D. Preziosi, and S. Trombulak. 2012. The role of landscape connectivity in planning and implementing conservation and restoration priorities. Issues in ecology **16**:1-20.

Sahlsten, J., H. Thorngren, and J. Hoglund. 2008. Inference of hazel grouse population structure using multilocus data: a landscape genetic approach. Heredity **101**:475-482.

Sawyer, S. C., C. W. Epps, and J. S. Brashares. 2011. Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes? Journal of Applied Ecology **48**:668-678.

Schaller, G. B. 1972. The Serengeti Lion. University of Chicago Press, Chicago.

Schick, R. S., S. R. Loarie, F. Colchero, B. D. Best, A. Boustany, D. A. Conde, P. N. Halpin, L. N. Joppa, C. M. McClellan, and J. S. Clark. 2008. Understanding movement data and movement processes: current and emerging directions. Ecology Letters **11**:1338-1350.

Schuette, P., S. Creel, and D. Christianson. 2013. Coexistence of African lions, livestock, and people in a landscape with variable human land use and seasonal movements. Biological Conservation **157**:148–154.

Schwartz, M. K., J. P. Copeland, N. J. Anderson, J. R. Squires, R. M. Inman, K. S. McKelvey, K. L. Pilgrim, L. P. Waits, and S. A. Cushman. 2009. Wolverine gene flow across a narrow climatic niche. Ecology **90**:3222-3232.

Selonen, V. and I. K. Hanski. 2006. Habitat exploration and use in dispersing juvenile flying squirrels. Journal of Animal Ecology **75**:1440-1449.

Skinner, J. D. and R. H. N. Smithers. 1990. The Mammals of the Southern African Subregion. 2nd edition. University of Pretoria, 736 pp.

Smale, L., S. Nunes, and K. Holekamp. 1997. Sexually dimorphic dispersal in mammals: patterns, causes, and consequences. Pages 181-250 *in* P. J. B. Slater, J. S. Rosenblatt, C. T. Snowdon, and M. Milinski, editors. Advances in the Study of Behavior. Academic Press.

Smallwood, K. S., L. Rugge, and M. L. Morrison. 2009. Influence of behavior on bird mortality in wind energy developments. Journal of Wildlife Management **73**:1082-1098.

Smith, J. L. D. 1993. The role of dispersal in structuring the Chitwan tiger population. Behaviour **124**:165-195.

Smuts, G. L. 1982. Lion. Macmillan, South Africa Publishers Ltd. (Pty)

Smuts, G. L., G. A. Robinson, and I. J. Whyte. 1980. Comparative growth of wild male and female lions (*Panthera leo*). Journal of Zoology **190**:365-373.

Soulé, M. E. 1991. Theory and strategy.*in* W. E. Hudson, editor. Landscape linkages and biodiversity. Island Press, Washington, D.C.

Soulsbury, C., P. Baker, G. Iossa, and S. Harris. 2008. Fitness costs of dispersal in red foxes (*Vulpes vulpes*). Behavioral Ecology and Sociobiology **62**:1289-1298.

Sparkman, A. M., J. R. Adams, T. D. Steury, L. P. Waits, and D. L. Murray. 2011. Direct fitness benefits of delayed dispersal in the cooperatively breeding red wolf (*Canis rufus*). Behavioral Ecology **22**:199-205.

Spong, G. and S. Creel. 2001. Deriving dispersal distances from genetic data. Proceedings of the Royal Society of London. Series B: Biological Sciences **268**:2571-2574.

Squires, J. R., N. J. DeCesare, L. E. Olson, J. A. Kolbe, M. Hebblewhite, and S. A. Parks. 2013. Combining resource selection and movement behavior to predict corridors for Canada lynx at their southern range periphery. Biological Conservation **157**:187-195.

Stamps, J. A. 1988. Conspecific attraction and aggregation in territorial species. American Naturalist **131**:329-347.

Stamps, J. A. 2001. Habitat selection by dispersers: integrating proximate and ultimate approaches. Pages 230-242 *in* J. Clobert, E. Danchin, A. Dhondt, and J. Nichols, editors. Dispersal. Oxford University Press, Oxford.

Stamps, J. A. 2006. The silver spoon effect and habitat selection by natal dispersers. Ecology Letters **9**:1179-1185.

Stamps, J. A. and V. V. Krishnan. 1999. A learning-based model of territory establishment. The Quarterly Review of Biology **74**:291-318.

Stamps, J. A., V. V. Krishnan, and M. L. Reid. 2005. Search costs and habitat selection by dispersers. Ecology **86**:510-518.

Stamps, Judy A., V. V. Krishnan, and Neil H. Willits. 2009. How different types of natal experience affect habitat preference. American Naturalist **174**:623-630.

Stander, P. E. 1990. A suggested management strategy for stock-raiding lions in Namibia. South African Journal of Wildlife Research **20**:37-43.

Sterck, E. H. M., E. P. Willems, J. A. R. A. M. van Hooff, and S. A. Wich. 2005. Female dispersal, inbreeding avoidance and mate choice in Thomas langurs (*Presbytis thomasi*). Behaviour **142**:845-868.

Stevens, V. M., A. Trochet, S. Blanchet, S. Moulherat, J. Clobert, and M. Baguette. 2013. Dispersal syndromes and the use of life-histories to predict dispersal. Evolutionary Applications **6**:630-642.

Strickland, D. 1991. Juvenile dispersal in gray jays: dominant brood member expels siblings from natal territory. Canadian Journal Of Zoology **69**:2935–2945

Stutchbury, B. J. 1991. Floater behaviour and territory acquisition in male purple martins. Animal Behaviour **42**:435-443.

Swenson, J. E., F. Sandegren, A. Soderberg, A. Bjarvall, R. Franzen, and P. Wabakken. 1997. Infanticide caused by hunting of male bears. Nature **386**:450-451.

Szulkin, M. and B. C. Sheldon. 2008. Dispersal as a means of inbreeding avoidance in a wild bird population. The royal society **10**.

Tallmon, D. A., G. Luikart, and R. S. Waples. 2004. The alluring simplicity and complex reality of genetic rescue. Trends in Ecology & Evolution **19**:489-496.

Tarwater, C. E. and J. D. Brawn. 2010. Family living in a Neotropical bird: variation in timing of dispersal and higher survival for delayed dispersers. Animal Behaviour **80**:535-542.

Thompson, C. and K. McGarigal. 2002. The influence of research scale on bald eagle habitat selection along the lower Hudson River, New York (USA). Landscape Ecology **17**:569-586.

Thomson Reuters. 2013. Web of Knowledge http://apps.webofknowledge.com/. 15 August 2013

Trainor, A. M., J. R. Walters, W. F. Morris, J. Sexton, and A. Moody. 2013. Empirical estimation of dispersal resistance surfaces: a case study with red-cockaded woodpeckers. Landscape Ecology **28**:755-767.

Travis, J. M. J., K. Mustin, K. A. Bartoń, T. G. Benton, J. Clobert, M. M. Delgado, C. Dytham, T. Hovestadt, S. C. F. Palmer, H. Van Dyck, and D. Bonte. 2012. Modelling dispersal: an eco-evolutionary framework incorporating emigration, movement, settlement behaviour and the multiple costs involved. Methods in Ecology and Evolution **3**:628-641.

Trinkel, M. 2013. Climate variability, human wildlife conflict and population dynamics of lions *Panthera leo*. Naturwissenschaften:1-9.

Trivers, R. 1985. Social evolution. Benjamin Cummings, Menlo Park.

Tumenta, P. N., H. H. de Iongh, P. J. Funston, and H. A. Udo de Haes. 2013. Livestock depredation and mitigation methods practised by resident and nomadic pastoralists around Waza National Park, Cameroon. Oryx **47**:237-242.

Valeix, M., S. Chamaillé-Jammes, A. J. Loveridge, Z. Davidson, J. E. Hunt, H. Madzikanda, and D. W. Macdonald. 2011. Understanding patch departure rules for large carnivores: lion movements support a patch-disturbance hypothesis. American Naturalist **178**:269-275.

Valeix, M., H. Fritz, S. Chamaille-Jammes, M. Bourgarel, and F. Murindagomo. 2008. Fluctuations in abundance of large herbivore populations: insights into the influence of dry season rainfall and elephant numbers from long-lterm data. Animal Conservation **11**:391-400.

Valeix, M., G. Hemson, A. J. Loveridge, G. Mills, and D. W. Macdonald. 2012a. Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. Journal of Applied Ecology **49**:73-81.

Valeix, M., A. Loveridge, H. Madzikanda, H. Fritz, and D. Macdonald. 2010. How key habitat features influence large terrestrial carnivore movements: waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. Landscape Ecology **25**:337–351.

Valeix, M., A. J. Loveridge, S. Chamaille-Jammes, Z. Davidson, F. Murindagomo, H. Fritz, and D. W. Macdonald. 2009. Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. Ecology **90**:23-30.

Valeix, M., A. J. Loveridge, and D. W. Macdonald. 2012b. Influence of prey dispersion on territory and group size of African lions: a test of the resource dispersion hypothesis. Ecology **93**:2490-2496.

Van Dyck, H. and M. Baguette. 2005. Dispersal behaviour in fragmented landscapes: Routine or special movements? Basic and Applied Ecology **6**:535-545.

VanderWaal, K. L., A. Mosser, and C. Packer. 2009. Optimal group size, dispersal decisions and postdispersal relationships in female African lions. Animal Behaviour **77**:949-954.

Vanschoenwinkel, B., S. Gielen, M. Seaman, and L. Brendonck. 2008. Any way the wind blows - frequent wind dispersal drives species sorting in ephemeral aquatic communities. Oikos **117**:125-134.

Vuilleumier, S. and N. Perrin. 2006. Effects of cognitive abilities on metapopulation connectivity. Oikos **113**:139-147.

Walls, S. S., R. E. Kenward, and G. J. Holloway. 2005. Weather to disperse? Evidence that climatic conditions influence vertebrate dispersal. Journal of Animal Ecology **74**:190-197.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature **416**:389-395.

Waser, P. M., S. R. Creel, and J. R. Lucas. 1994. Death and disappearance: estimating mortality risks associated with philopatry and dispersal. Behavioral Ecology **5**:135-141.

Waser, P. M. and W. T. Jones. 1983. Natal philopatry among solitary mammals. The Quarterly Review of Biology **58**:355-390.

Wasserman, T., S. Cushman, M. Schwartz, and D. Wallin. 2010. Spatial scaling and multi-model inference in landscape genetics: *Martes americana* in northern Idaho. Landscape Ecology **25**:1601-1612.

Whitman, K., A. M. Starfield, H. S. Qadling, and C. Packer. 2004. Sustainable trophy hunting of African lions. Nature **428**:175-178.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology **3**:385-397.

Wiens, J. A. 2001. The landscape context of dispersal Pages 96-110 *in* J. Clobert, E. Danchin, A. Dhondt, and J. Nichols, editors. Dispersal. Oxford University Press, Oxford.

Winterbach, H. E. K., C. W. Winterbach, M. J. Somers, and M. W. Hayward. 2013. Key factors and related principles in the conservation of large African carnivores. Mammal Review **43**:89-110.

Wolff, J. O., K. I. Lundy, and R. Baccus. 1988. Dispersal, inbreeding avoidance and reproductive success in white-footed mice. Animal Behaviour **36**:456-465.

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

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

Wright, S. 1969. The Theory of Gene Frequencies. University of Chicago Press, Chicago.

Yoder, J. M., E. A. Marschall, and D. A. Swanson. 2004. The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. Behavioral Ecology **15**:469-476.

Zeller, K. A., K. McGarigal, and A. R. Whiteley. 2012. Estimating landscape resistance to movement: a review. Landscape Ecology **27**:777-797.

Zollner, P. A. and S. L. Lima. 1999. Search strategies for landscape-level interpatch movements. Ecology **80**:1019-1030.

Zollner, P. A. and S. L. Lima. 2005. Behavioral tradeoffs when dispersing across a patchy landscape. Oikos **108**:219-230.

Zonum Solutions. 2010. DigiPoint 3. http://www.zonums.com/gmaps/digipoint.php.

Appendix A

Appendix I: Gene flow and immigration: Genetic diversity and population structure of lions (*Panthera leo*) in Hwange National Park, Zimbabwe

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Statement of authorship: NE collected data, assisted logistically and with interpretations; AL collected data; AL, JH and DM oversaw this project; CM and AL wrote the first draft of the manuscript and all authors contributed to revisions

Abstract

The genetic diversity and population structure of a population of African lions in Hwange National Park, Zimbabwe, was studied using 17 microsatellite loci. Spatial genetic analysis using Bayesian methods suggested a weak genetic structure within the population and high levels of gene flow across the study area. We were able to identify a few individuals with aberrant or admixed ancestry, which we interpreted as either immigrants or as descendants thereof. This, together with relatively high genetic diversity, suggests that immigrants from beyond the study area have influenced the genetic structure within the park. We suggest that the levels of genetic diversity and the observed weak structure are indicative of the large and viable Okavango-Hwange population (of which our study population is a part), and is attributable to the high (but now threatened) levels of habitat connectivity that still exists between Protected Areas in this region. Given expected increases in human populations and anthropogenic impacts, efforts to identify and maintain existing movement corridors between regional lion populations will be important in retaining the currently healthy genetic status of this population. Our results show that understanding existing levels of genetic diversity and genetic connectivity has implications, not only for this lion population, but also for management and conservation of wild populations in other taxa.

Introduction

A range of factors influences the genetic structure of populations. Processes such as mutations, genetic drift, constant migration over time and selection influence populations over evolutionary time scales while ecological factors such as social behavior, mating systems and human impact, including harvesting, management and habitat alterations, operate at ecological time scales (Ross 2001). The design of effective and sustainable conservation and management plans thus depends to a great extent on the correct identification of population genetic structure and the factors influencing it.

Isolation of populations is increasingly a result of human pressure on habitats (Ceballos and Ehrlich 2002). When a previously large and widespread population becomes fragmented, it is important to identify conservation units correctly (Kraaijeveld-Smit 2005) in order to mitigate threats and foster long-term population viability. As a species range becomes increasingly fragmented, movements between sub-populations may become scarce and hence overall population size decreases. This may lead to a loss of genetic diversity and hence impair evolutionary potential, which in extreme cases may lead to extinction (Coulon *et al.* 2004). Additionally, in small and isolated populations, increased levels of inbreeding will accelerate loss of genetic variability and negatively affect life history traits such as survival, reproductive success, and fecundity (Charlesworth and Charlesworth 1987). Genetic diversity of small populations can be increased, and the negative effects of inbreeding may be mitigated, by the immigration of even a single individual to a focal population, highlighting the crucial importance of inter-population connectivity (Brown and Kodric-Brown 1977; Vilà *et al.* 2003; Madsen *et al.* 1999). In many species, individuals avoid inbreeding by migrating away from their natal area and thus dispersal might be viewed as an inbreeding avoidance mechanism (Perrin and Goudet 2001).

Lions, like most wild felids, are faced by a suite of anthropogenic threats, usually a combination of habitat loss leading to fragmentation of populations, conflict with people and over-exploitation (Loveridge *et al.* 2010a). Isolation and diminution of populations are both likely to be reflected in their genetic structure and diversity. The impacts of human activities on dispersal, and hence gene flow, may be hard to predict. Habitat fragmentation and isolation of populations will constrain dispersal while removal of individuals may facilitate it through indirect effects on the social structure. In this study we assess the potential genetic impacts of anthropogenic threats on a population of lions in Hwange National Park (HNP), Zimbabwe. The HNP population has faced high mortality through trophy hunting of adult and sub-adult males (Loveridge *et al.* 2007, Packer *et al.* 2010) and through illegal retaliatory killing and officially sanctioned problem animal control of livestock-raiding lions of all ages and both sexes (Loveridge *et al.* 2010b). High levels of mortality in the localities surrounding protected areas may serve to isolate such areas from surrounding populations.

Throughout Africa, lion populations are increasingly fragmented with an estimated 75% range loss in the last 500 years (Riggio *et al.* 2013). In lions, as in most polygynous mammals, males are the dispersing sex, although around a third of females may disperse (Pusey and Packer 1987). Lions not only exhibit sex-biased dispersal but also opportunistic territory acquisition by males (Funston *et al.* 2003). Furthermore, dispersing lions range widely and have the potential to disperse between populations (Macdonald *et al.* 2010, A. Loveridge unpublished data). Long distance dispersal may lead to increased gene flow and increased genetic diversity in a locality, while short distance dispersal might heighten the risk of inbreeding and loss of diversity. These attributes make lions an excellent model species to study socio-ecological effects on genetic diversity and population structure (Fraser *et al.* 2004).

Conflict with agro-pastoralists accounts for many of the deaths of lions and other large carnivores that leave the safety of protected areas. Dispersing animals are particularly vulnerable. Intense conflict occurred between local people and lions around HNP resulting in high levels of mortality in the lion population. Between 2000 and 2012 we recorded 73 lion mortalities (22% of all mortality records) due to illegal retaliatory killing and problem animal control in the areas directly adjacent to the park (Loveridge, unpublished data). This is likely to underestimate the number of mortalities because illegal killing is often concealed to avoid prosecution (see Liberg *et al.* 2011 for a European example). Such high levels of mortality could potentially pose a barrier to dispersing animals. Over the 12 years that lions have been monitored in HNP only two successful inter-population dispersals of radio-collared study animals have been recorded (A. Loveridge pers. obs.).

Here we describe the genetic diversity and population structure of the lion population in Hwange National Park. Levels of immigration to and from HNP are unknown, but evidence from our long-term study reveal that animals dispersing to areas outside the protected area and into human settlement areas to the North and East rarely survive. Landscape genetic analysis provides the opportunity to determine whether immigration into the population is occurring and thus to assess levels of connectivity or isolation in the population. We deduced that despite the human dominated landscapes preventing inward or outward dispersal on the northern and eastern boundaries of HNP, dispersal would be unrestricted across the western and north-western boundaries which are adjacent to wildlife areas in Botswana and Zimbabwe respectively. Thus we predicted that dispersal events would be detected in the genetic structure of the population. In this paper we estimate genetic diversity and examine population structure using multilocus microsatellite markers within HNP and compare this estimate with data from other studies.

Furthermore, we examine whether there is evidence of inbreeding or recent immigration to HNP.

Methods

Study Area

The study was carried out in Hwange National Park (HNP) which covers 14 900 km^2 of savannah in Northwestern Zimbabwe (19°00´S, 26°30´E). The vegetation is principally woodland and bushland savanna with less than 10% composed of grassland patches (Rogers 1993), and is mostly dominated by *Colophospermum mopane*, *Combretum* spp., *Acacia* spp., *Baikiaea plurijuga* and *Terminalia sericea* (Rogers 1993). HNP is a semi-arid ecosystem, with most rainfall between November and April. During the dry season, in years of normal rainfall, no water remains in the southern part of the park and around 50 water holes in the northern area are artificially supplied with water (Valeix *et al.* 2009, 2010). The park is entirely unfenced and agro-pastoralist communities live on the northern and eastern sides of the park (Fig. 1) the western boundary is formed by the Botswana- Zimbabwe border, which is the easternmost boundary of the arid Kalahari ecosystem. The study area covered more than 5000 km^2 in the northern part of the Park and estimates of lion density varied over the 12-year study from 2.7 to 4.1 lions per 100 km^2 (Loveridge *et al.* 2007, Loveridge, unpublished data).

Collection and Storage of Samples

Blood samples were collected from 91 individual lions from HNP between 2001 and 2009, when lions were immobilized to be fitted with radio-collars. In 2005, 80% of the prides in the study area included at least one collared individual. Blood samples were either frozen or stored in 95% ethanol at room temperature. We also obtained samples from 24 lions from the Kolmården Zoo in central Sweden to provide a comparison between the genetic diversity of a wild and a small, potentially genetically limited captive population.

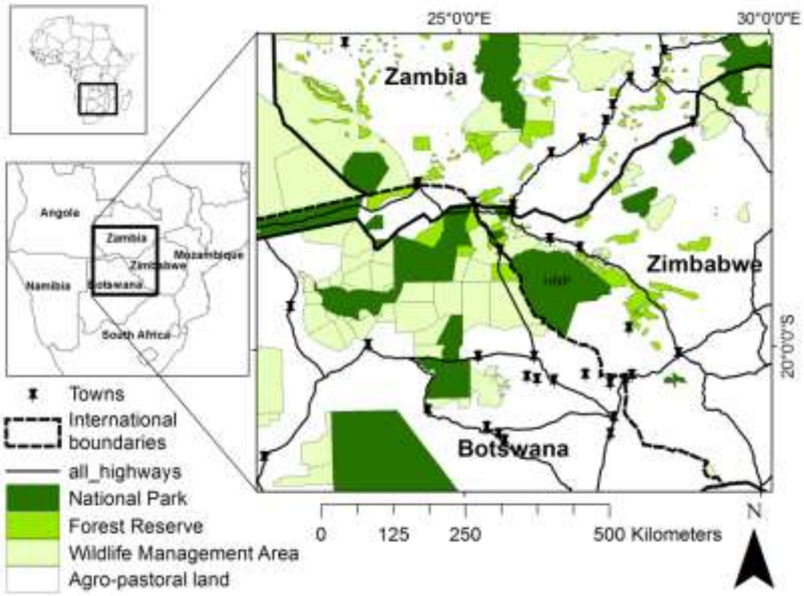

Fig. 1: Map of HNP and its surrounding, showing protected areas and towns.

Genotyping

DNA extractions were performed using the blood and tissue Qiagen extraction kit following the manufacturer's instructions (Qiagen, DNeasy kit). We selected 29 pairs of polymorphic microsatellite loci, which have been used successfully in previous studies (Spong and Creel 2001)**.** These were FCA205, FCA91, FCA006, FCA567, FCA085, FCA229, FCA001, FCA628, FCA69, FCA139, FCA105, FCA272, FCA441, FCA31, FCA275, FCA224, FCA211, FCA247, F115, FCA126, FCA014, FCA391, FCA230, FCA008, FCA208, FCA077, FCA129, FCA506, FCA045 (Menotti-Raymond *et al.* 1999). 26 of these microsatellites loci were dinucleotide repeats and 3 were tetranucleotide repeats (FCA391, FCA441 and F115) (Menotti-Raymond *et al.* 1999). Details on the multiplex compositions can be found in Table 1. The markers were labelled with fluorescent dyes (HEX, NED or FAM) and were divided into four multiplexes according to their size (Table 1). Multiplex Polymerase Chain Reaction (PCR) reactions were run in 10 µL volumes containing 1 µL of each multiplex mix, 1 µL of diluted DNA, 5 µL of PCR mastermix and 3 µL of Rnase free water. PCR conditions were an initial denaturation cycle at 95ºC for 15mins, followed by 35 cycles at 94ºC for 30s, annealing at 62ºC for 90s and 72ºC for 90s. PCRs then had a final extension at 72ºC for 10mins. Genotyping was run on a MegaBACE 1000 (Amersham Biosciences). To ensure correct genotyping, samples were run at least three times. Alleles scoring for each sample were done using the software Fragment Profiler (Fragment Profiler 1.2, Amersham Biosciences, 2003) and confirmed visually.

Data analyses

Using GENEPOP (Raymond and Rousset 1995), we tested for deviation from Hardy–Weinberg equilibrium (HWE) for each locus and applied a global test for heterozygote deficiency or excess at every locus and tested for genotypic linkage disequilibrium for each pair of loci. We performed all standard population genetic analyses (Mean number of alleles, allele frequencies for each locus, observed (H_o) and expected (H_e) heterozygosity levels, F_{IS}) using the GENETIX 4.02 software package (Belkhir *et al.* 2004). A factorial correspondence analysis was performed using the AFC 2D option implemented in GENETIX (Belkhir *et al.* 2004) on the matrix of individual genotypes to visualize individuals and how the genetic characteristics of each individual were organized in a multidimensional space based on allelic data.

The genetic structure of the HNP population was assessed using two different methods. First, we used the software package STRUCTURE v.2.3 (Pritchard *et al.* 2000) to find the most likely number of independent genetic clusters (K). Each cluster represents a sample of individuals characterized by a set of allelic frequencies for each locus, which are in Hardy Weinberg and linkage equilibrium. Initially, we ran STRUCTURE without any prior information on the sampling location. For this, the user provides a range of K (the number of clusters), and the software runs multiple Markov Chain Monte Carlo

Table 1. PCR multiplex composition.

Locus	Sequence		DYE	Size range	Multiplex
	Forward	**Reverse**			
FCA001	TGCTTGTCCTCTCCCTCG	TGACTGCGCCATAGCTTTC	FAM	190 - 212	1
FCA006	GACTTCTGCCTTCTTGTGGC	CCCCTAATGTGACTACAGATAGGG	HEX	180 - 184	1
FCA008	ACTGTAAATTTCTGAGCTGGCC	TGACAGACTGTTCTGGGTATGG	HEX	122 - 148	4
FCA014	AGCCAAGAGGGGAAACAACT	TGTCACAAATGGCAGGTTGT	FAM	160 - 190	3
FCA031	GCCAGGGACCTTTAGTTAGATT	GCCCTTGGAACTATTAAAACCA	FAM	221 - 241	2
FCA045	TGAAGAAAAGAATCAGGCTGTG	GTATGAGCATCTCTGTGTTCGTG	NED	146 - 160	4
FCA069	AATCACTCATGCACGAATGC	AATTTAACGTTAGGCTTTTTGCC	HEX	108 - 118	2
FCA077	GGCACCTATAACTACCAGTGTGA	ATCTCTGGGGAAATAAATTTTGG	HEX	143 - 155	4
FCA085	CTGTACATTTCTCTTCCCATTGC	CCCCTACTGGGTGCACTG	FAM	134 - 140	1
FCA091	TGAGAACAAGCCATTAATAGCA	CCCAAACATAAGGCTGCATT	HEX	134 - 146	1
FCA105	TTGACCCTCATACCTTCTTTGG	TGGGAGAATAAATTTGCAAAGC	HEX	189 - 197	2
FCA126	GCCCCTGATACCCTGAATG	CTATCCTTGCTGGCTGAAGG	FAM	139 - 145	3
FCA129	ACATAGAGCCGACACGGG	CGCCTATGTTTACTGCAGCA	HEX	174 - 180	4
FCA139	AGCATGTTTTTGAGGCAGCT	TTATGGGTAGTGTGAAGTCAGGG	HEX	141 - 147	2
FCA205	CCTGCTCTCAAGGAGCTCC	CCCATTTCTCCTACCAGTTCC	HEX	93 - 109	1
FCA208	TCAGGGTTCAAAAAAAGAAAAA	CAAAGCACCAGCTTAGAAGTCA	HEX	304 - 314	4
FCA211	TGTAGAACATAATGCCTCAGCC	TCTTGAACCTATTTCCCCACA	HEX	111 - 119	3
FCA224	CTGGGTGCTGACAGCATAGA	TGCCAGAGTTGTATGAAAGGG	NED	154 - 162	2
FCA229	CAAACTGACAAGCTTAGAGGGC	GCAGAAGTCCAATCTCAAAGTC	FAM	160 - 170	1
FCA230	AAGAATGGACTTGGGAAATGG	AAACCACAACAGGCAAAAGG	NED	128 - 158	3
FCA247	GGAAATTAGGAGCTCTGCCA	AAGATTTACCCAGTTGCCCC	HEX	145 - 151	3
FCA272	ACTTTACCTCCTTCCAAAAAG	CACCTTTCCATCCAATAAATTC	FAM	109 - 129	2
FCA275	TTGGCTGCCCAGTTTTAGTT	ACGAAGGGGCAGGACTATCT	NED	111-139	2
FCA391	GCCTTCTAACTTCCTTGCAGA	TTTAGGTAGCCCATTTTCATCA	FAM	237 - 273	3
FCA441	ATCGGTAGGTAGGTAGATATAG	GCTTGCTTCAAAATTTTCAC	FAM	153 - 183	2
FC506	AATGACACCAAGCTGTTGTCC	AGAATGTTCTCTCCGCGTGT	HEX	232 - 258	4
FCA567	TCAGGGTTTTCCAGAGAAACA	TAGACACATACAGATGGGGTGC	FAM	92 - 106	1
FCA628	CCCCTGCTCATTCTCTCTCA	GTGCCTGGCACAGCATAAG	NED	85 - 155	1
F115	CTCACACAAGTAACTCTTTG	CCTTCCAGATTAAGATGAGA	HEX	193 - 217	3

MCMC iterations with different values of K. We ran ten independent replicates with each K from 1 to 10. Every run consisted of 100 000 burn-in-steps, 500 000 MCMC iterations (following Pritchard and Wen 2003). As we were primarily interested in detecting possible genetic structure and to detect migrants (as opposed to clinal variation) we applied the no-admixture model, and used the approach suggested by Evanno *et al.* (2005) to infer the most likely number of clusters, K. Second, we used the clustering algorithm implemented in the software BAPS (Corander *et al.* 2008; version 5.4) which incorporates spatial coordinates denoting the origin of each individual specimen to deduce the number of clusters. We performed 30 replicate runs of the algorithm, with the a priori upper boundary for the number of clusters ranging between 2 and 15. Again we used a model without allowing for admixture.

Results

We used the genotypes from a total of 17 microsatellite loci in the analyses since a few of the loci did not amplify well. Four individuals failed to amplify at more than 3 loci and were removed from the analyses. We thus included a total of 87 individuals from HNP in our analyses, (42 females and 45 males) in addition to the 24 individuals from the Kolmården Zoo.

Genetic diversity

All loci were polymorphic and the number of alleles per locus varied between 5 and 17, the average number was 10.47. There was no significant linkage disequilibrium between loci (all $p>0.05$). The average expected heterozygosity was 0.75 ± 0.10 and the observed heterozygosity was 0.73 ±0.10. There was thus a slight but significant heterozygote deficiency with a correspondingly significant F_{IS} ($p<0.001$). When we compared the genetic diversity of the Hwange lions with two other studies: the captive bred population at the Kolmården Zoo, and previously published genetic data from Selous

Game Reserve (Spong *et al.* 2002), we observed that the Hwange and Selous lions displayed similar levels of genetic variation whereas the genetic diversity of the zoo population was significantly lower (Table 2).

Table 2. Comparison of standard population genetic parameters in three different lion populations (means □ 1. S.D.). Data on heterozygosities from Selous were taken from Spong et al. (2002).

	Hwange National Park, Zimbabwe	Selous Game Reserve, Tanzania	Kolmården Zoo, Sweden
Number of individuals	87	70	24
Number of loci used	17	14	21
Mean number of alleles per locus	10.47	8.9	3.38
H_{exp}	0.75 ± 0.10	0.75 ± 0.10	0.53 ± 0.19
H_{obs}	0.73 ± 0.10	0.69 ± 0.16	0.59 ± 0.29
F_{IS}	0.03	0.08	-0.04

HNP Population Genetic Structure

Analyses using STRUCTURE gave the highest probability for three distinct genetic clusters (K=3). The variance between runs was at its lowest for K=2 and 3 with variances much higher for K > 3 further indicating a genetic structure of 2-3 clusters. Similarly, when using the Evanno method (□K) (Evanno *et al.* 2005) we identified K=2 or 3 as the most probable number of clusters (Fig. 2). Since the data for K = 2 and K = 3 were similar, graphical analyses of the STRUCTURE plots were conducted for both values of K.

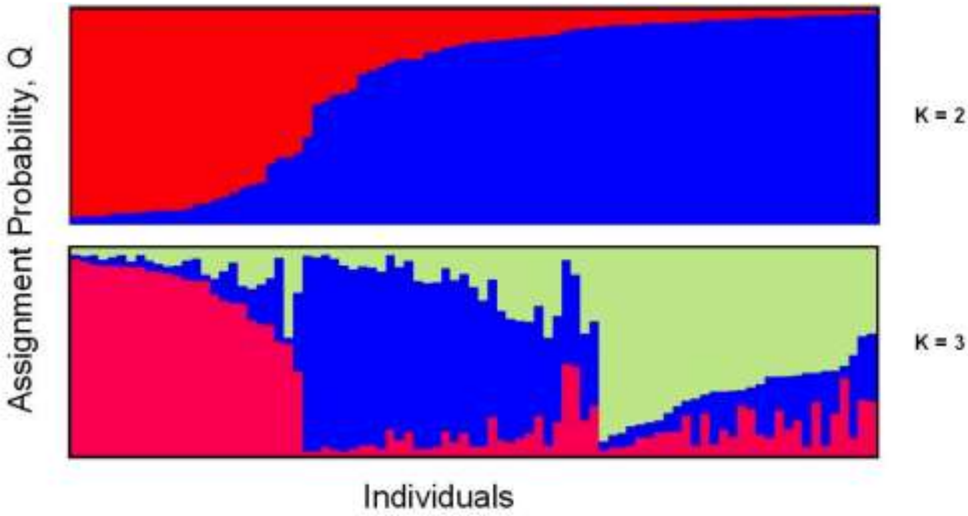

Fig. 2: Bar Plot output from STRUCTURE of K=2 and K=3. The probability of assignment to each cluster is given by the height of the different colors and is based on an average of 10 runs, for the 87 individuals.

The spatial arrangement of assignment probabilities for K=2 are shown in Fig. 3. In the two clusters model, K=2, the majority of individuals was assigned to a main cluster (blue n =55, Fig. 3). The spatial arrangement of individuals appears to be random. Along an East-West axis through the park the correlation between assignment probability and longitude was non significant (r=-0.11, n=87, NS) as it was along a North-South axis (correlation of assignment probability and latitude: r=0.04, n=87, NS). Similarly, a map with the admixture coefficients for K=3 did not show any significant spatial patterns (data not shown).

Although there was evidence for three genetic clusters (K=3) in this study, two clusters (K=2) seems to be the most likely for a number of reasons: Pritchard *et al.* (2000) demonstrated that in simulations where STRUCTURE finds different solutions at multiple values of K with reasonably similar probabilities, the lowest value is usually the most reliable. Over-estimation of the true value of K can also be due to the presence of related individuals (Pritchard and Wen 2003). Our samples were obtained during the placement of radio-collars on individuals; some individuals were sampled within the same pride or coalitions, and therefore are likely to be related to each other. We therefore favour the two clusters solution (K = 2) for inferring the genetic structure of this lion population.

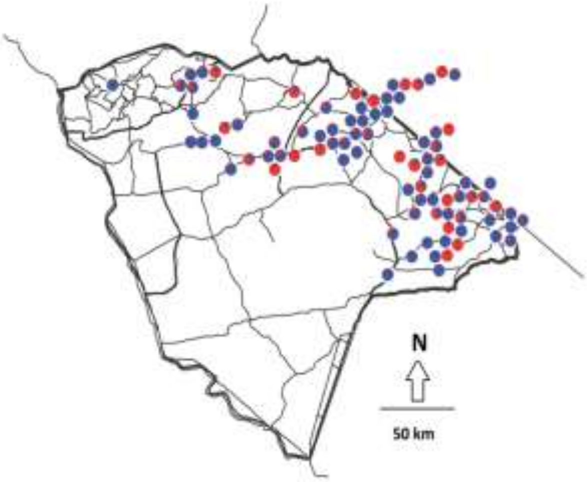

Fig. 3: Geographical distribution of the 87 individuals sampled across Hwange National Park and individual assignment probabilities of the two clusters inferred by STRUCTURE. Assignment probabilities to either of the two clusters are proportional to the colour of each pie chart. Cluster one and two are represented in blue and red respectively. The placements of each pie chart indicate the sampling locality of an individual.

When using spatial coordinates as prior information, BAPS generated a posterior probability of 0.983 for 10 genetic clusters. The inferred clusters were, however, consistent with the STRUCTURE results in showing the presence of one main cluster (n = 69) and 9 small clusters containing at maximum 3 individuals and the individuals assigned to the main cluster by each method largely. Six of the nine small clusters were concentrated on the edge of the protected area (Fig. 4).

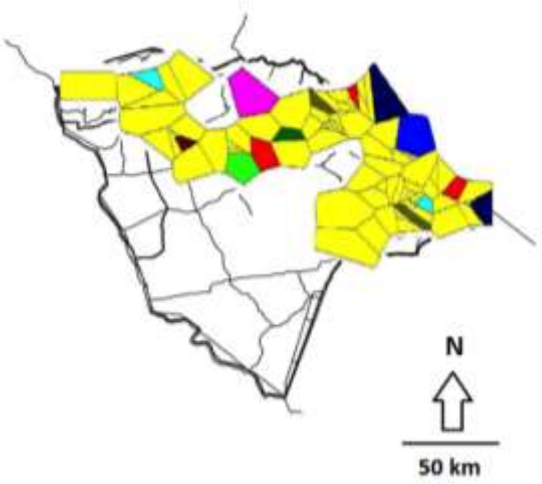

Fig. 4: Illustrative spatial representation of the 87 individuals using the BAPS no-admixture algorithm. Each polygon represents one or more individuals assigned to the same clusters. Although based upon sampling location the figure is not intended to represent social or territorial structure of the population, though both are expected to influence the distribution of related individuals within the population. Polygons with different colours correspond to genetically differentiated clusters, while identical colours identify individuals belonging to the same cluster. The best model identified 10 clusters, with one main cluster (yellow, n = 69) and 9 small clusters containing at maximum 3 individuals.

In the two dimensional factorial correspondence analysis implemented in GENETIX, 11 males were identified as outliers, and thus as putative immigrants. The corresponding numbers for females was 3 (Fig. 5). Of these 14 individuals, putatively identified as immigrants, 11 were also identified as divergent by BAPS, and all 14 were identified as divergent using STRUCTURE (Table 3).

Table 3: Summary of immigrant status as inferred from observations and genetic analyses.

	Observed as immigrant	Inferred immigrant with STRUCTURE	Inferred immigrant with BAPS	Identified as divergent by AFC
Males				
NKWaM1	No	Yes	Yes	Yes
KANM1	Yes	Yes	Yes	Yes
LIVaM1	Unknown	Yes	Yes	Yes
ULAM1	Yes	Yes	Yes	Yes
SHUaM1	No	Yes	Yes	Yes
LINM1	No	Yes	Yes	Yes
UDLM2	Yes	Yes	Yes	Yes
GUVbM1	No	Yes	No	Yes
DETaM1	No	Yes	No	Yes
AIRM1	Unknown	Yes	Yes	Yes
GUVbM3	No	Yes	No	Yes
Females				
NKWaF1	No	Yes	No	Yes
XMAF1	Unknown	Yes	No	Yes
NEHF2	Unknown	Yes	Yes	Yes

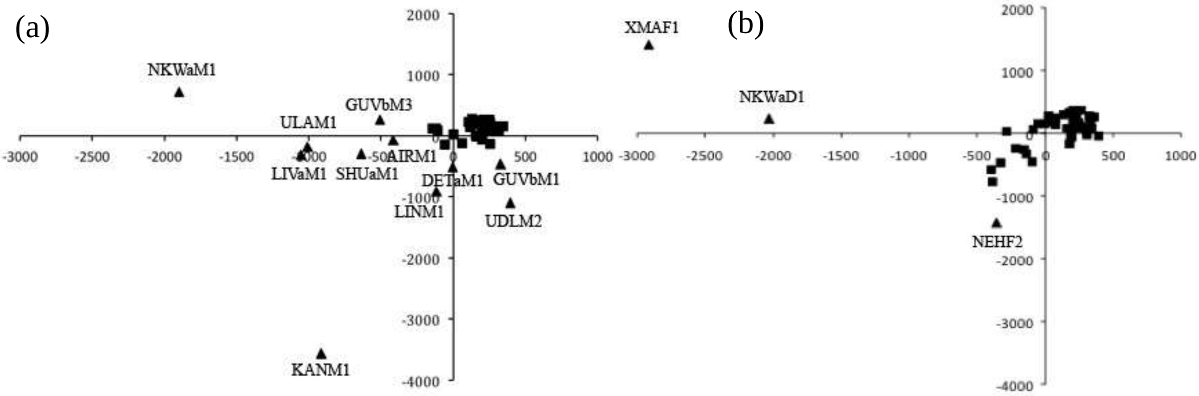

Fig. 5: Two-dimensional Factorial Correspondence Analysis of individual multilocus genotypes computed using 17 microsatellite loci for each of the sexes (a) males n=44, b) females n=43). The individuals considered as immigrants are indicated with triangles and the ID for such individuals are indicated.

Discussion

The extinction of wild mammal populations may be brought about by human activities such as hunting or agriculture, and this may be amplified were human populations occur at high density (Ceballos and Ehrlich 2002). Globally, natural populations face scenarios where many organisms can survive only in reserves or other protected areas. Migration between such semi-isolated areas is increasingly a concern for conservation. African lions have experienced both significant population decline and reduction in geographic range in recent decades (Macdonald *et al.* 2010) with most viable populations occurring in large protected areas (IUCN-SSG 2006). Fragmentation of lion populations in the face of increasing pressure of habitat conversion and conflicts with pastoralists and ranchers makes conservation and management of this species a challenge that requires significant resources (Packer *et al.* 2013). An understanding of prevailing levels of genetic integrity and potential genetic connectivity may help conceive and prioritize future conservation efforts.

Genetic Diversity

Genetic diversity in the lion population of HNP was moderately high, with an average expected heterozygosity of 0.75, indicating a large local population size and/or high levels of gene flow. This is in accord with the findings of Dubach *et al.* (2013) whose analysis of Africa-wide lion population genetics show the Botswana/ Zimbabwe sub population (LCU 46, IUCN-SSG 2006) to be genetically heterogeneous with high levels of gene flow. HNP forms the easternmost portion of the wider Okavango-Hwange sub-population of lions, which occupies an area of 95170km^2 and is estimated to hold around 2300 lions (IUCN-SSC 2006). This is one of only four ‘Lion Conservation Units’ (LCUs) in Africa to hold > 2000 animals and one of only two in southern Africa (IUCN-SSC 2006). Thus the finding that genetic diversity and probable gene flow were both high is consistent with the current geographic extent and size of the population.

The levels of genetic diversity within HNP were comparable to the level of genetic diversity found in Selous Game Reserve (Spong *et al.* 2002). The Selous ecosystem holds the largest population of lions (~ 5500) in Africa in an area of 190 000km^2 (IUCN-SSC 2006) and is thus presumably a lion population where evidence of either inbreeding or genetic isolation is least likely to be found. This suggests that at a continental level, with comparable measures of heterozygosity, the Hwange-Okavango population is similarly free of genetic problems. Interestingly, in both Hwange and Selous the observed heterozygosities were lower than expected leading to significant population inbreeding coefficients (F_{IS}). Deviations from Hardy-Weinberg expectations may be caused by a Wahlund effect and occur if two or more subpopulations have different allele frequencies reducing overall heterozygosity, even if the subpopulations themselves are in a Hardy-Weinberg equilibrium (Wahlund 1928). In the case of HNP this might be explained by hidden population structure, family group structure or a biased representation of close relatives in our study sample. Our samples were obtained during the placement of radio-collars on individuals; some individuals were sampled within the same pride or coalitions, and therefore are likely to be related to each other as it has been demonstrated in previous studies (Spong and Creel 2001; Pusey and Packer 1987). By comparison, the genetic diversity of the captive lion population was low compared to the two natural populations. Individuals in captive populations are limited in number and despite efforts to increase the genetic diversity by exchanging individuals among zoos, this zoo population appears to have lost genetic diversity. However, it does not seem to experience inbreeding insofar as observed and expected heterozygosities were similar (and hence F_{IS} was zero); presumably due to active outbreeding approaches conducted by numerous zoos.

The consequences of high levels of hunting and anthropogenic mortality for population genetics are difficult to assess as this may be influenced by many factors such as potential reductions in population size and the duration over which any population bottlenecks occur (Frankham *et al.* 2002). Furthermore, high mortality in habitat corridors connecting sub-populations could potentially result in population isolation and inbreeding. However, based on our marker set, results suggest that despite intense hunting (prior to 2004) and overall high anthropogenic mortality (Loveridge 2010b), the Hwange lion population has not experienced significant loss of genetic diversity. This is likely to be a consequence of a relatively large population size and landscape connectivity that allows dispersal between sub-populations, particularly with the wildlife areas to the West of HNP.

HNP Population Structure

We did not find any evidence for a geographical division within the population, which was unsurprising given that no geographic or artificial barriers such as fences limit this population. The two different Bayesian methods identified distinct genetic clusters. Both methods described one main population including the majority of the sampled individuals, and one or more sub-clusters.

The presence of weak genetic structure suggests that gene flow is occurring in the area or that there has been only a very recent separation of populations (Bulgin *et al.* 2003). Aside from geographical barriers, dispersal of breeding individuals between populations may be the main determinant of the genetic structure of the population (Coulon *et al.* 2006). In the Serengeti ecosystem approximately 30% of female lions dispersed (Pusey and Packer 1987) while in the Selous ecosystem, around 20% of females did (Spong and Creel 2001). In HNP, it is likely that up to 60% of females may disperse (Loveridge, unpublished data), likely due to the high off-take of territorial males (Loveridge 2010). This high level of female dispersal may account for the three potential female imigrants identified in this study. Sub-adult males on the other hand will always disperse, generally over relatively short distances, settling within or near the natal range (Pusey and Packer 1987, Spong and Creel 2001, Funston *et al.* 2003). The weak population structure found in our study suggest that dispersal distances in the area are longer. This is consistent with our field observations as we have observed several males dispersing more than 150km from the study area, often through vast areas of agro-pastoral land.

Immigrant individuals, whom reproduce within the study area, may have an effect on the genetic diversity (Vilà *et al.* 2003), but only if the migrants carry alleles that are not already present in the population (Ehrlich and Raven 1964). Packer and Pusey (1993) determined that 69% of the males, which reproduced in their study area, originated elsewhere. In HNP, based on the factorial correspondence and BAPS analyses, there was strong evidence that eleven individuals (nine males and three females) were genetically distinct from the rest of the population. We could confirm with observed behavioural data that 3 of them were indeed likely to be immigrants while for 7 others we had observational evidence that they were resident animals that had been born in prides resident within the study area. For the remaining 4, we had no evidence either way. It is possible that the individuals identified by genetic analysis as putative immigrants, but known to have been born within the study area, might have descended from immigrants, suggesting that historical immigration has occurred.

Interestingly 6 of the 9 small clusters identified in the BAPS analysis were located close to the edge of the population, near the park boundary (Fig. 4). Prides living on the edge of the park experience significantly higher mortality, have lower chances of persistence and have higher male turnover (due to high male mortality on the park boundary) (Loveridge *et al.* 2010b). It is possible that opportunities for dispersing individuals to acquire a territory and breed are higher in peripheral areas where territorial vacuums are created by anthropogenic mortality, (Loveridge *et al.* 2007) and high levels of conflict with people increases the chances entire prides will be removed. Thus the influx of new genes derived from immigrants is more likely closer to the perimeter of the park.

Conservation Genetic Implications

In order to design appropriate management strategies it is necessary to understand both the history and the structure of the study population and also the level and distribution of genetic diversity (O’Brien 1994). Genetic diversity plays an important part in the adaptation of populations to changing environmental conditions (Reed and Frankham 2003). Frankham (1998) also suggested that loss of genetic diversity could add to the risks of extinction for endangered or managed populations. In this study genetic diversity was high and we could infer that gene flow to and from the study site was likely.

Relatively high levels of heterozygosity found in this population suggest that either the area and population are large enough to sustain genetic diversity, or the population is already connected to other sub populations. Probably immigration into HNP occurs from Protected Areas to the West and North-West through habitat corridors formed by Wildlife Management and Safari Areas. Connectivity is less certain to the North and East of HNP where there is significant human settlement (Fig. 1). Nevertheless recent records of radio-tagged lions from HNP migrating into Zambia (straight line distance of 120 km from HNP) and to Chete Safari Area (Zimbabwe, 150 km from HNP) suggest that at least a few lions are still able to traverse these areas, which in turn suggests that genetic linkages may remain between protected areas within the wider sub-region. Further studies should focus on detecting genetic structure at a larger scale and try to identify putative corridors of connectivity and maintain them.

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References

Belkhir K, Borsa P, Chikhi L, *et al.* Laboratoire Génome, Populations, Interactions, CNRS UMR 5000. Université de Montpellier II; Montpellier: 2004. GENETIX 4.05, logiciel sous Windows pour la génétique des populations. (http://www.univmontp2.fr/~genetix/genetix.htm)

Bulgin NL, Gibbs HL, Vickery P, Baker AJ (2003) Ancestral polymorphisms in genetic markers obscure detection of evolutionarily distinct populations in the endangered Florida grasshopper sparrow (*Ammodramus savannarum floridanus*). *Molecular Ecology* **12,** 831–844.

Brown JH, Kodric-Brown A (1977) Turnover Rates in Insular Biogeography: Effect of Immigration on Extinction. *Ecology* **58**, 445-449.

Ceballos G, Ehrlich PR (2002) Mammal Population Losses and the Extinction Crisis. *Science* **296**, 904-907.

Charlesworth D, Charlesworth B (1987) Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology and Systematics* **18**, 237-268.

Corander J, Sirén J, Arjas E (2008) Bayesian Spatial Modelling of Genetic Population Structure. *Computational Statistics* **23**, 111-129.

Coulon A, Cosson JF, Angibault JM, Cargnelutti B, Galan M, Morellet N, Petit E, Aulagnier S, Hewison AJM (2004) Landscape connectivity influences gene flow in a roe deer population inhabiting a fragmented landscape: an individual-based approach. *Molecular Ecology* **13**, 2841–2850.

Coulon A, Guillot G, Cosson J *et al.* (2006) Genetic structure is influenced by lansdcape features. Empirical evidence from a roe deer population. *Molecular Ecology* **15**, 1669–1679.

Davidson Z, Valeix M, Loveridge AJ, Madzikanda H, Macdonald D (2011) Socio-spatial behaviour of an African lion population following perturbation by sport hunting. *Biological Conservation*, **144**: 114-121

Dubach, J.M., Briggs, M.B., White, P.A., Ament, B.A., & Patterson, B.D. (2013). Genetic perspectives on 'lion conservation units' in Eastern and Southern Africa. *Conservation Genetics, DOI 10.1007/s10592-013-043-3.*

Ehrlich PR, Raven PH (1964) Butterflies and plants: a study in coevolution. *Evolution* **18**, 586-608.

Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Molecular Ecology* **14**, 2611–2620.

Frankham R (1998) Inbreeding and Extinction: Island Populations. *Conservation Biology* **12**, 665-675.

Frankham R, Ballou JD, Briscoe DA (2002) Introduction to Conservation Genetics. Cambridge University Press: Cambridge, UK.

Fraser DJ, Lipp C, Bernatchez L (2004) Consequences of unequal population size, asymmetric gene flow and sex-biased dispersal on population structure in brook charr (*Salvelinus fontinalis*). *Molecular Ecology* **13**, 67-80.

Funston PJ, Micheal G, Mills L, Richardson PRK, Van Jaarsveld AS (2003) Reduced dispersal and opportunistic territory acquisition in male lions (*Panthera leo*). *Journal of Zoology* **259,** 131-142.

Hanby JP, Bygott JD (1987) Emigration of subadult lions. *Animal Behaviour* **35**, 161-169.

IUCN-SSC. (2006). Conservation strategy for the lion *Panthera leo* in eastern and southern Africa (pp. 55). www.felidae.org: IUCN SSC Cat Specialist Group.

Kraaijeveld-Smit FJL, Beebee TJC, Griffiths RA, Moore RD, Schley L (2005) Low gene flow but high genetic diversity in the threatened Mallorcan midwife toad *Alytes muletensis*. *Molecular ecology* **14**, 3307-3315.

Liberg, O., C. Chapron, P. Wabakken, H. C. Pedersen, N. T. Hobbs & H. Sand (2011) Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. *Proceedings of the Royal Society B: Biological Sciences* **279**, 910-915.

Loveridge AJ, Searle AW, Murindagomo F, Macdonald DW (2007) The impact of sport-hunting on the lion population in a protected area. *Biological Conservation* **134**, 548–558.

Loveridge, A. J., S. W. Wang, L. G. Frank & J. Seidensticker, (2010a) People and wild felids: conservation of cats and management of conflicts. In: *Biology and Conservation of Wild Felids*: 161. D. W. Macdonald & A. J. Loveridge (Eds.). Oxford University Press, Oxford.

Loveridge, A. J., G. Hemson, Z. Davidson & D. W. Macdonald, (2010b) African lions on the edge: Reserve boundaries as 'attractive sinks'. In: *Biology and Conservation of Wild Felids*: 283. D. W. Macdonald & A. J. Loveridge (Eds.). Oxford University Press, Oxford.

Macdonald, D. W., A. J. Loveridge & A. Rabinowitz, (2010) Felid futures: crossing disciplines, borders, and generations. In: *Biology and Conservation of Wild Felids*: 599. D. W. Macdonald & A. J. Loveridge (Eds.). Oxford University Press, Oxford.

Madsen T, Olsson M, Shine R, Wittzell H (1999) Restoration of an inbred population of adder (*Vipera berus*). *Nature* **402,** 34–35.

Menotti-Raymond M, David VA, Lyons LA, Schaffer AA, Tomlin JF, Hutton MK, O'Briend SJ (1999) A genetic linkage map of microsatellites in the domestic cat (*Felis catus*). *Genomics* **57**, 9-23.

O'Brien SJ (1994) A role for molecular genetics in biological conservation. *Proceedings of the Natlional Acadademy of Sciences USA* **91**, 5748-5755.

Packer C, Pusey AE (1993) Dispersal, kinship and inbreeding in African lions. N.W. Thornhill editor, 375-391. The natural history of inbreeding and outbreeding: theoretical and empirical perspectives. University of Chicago Press, Chicago, Illinois.

Packer C, Whitman K, Loveridge AJ, Jackson J, Funston PJ (2006) Impacts of Trophy Hunting on Lions in East and Southern Africa. Recent offtake and future recommendations. In: Eastern and Southern African Lion Workshop, Johannesburg.

Packer C, Brink H, Kissui BM, Maliti H, Kushnir H, Caro T (2010) Contributed Paper: Effects of Trophy Hunting on Lion and Leopard Populations in Tanzania. *Conservation Biology* **25**, 142-153.

Packer C, Swanson A, Canney S, Loveridge A, Garnett S, Pfeifer M, Burton AC, Bauer H, MacNulty D (2013) The case for fencing remains intact. *Ecology Letters* doi: 10.1111/ele.12171.

Perrin N, Goudet J (2001) Inbreeding, kinship and the evolution of natal dispersal. In: J. Clobert, E. Danchin, AA Dhondt, JD Nichols: *Dispersal*. Oxford Univ. Press, Oxford. pp. 452

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. *Genetics* **155**, 945–959

Pritchard JK, Wen W (2003) Documentation for STRUCTURE software: Version *2*. Available from http://www.pritch.bsd. uchicago.edu.

Pusey AE, Packer C (1987) The evolution of sex-biased dispersal in lions. *Behaviour* **101**, 275-310.

Raymond M. & Rousset F, 1995. GENEPOP (version 1.2): Population genetics software for exact tests and ecumenicism. J. Heredity, **86**:248-249. (http://genepop.curtin.edu.au/)

Reed DH, Frankham R (2003) Correlation between fitness and genetic diversity. *Conservation Biology* **17**, 230–237.

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

Rogers CML (1993) A woody vegetation survey of Hwange National Park. Dept of National Parks and Wildlife Management, Zimbabwe.

Ross KG (2001) Molecular ecology of social behaviour: analyses of breeding systems and genetic structure. *Molecular Ecology* **10**, 265–284.

Spong G, Creel S (2001) Deriving dispersal distances from genetic data. *Proceedings of the Royal Society B: Biological Sciences* **268**, 2571–2574.

Spong G, Creel S, Stone J, Björklund M (2002) Genetic structure of lions (*Panthera leo*) in the Selous Game Reserve: implications for the evolution of sociality. *Journal Evolutionary Biology* **15**, 945–953.

Valeix, M., A. J. Loveridge, S. Chamaillé-Jammes, Z. Davidson, F. Murindagomo, H. Fritz & D. W. Macdonald (2009) Behavioural adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. *Ecology* **90,** 23-30.

Valeix, M., A. J. Loveridge, Z. Davidson, H. Madzikanda, H. Fritz & D. W. Macdonald (2010) How key habitat features influence large terrestrial carnivore movements: waterholes and African lions in a semi arid savanna of north-western Zimbabwe. *Landscape Ecology* **25,** 337-351.

Vilà C, Sundqvist AK, Flagstad Ø, Seddon J, Björnerfeldt S, Kojola I, Casulli A, Sand H, Wabakken P, Ellegren H (2003) Rescue of a severely bottlenecked wolf (*Canis lupus*) population by a single immigrant. *Proceedings of the Royal Society B: Biological Sciences* **1510,** 91-97.

Wahlund, S. (1928). Zusammensetzung von Population und Korrelationserscheinung vom Standpunkt der Vererbungslehre aus betrachtet. *Hereditas* **11**, 65–106.

Appendix II: Influence of immediate predation risk by lions on the vigilance of prey of different body size

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Original Article

Influence of immediate predation risk by lions on the vigilance of prey of different body size

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The effects on vigilance behavior of environmental cues that affect perceived risk of predation have been widely measured in gregarious herbivores. How extrinsic (e.g., predator activity within certain habitats) and intrinsic (e.g., within-group competition) cues interact depends on the biology of the prey species. However, very little is known about the impact of the actual presence of the predator in the vicinity on fine scale prey vigilance behavior. For this study, we monitored the vigilance of plains zebra (*Equus quagga*) and impala (*Aepyceros melampus*) in and around Hwange National Park, Zimbabwe. We assessed how the presence of radio-collared lions (*Panthera leo*) affected the vigilance of their prey. To evaluate the factors affecting vigilance behavior, we measured routine and intense vigilance. Routine vigilance can be conducted while chewing, although during intense vigilance chewing is halted and thus imposes foraging costs as food processing is delayed. As the most acute form of vigilance, we predicted that the presence of lions would lead to an increase in intense vigilance in both species. We found this to be the case for zebra, a key prey species for lions, while impala adjusted their intense vigilance to risk cues less specific to the presence of lions. Potential predation risk posed by lions in the immediate vicinity differs not only between species but also for a given species in different contexts. Our results also reveal how other environmental risk indicators influence the structure of vigilance behavior of large prey species in a manner that reflects their respective ecologies. *Key words:* antipredatory behavior, impala, intense vigilance, *Panthera leo*, zebra. *[Behav Ecol]*

INTRODUCTION

Vigilance behavior contributes to herbivore fitness in several ways, including avoidance of within-group competition (Blanchard et al. 2008), facilitation of group cohesion (Treves 1999), and predator detection (FitzGibbon 1989). In the latter, it is part of a suite of behavioral adaptations that facilitate increased prey fitness via predation avoidance (Lima and Dill 1990; Hunter and Skinner 1998). These adaptations have repercussions for the ecology of prey species, including effects on group size (Hamilton 1971; Pulliam 1973; Childress and Lung 2003), spatial, and temporal habitat use (Ripple and Beschta 2004; Valeix, Fritz, et al. 2009; Valeix, Loveridge, et al. 2009).

The majority of observational studies of antipredatory vigilance are limited by the fact that accurate behavioral data on prey, which are generally abundant and easy to observe, are rarely complemented by comparable information on their predators, which are often rare and difficult to observe (Lima 2002). Group size and distance to cover have been widely used as proxies for the risk of predation (Pays et al. 2012), but recent work indicates that the physical presence of predators itself influences prey behavior (Creel and Winnie 2005; Valeix, Fritz, et al. 2009; Valeix, Loveridge, et al. 2009; Périquet et al. 2010), with prey adjusting antipredator vigilance differently to these parameters when a predator is detected in the immediate vicinity.

Vigilance generally involves foraging costs (Brown 1999; Fortin, Boyce, Merrill, et al. 2004). Time spent vigilant can conflict with foraging, thereby reducing rate of food intake (Houston et al. 1993). Optimal foragers should therefore reduce their vigilance as the marginal value of energy increases (Brown 1999; Fortin, Boyce, and Merrill 2004). Seasonality in forage quality (Blanchard and Fritz 2008) implies that costs of vigilance are most pronounced in the dry season because forage quality is lower and therefore intake needs to be greater, a phenomenon hereafter referred to as the forage quality hypothesis (see Rubenstein 1994 and Blanchard et al. 2008 for social amplification of this effect in zebra, *Equus quagga* and impala, *Aepyceros melampus*, respectively).

In some species, such as maras (*Dolichotis patagonum*), vigilance costs are shared among mates, as males keep guard while their female is feeding (Taber and Macdonald 1992). Other prey mitigate foraging costs by being vigilant while handling food. This antipredatory behavior has been referred

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to as a routine vigilance (sensu Blanchard and Fritz 2007). Such multitasking can be observed in birds handling seeds (Baker et al. 2010, 2011) or herbivores swallowing or chewing food while vigilant (Fortin, Boyce, Merrill, et al. 2004; Blanchard and Fritz 2007; Pays et al. 2012). The main disadvantage of routine vigilance is that the quality of information gathered for predator detection is impaired as the chewing process disturbs both hearing and, to a lesser extent, vision (Fortin, Boyce, and Merrill 2004; Molinari-Jobin et al. 2004; Amft et al. 2005). Therefore, it might not be an optimal strategy for predator detection if routine vigilance does not allow prey to detect the predator in time. In some cases, such as when a specific risk-stimulus is detected, a more acute form of vigilance can be advantageous (Brown 1999). During such "intense vigilance" (induced vigilance, sensu Blanchard and Fritz 2007), the individual postpones all other activities while conducting vigilance, including chewing. As it is exclusive, this high-quality vigilance therefore involves higher immediate foraging costs than does routine vigilance (Blanchard and Fritz 2007) that can be performed while continuing to eat. Very few studies have made such a distinction between the 2 vigilance types. This is despite their relative contributions to total vigilance being different in that the costs of intense vigilance in terms of forging are much higher than the ones of routine vigilance (Fortin, Boyce, and Merrill 2004). To understand the ecological role of vigilance, it might be advantageous to distinguish between routine vigilance and intense vigilance because these 2 vigilance types impose different foraging costs and provide information of different quality on predation risk. Accordingly, the functional relationships between the optimal level of vigilance and habitat features should vary depending on the type of vigilance examined (Fortin, Boyce, and Merrill 2004). Nonetheless, few vigilance studies have made this distinction.

Here, we used radiotelemetry data from African lions (*Panthera leo*) to measure the effect of immediate predator presence on both components of individual vigilance: routine vigilance and intense vigilance. Because of the high quality of intense vigilance, we tested the hypothesis that prey increase their intense vigilance rather than their routine vigilance when a predator is known to be in the vicinity. We also explored the role of body size and associated vulnerability to predation in vigilance behavior by studying 2 contrasting herbivore species: zebra and impala whose average body masses are 200 and 45 kg, respectively (Cumming D and Cumming G 2003). Although both species are potential prey for lions (Owen-Smith and Mills 2008), lions preferentially prey on species within a weight range of 190–550 kg (Hayward and Kerley 2005), and zebras are known to be highly preferred prey of lions. This is the case in Hwange National Park (HNP) where zebra represent ~7.1% of all prey killed by lions, whereas impala represent only 2.5% (Loveridge et al. 2006) while both species are approximately equally abundant in the study area (1.15 zebras/km^2 [standard deviation {SD} 0.42]; 1.43 impalas/km^2 [SD 0.63], Chamaillé-Jammes et al. 2009). Additionally, lions account for most predation of zebra, but impala are more often taken by other predator species. Indeed, impala are significantly preferred by African wild dogs, cheetahs, and leopards (Hayward and Kerley 2008). In light of this, we expected these 2 species, which differ in their body size, perception of predation risk, predator preference, and energy requirements to differ in their strategy for dealing with predation risk (i.e., to optimize their survival) and limiting costs on foraging. Additionally, we expected vigilance to be negatively associated with group size, and as lions are ambush predators, we expected zebra vigilance to increase when close to cover. We did not expect impala to react strongly to the presence of lions because they are preyed on by predator species with a wide range of hunting tactics (Pays et al. 2012). However, we expected them to adjust their behavior according to their group size and distance to cover in the same way as do zebra.

MATERIALS AND METHODS

Study site

Data collection was carried out in the Main Camp area of Hwange National Park (HNP), located in north-west Zimbabwe, 19°00′S, 26°30′E. The habitat is dystrophic semiarid savannah, composed primarily of vegetation characteristic of woodland and bushland, though this is interspersed with small grassland patches (Roger 1993). The long-term mean annual rainfall for the area is 606 mm and characterized by high variability. During the dry season, natural water is scarce, and surface water available to animals is mainly found in artificial water holes, which are pumped with ground water. Lion density in HNP has been estimated at 2.7 lions/100 km^2 (Loveridge, Searle, et al. 2007). The rainy season occurs from the end of October to the end of April. Field observations were conducted in both the wet season from February to April 2008 and in the early dry season from mid-July to September 2010.

Vigilance monitoring

Vigilance data were collected from plains zebra and impala. Both are gregarious ungulates that form harem groups. Whereas zebras are grazers and usually stay in grassland areas, impalas are mixed feeders utilizing grassland and bushland habitats. Due to the practicalities of maintaining visual contact with the focal individual throughout the observation period, data collection was conducted when animals were feeding in areas open enough to film for 5 min. Filming was conducted from a parked vehicle between 100 and 150 m from the focal individual, following a period of habituation (the observers waited until no vigilance was directed toward them, usually between 2 and 5 min) allowed between switching off the vehicle's engine and data collection, so as best to capture their natural behavior.

Focal individuals were chosen randomly within the pool of animals corresponding to criteria designed to remove intraspecific variation in vigilance levels. First, observations focused on adult females without dependent offspring (Burger and Gochfeld 1994). Second, selecting individuals from the center of their group meant that we collected conservative estimates, without amplification of vigilance levels as a product of within-group positioning (Blanchard et al. 2008).

For each 5-min filming session, additional information was collected for individuals successfully recorded. This included date, time of day, location (GPS coordinates), and whether lions could be detected using a very high frequency receiver (if no detection, it meant than no radio-tagged lion was present within 2 km of the prey). Individual's species and group size were also recorded (group size was defined as the number of individuals foraging within 50 m of each other). Additionally, the distance between the focal individual and the closest cover was determined using a range finder.

For impala, pseudoreplication was avoided by only filming an individual from a given group once per day. As impala groups are very dynamic in terms of composition and numbers, this method reduced the chance of focusing on the same individual twice. For zebra, we avoided pseudoreplication by focusing on different individuals, based on their unique stripe patterns.

Using the footage collected from appropriate individuals, the type, order, and duration of behavior categories were recorded. Analysis of film footage was carried out without reference to individual- and case-specific data to avoid introducing bias. Vigilance types were distinguished using the following criteria:

Routine vigilance

Individual's head is raised above shoulder height in an alert posture, usually with ears pushed forwards, and the individual is scanning its environment while chewing or walking. Routine vigilance could be used to detect food competition between conspecifics or be an antipredatory behavior.

Intense vigilance

Individual's head is raised above shoulder height in an alert posture, both ears pushed forwards fully, exclusively scanning their surroundings without chewing or moving. This type of vigilance is often referred to as "induced" vigilance (Blanchard and Fritz 2007) and is mainly used to describe antipredatory behavior. We chose to use the term "intense" as the cause of the vigilance is not always known.

Each observation period began when the focal individual was displaying feeding behavior. All forms of vigilance bout were considered finished when the individual had lowered its head, even momentarily. Similarly, intense vigilance bouts were considered finished when one or both ears were pushed back, even briefly, or the animal began chewing again.

Lion data

Data on lion presence in the study area were collected from radio-collared lions. We used data from 17 female and 10 male adults that were already instrumented with GPS radio collars in the framework of the long-term monitoring of the lion population in HNP (for details, see Loveridge, Davidson et al. 2007). Consequently, we could detect whether lions were in the vicinity during the observations. The presence of lions was detected during observations by radio tracking using a four-element yagi antenna (Sirtrack Ltd.) and either a Telonics TR4 or TR5 (Telonics Inc., Mesa, AZ) or Televilt RX900 telemetry receiver (Televilt Positioning AB). Such radio tracking permits detection of collared lions within a range of ~ 2 km. Even though the cues on which herbivores base their knowledge of the presence of the lions in this vicinity are far from being understood, previous studies have shown that herbivores adjust their behavior to lion presence within such a radius (Valeix, Fritz, et al. 2009; Valeix, Loveridge, et al. 2009). Hence, hereafter, presence of lions in the vicinity is taken to mean the presence of radio-tagged lions within 2 km of the observation site.

The presence of undetected lions or other predators may be a source of noise in our data. However, we feel that this noise is likely to be minimal. Indeed, there was at least one collared lion in all known lion prides and coalitions in the study area, and preliminary analyses revealed that lions from the same group stay together most of the time (with all females from a pride sighted together in 89.2 ± 7.4% of sightings). No comparable data were available for other large predators in the area, but the presence of untagged large predators would simply make any vigilance response to lion less detectable rather than create an artificial effect. Our assumptions are therefore conservative in terms of the hypothesis we are testing.

Statistical analyses

We considered a baseline model that accounted for group size, absence or presence of lion, distance to cover, and season to determine how these parameters influenced the proportion of time spent in intense vigilance and routine vigilance as well as the frequency of intense vigilance and routine vigilance bouts. Whenever needed, these independent variables were transformed to linearize the relationship. We also tested the interaction between these variables and only presented the significant ones ($P \leq 0.05$). We used the function lm in the package nlme in R (version 2.13.1 for Mac OS X 10.7.2).

RESULTS

Impala

The proportion of time spent in routine vigilance per observation period averaged 27.5% (confidence interval [CI] 95% 24.5–30.4) and was best predicted by log group size and season (Table 1, Figure 1). Similarly, the group size and season influenced the frequency of routine vigilance bouts (Table 2). In both cases, vigilance was negatively associated with group size and higher in the wet season relative to the dry season. The proportion of intense vigilance per observation period averaged 8.8% (CI 95% 6.4–11.2) and was determined by group size and distance to cover (Table 1, Figure 1). Impala spent less time in intense vigilance when they were in larger groups or farther from cover. None of the variables explained variations in the frequency of intense vigilance bouts (Table 2).

None of the interactions tested had a significant impact on impala vigilance behavior.

Zebra

The proportion of routine vigilance per observation period was negatively associated with group size as was the frequency of routine vigilance bouts (Tables 1 and 2) and averaged 24.5%

Table 1

Average coefficient for multiple regressions relating the effect of different parameters on the proportions of routine and intense vigilance

	Proportion of routine vigilance				Proportion of intense vigilance			
	Zebra		Impala		Zebra		Impala	
Parameter	Value	SE	Value	SE	Value	SE	Value	SE
Intercept	0.40	0.05	0.57	0.07	0.02	0.03	0.27	0.06
Log(group size)	−0.22***	0.05	−0.15***	0.03	−0.01	0.04	−0.09*	0.04
Season[a]	NS	NS	−0.15***	0.04	NS	NS	NS	NS
Lion	NS	NS	NS	NS	0.33 ***	0.07	−0.02	0.03
Distance cover[2]	NS	NS	NS	NS	NS	NS	−0.00006*	0.00002
Log(Gr size) × lions	NS	NS	NS	NS	−0.29***	0.07	NS	NS

SE, standard error.

[a] Dicotomic variable with wet season being the season of reference.

$*P \leq 0.05$, $**P \leq 0.01$, $***P < 0.001$, and NS, not significant

Table 2

Average coefficient for multiple regressions relating the effect of different parameters on the frequencies of routine and intense vigilance

	Frequency of routine vigilance				Frequency of intense vigilance			
	Zebra		Impala		Zebra		Impala	
Parameter	Value	SE	Value	SE	Value	SE	Value	SE
Intercept	1.13	0.2	2.65	0.39	0.078	0.062	0.48	0.18
Log(group size)	−0.63**	0.2	−0.90***	0.24	NS	NS	NS	NS
Season^a	NS	NS	−0.62**	0.19	−0.02	0.05	NS	NS
Lion	NS	NS	NS	NS	0.032	0.05	NS	NS
Distance cover^2	NS	NS	NS	NS	0.00007 *	0.00003	NS	NS
Season × lion	NS	NS	NS	NS	0.55 ***	0.01	NS	NS

SE, standard error.

[a] Dicotomic variable with wet season being the season of reference.

*$P \leq 0.05$, **$P \leq 0.01$, ***$P < 0.001$, and NS, not significant.

(CI 95% 21.6–27.4). The proportion of time spent in intense vigilance, averaging 4.7% (CI 95% 2.8–6.6), was best predicted by the model that contained the group size × lion presence interaction term (i.e., the proportion of time spent in intense vigilance increased in the presence of lions more in small than large groups, Figure 2) and positively associated with distance from cover (Table 1). The frequency of routine vigilance bouts was only influenced by group size, with members of larger groups raising their head less frequently to scan their surroundings (Table 2). The intense vigilance bouts frequency was best predicted by the model with the season × lion presence interaction term, where lion presence increased intense vigilance frequency more in the dry than the wet season (Table 2, Figure 3).

None of the other interactions tested had a significant impact on zebra vigilance behavior.

DISCUSSION

The body size of prey species largely determines the suite and characteristics of their predators, and consequently, prey of different body sizes have different susceptibility to predation (Sinclair et al. 2003; Owen-Smith and Mills 2008; Fritz et al. 2011). Our study revealed size-dependent differences in the vigilance behavior of 2 herbivore species in response to dynamic and static features of their habitat. We found that the presence of lions in the vicinity, which varies dynamically over time and space, led to a 5.2-fold increase in frequency of intense vigilance bouts in zebra and a 3-fold increase in the average proportion of intense vigilance. In contrast, we detected no change in the vigilance of impala in the presence versus absence of lions. This predator might be a greater threat for zebra than impala, given that lions would be responsible for at least 80% of zebra mortality but cause only less than 25% of impala mortality (Hayward et al. 2007; Owen-Smith and Mills 2008; Thaker et al. 2011). Furthermore, as impala and zebra are approximately equally abundant in HNP (Chamaillé-Jammes et al. 2009) but impala are found in larger groups (impalas mean group size: 23.3 [CI 95% 20–26.6, n = 122], zebras mean group size: 9.2 [CI 95% 8–10.5; n = 131]), a given attack would represent a smaller "per capita" risk for impala than for zebra. Our finding that impala do not reduce the risk imposed by the proximity of lions through changes in individual vigilance supports the hypothesis that they react in a different way to zebras to the presence of the predator. Finally, it is also possible that their antipredatory behavior to decrease the risk of predation by lions is based on other behavioral

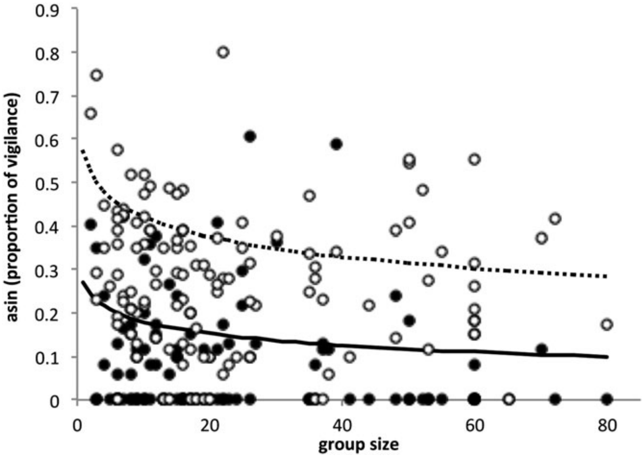

Figure 1
Proportion (arcsine transformed) of routine (solid line and filled circles) and intense (dotted line and empty circles) vigilance for impala in function of their group size.

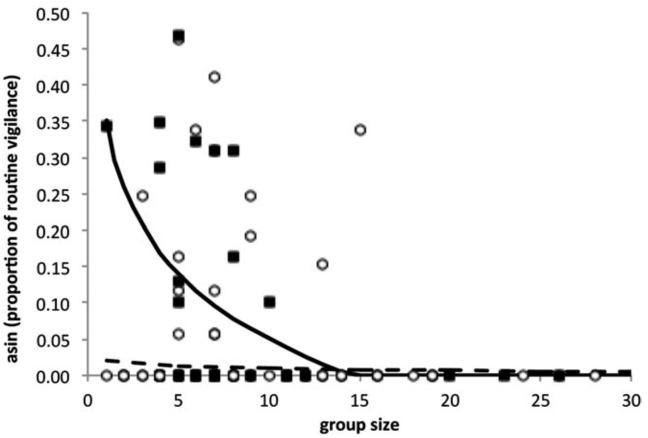

Figure 2
Proportion of intense vigilance (arcsine transformed) for zebra in function of the group size with (filled squares) and without lions (empty circles) in the vicinity.

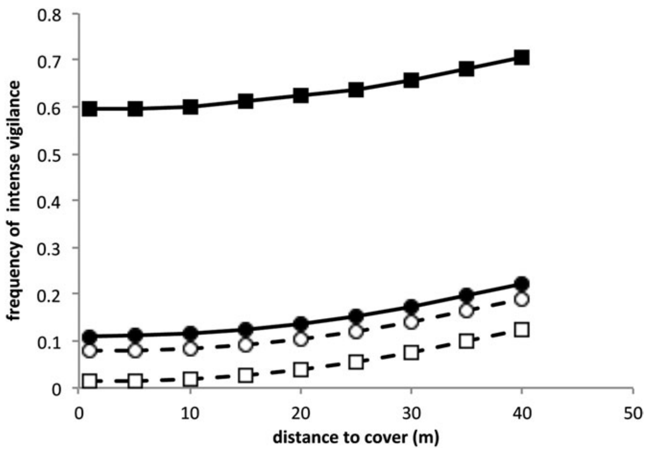

Figure 3
Frequency of intense vigilance for zebra in function of the distance to cover during the 2 seasons (squares: dry season; circles: wet season) with (filled symbols) and without lions (empty symbols) in the vicinity.

adjustments, such as changes in habitat selection or group formation.

As we expected in the presence of lions, zebra increased their use of intense vigilance. Intense vigilance is a high quality process of information acquisition to improve predator detection, thus allowing prey to respond to an immediate temporal and spatial predator risk. However, they avoid using intense vigilance when lions are not in the vicinity because it is a costly posture. Thus, they limit foraging costs of vigilance.

We further observed a 13-fold increase in the proportion of intense vigilance in the presence of lions in the dry season compared with only a 2-fold increase in the wet season, indicating that zebra perceive lions as a greater threat during the dry than the wet season. This conclusion is supported by lion kill data from HNP, which indicates that lions consume a greater proportion of zebra in the dry (6% in the early dry season, increasing to 13% in the late dry season) than the wet season (4%) (Hwange Lion Research Project, unpublished data). No such seasonal pattern in predation risk was detected for impala. The seasonal effect for zebra is also consistent with the food quality hypothesis: because there is more high-quality forage available in the wet than the dry season at our study site (Blanchard and Fritz 2008), the foraging costs of vigilance should have a greater impact on herbivore behavior in the dry season (Fortin, Boyce, Merrill, et al. 2004). Indeed, optimality principles predict a decrease in vigilance following an increase in the marginal value of food (Brown 1999).

In the dry season, herbivores have to face several constraints: low forage quality but also the need to access surface water regularly to meet their drinking requirements. As a consequence, herbivore distribution is largely influenced by the distance to a water source in the dry season (Redfern et al. 2005; Valeix, Loveridge, et al. 2009) and predators such as lions tend to hunt and ambush their prey in the vicinity of these water sources (Valeix, Fritz, et al. 2009; Valeix et al. 2011). Hence, vigilance behavior in herbivores is likely to be maximal when in the vicinity of a water source: in Hwange, kudu and giraffe spend on average 30% and 40% of their time at water sources being vigilant (Périquet et al. 2010). Although our study did not address the interplay between season, food quality, and distance to a water source, these factors are likely to interact in the prey to exhibit vigilance.

In addition to the effect of the presence of lions and season, we found that group size and distance to cover also affected the structure of individual vigilance both in zebra and impala. The negative correlation between vigilance and group size has become a classic example of adjustable predator avoidance behavior (Roberts 1996). A number of mechanisms are thought to contribute to this, including Hamilton's (1971) dilution effect, the confusion effect (Welty 1934), and Pulliam's (1973) "many eyes" effect. The reduction in individual risk that these factors collectively convey is widely considered as a driving force behind the evolution of aggregation behavior in social herbivores (Turchin and Kareiva 1989; Reluga and Viscido 2005; Wood and Ackland 2007). In addition, interindividual competition for food access in large groups might also force individuals to reduce the time spent in intense vigilance. Indeed, in such groups constrained by a large number of competitors but taking advantage of a dilution effect, the best strategy should be an increase of the foraging time limiting vigilance posture and using the low-cost posture (i.e., routine vigilance). A group-size effect can also interact with individual choice to determine time allocated to vigilance (intense or routine vigilance), as individuals might bet on a dilution effect (and collective detection) in large groups, thereby limiting intense vigilance. This is in accordance with our result that the effect of group size on zebra intense vigilance only became evident in the presence of lions (Figure 2). However, the group-size effect was a far more dominant factor for impala in shaping intense vigilance levels. This suggests that, because they have more potential predators than do zebra, impala assess their predation risk based more on their group size rather than the actual presence or absence of one of these predators in the vicinity. In contrast to our predictions, and other results (Burger et al. 2000; Beauchamp 2010), distance to cover was positively associated with zebra vigilance (Figure 3), though the effect was comparatively small.

Finally, the way in which impala and zebra adjust their intense vigilance in response to risk cues is noteworthy. Zebra do so primarily by changing vigilance bout frequency. This strategy minimizes the length of time spent with the head lowered, hence increasing the likelihood of detecting an ambush predator, such as a lion. In contrast, impala adjusted the proportion of vigilance but not the frequency of bouts (Pays et al. 2007; Carter et al. 2009; Sirot and Pays 2011). This may reflect a more generalized approach to predator detection, fitting the risk posed by potential predators with a range of hunting strategies.

In conclusion, our results illustrate that prey body size and ecology influence how herbivores gage risk of predation, including from lions in the vicinity, and how they reduce this risk through changes in individual vigilance. These patterns are most obvious when the distinction is drawn between routine and intense types of vigilance. During the wet season, kudu (*Strepsiceros zambesiensis*) are the main prey of lions (Loveridge, Davidson, et al. 2007; Davidson 2009) so a study of their reaction to the presence of lions would add depth to the conclusions drawn here. To our knowledge, this study is one of the first to assess the effect of the immediate presence of a predator on prey behavior at such a fine scale.

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REFERENCES

Amft O, Stäger M, Lukowicz P, Tröster G. 2005. Analysis of chewing sounds for dietary monitoring. Lect Notes Comput Sci. 3660: 56–72.

Baker DJ, Stillman RA, Smith BM, Bullock JM, Norris KJ. 2010. Vigilance and the functional response of granivorous foragers. Funct Ecol. 24:1281–1290.

Baker DJ, Stillman RA, Smart SL, Bullock JM, Norris KJ. 2011. Are the costs of routine vigilance avoided by granivorous foragers? Funct Ecol. 25:617–627.

Beauchamp G. 2010. Relationship between distance to cover, vigilance and group size in staging flocks of semipalmated sandpipers. Ethology. 116:645–652.

Blanchard P, Fritz H. 2007. Induced or routine vigilance while foraging. Oikos. 116:1603–1608.

Blanchard P, Fritz H. 2008. Seasonal variation in rumination parameters of free-ranging impalas Aepyceros melampus. Wildl Biol. 14:372–378.

Blanchard P, Sabatier R, Fritz H. 2008. Within-group spatial position and vigilance: a role also for competition? The case of impalas *(Aepyceros melampus)* with a controlled food supply. Behav Ecol Sociobiol. 62:1863–1868.

Brown JS. 1999. Vigilance, patch use and habitat selection: foraging under predation risk. Evol Ecol Res. 1:49–71.

Burger J, Gochfeld M. 1994. Vigilance in African mammals: differences among mothers, other females, and males. Behaviour. 131:153–169.

Burger J, Safina C, Gochfeld M. 2000. Factors affecting vigilance in springbok: importance of vegetative cover, location in herd, and herd size. Acta Ethol. 2:97–104.

Carter AJ, Pays O, Goldizen AW. 2009. Individual variation in the relationship between vigilance and group size in eastern grey kangaroos. Behav Ecol Sociobiol. 64:237–245.

Chamaillé-Jammes S, Valeix M, Bourgarel M, Murindagomo F, Fritz H. 2009. Seasonal density estimates of common large herbivores in Hwange National Park, Zimbabwe. Afr J Ecol. 47:804–808.

Childress MJ, Lung MA. 2003. Predation risk, gender and the group size effect: does elk vigilance depend upon the behaviour of conspecifics? Anim Behav. 66:389–398.

Creel S, Winnie J. 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. Anim Behav. 69:1181–1189.

Cumming D, Cumming G. 2003. Ungulate community structure and ecological processes: body size, hoof area and trampling in African savannas. Oecologia. 134:560–568.

Davidson Z. 2009. Lion ecology and socio-spatial impacts of trophy hunting in Zimbabwe [doctorate thesis]. [Oxford]: University of Oxford.

FitzGibbon CD. 1989. A cost to individuals with reduced vigilance in groups of Thomson's gazelles hunted by cheetahs. Anim Behav. 37:508–510.

Fortin D, Boyce M, Merrill EH. 2004. Multi-tasking by mammalian herbivores: overlapping processes during foraging. Ecology. 85:2312–2322.

Fortin D, Boyce M, Merrill EH, Fryxell JM. 2004. Foraging costs of vigilance in large mammalian herbivores. Oikos. 107:172–180.

Fritz H, Loreau M, Chamaillé-Jammes S, Valeix M, Clobert J. 2011. A food web perspective on large herbivore community limitation. Ecography. 34:196–202.

Hamilton WD. 1971. Geometry for the selfish herd. J Theor Biol. 31:295–311.

Hayward MW, Kerley GIH. 2005. Prey preferences of the lion *(Panthera leo)*. J Zool. 267:309–322.

Hayward MW, Kerley GIH. 2008. Prey preferences and dietary overlap amongst Africa's large predators. S Afr J Wildl Res. 38:93–108.

Hayward MW, O'Brien J, Hofmeyr M, Kerley GIH. 2007. Testing predictions of the prey of lion derived from modeled prey preferences. J Wildl Manag. 71:1567–1575.

Houston AI, McNamara JM, Hutchinson J. 1993. General results concerning the trade-off between gaining energy and avoiding predation. Philos Trans R Soc B Biol Sci. 341:375–397.

Hunter LT, Skinner J. 1998. Vigilance behaviour in African ungulates: the role of predation pressure. Behaviour. 135:195–211.

Lima SL. 2002. Putting predators back into behavioral predator-prey interactions. Trends Ecol Evol. 17:70–75.

Lima SL, Dill LM. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. Can J Zool. 68:629–640.

Loveridge AJ, Davidson Z, Hunt JE, Valeix M, Elliot N, Stapelkamp B. 2007. Hwange Lion Research Project Annual Report 2007 Report prepared for the Zimbabwe Parks and Wildlife Management Authority. p. 1–55.

Loveridge AJ, Hunt JE, Murindagomo F, Macdonald DW. 2006. Influence of drought on predation of elephant *(Loxodonta africana)* calves by lions *(Panthera leo)* in an African wooded savannah. J Zool. 270:523–530.

Loveridge AJ, Searle A, Murindagomo F, Macdonald DW. 2007. The impact of sport-hunting on the population dynamics of an African lion population in a protected area. Biol Conserv. 134:548–558.

Molinari-Jobin A, Molinari P, Loison A, Gaillard J-M, Breitenmoser U. 2004. Life cycle period and activity of prey influence their susceptibility to predators. Ecography. 27:323–329.

Owen-Smith N, Mills MGL. 2008. Predator-prey size relationships in an African large-mammal food web. J Anim Ecol. 77:173–183.

Pays O, Blanchard P, Valeix M, Chamaillé-Jammes S, Duncan P, Périquet S, Lombard M, Ncube G, Tarakini T, Makuwe E, et al. Forthcoming 2012. Detecting predators and locating competitors while foraging: an experimental study of a medium-sized herbivore in an African savanna. Oecologia. doi:10.1007/s00442-011-2218-3.

Pays O, Jarman PJ, Loisel P, Gerard J-F. 2007. Coordination, independence or synchronization of individual vigilance in the eastern grey kangaroo? Anim Behav. 73:595–604.

Périquet S, Valeix M, Loveridge AJ, Madzikanda H. 2010. Individual vigilance of African herbivores while drinking: the role of immediate predation risk and context. Anim Behav. 79:655–671.

Pulliam HR. 1973. On the advantages of flocking. J Theor Biol. 38:419–422.

Redfern J, Grant C, Gaylard A, Getz W. 2005. Surface water availability and the management of herbivore distributions in an African savanna ecosystem. J Arid Environ. 63:406–424.

Reluga TC, Viscido S. 2005. Simulated evolution of selfish herd behavior. J Theor Biol. 234:213–225.

Ripple WJ, Beschta RL. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? BioScience. 54:755–766.

Roberts G. 1996. Why individual vigilance declines as group size increases. Anim Behav. 51:1077–1086.

Rogers CML, editor. 1993. A woody vegetation survey of Hwange National Park. Harare (Zimbabwe): Department of National Parks and Wildlife Management.

Rubenstein D. 1994. The ecology of female social behaviour in horses, zebras, and asse. In: Jarman P, Rossiter A, editors. Animal societies: individuals, interactions, and organization. Kyoto (Japan): Kyoto University Press. p. 13–28.

Sinclair ARE, Mduma S, Brashares J. 2003. Patterns of predation in a diverse predator–prey system. Nature. 425:288–290.

Sirot E, Pays O. 2011. On the dynamics of predation risk perception for a vigilant forager. J Theor Biol. 276:1–7.

Taber A, Macdonald D. 1992. Communal breeding in the mara, Dolichotis patagonum. J Zool. 227:439–452.

Thaker M, Vanak AT, Owen CR, Ogden MB, Niemann SM, Slotow R. 2011. Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. Ecology. 92:398–407.

Treves A. 1999. Vigilance and spatial cohesion among blue monkeys. Folia Primatol. 70:291–294.

Turchin P, Kareiva P. 1989. Aggregation in Aphis varians: an effective strategy for reducing predation risk. Ecology. 70:1008–1016.

Valeix M, Chamaillé-Jammes S, Loveridge AJ, Davidson Z, Hunt JE, Madzikanda H, Macdonald DW. 2011. Understanding patch departure rules for large carnivores: lion movements support a patch disturbance hypothesis. Am Nat. 178:269–275.

Valeix M, Fritz H, Loveridge AJ, Davidson Z. 2009. Does the risk of encountering lions influence African herbivore behaviour at waterholes? Behav Ecol Sociobiol. 63:1483–1494.

Valeix M, Loveridge AJ, Chamaillé-Jammes S, Davidson Z, Murindagomo F, Fritz H, Macdonald DW. 2009. Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. Ecology. 90:23–30.

Welty JC. 1934. Experiments in group behavior of fishes. Physiol Zool. 7:85–128.

Wood AJ, Ackland GJ. 2007. Evolving the selfish herd: emergence of distinct aggregating strategies in an individual-based model. Proc R Soc Lond Ser B Biol Sci. 274:1637–1642.