THE PERFORMANCE AND SPATIAL ECOLOGY OF THE CRITICALLY ENDANGERED BLACK RHINOCEROS, *DICEROS BICORNIS* L., POPULATION IN ITHALA GAME RESERVE, KWAZULU NATAL, SOUTH AFRICA

By

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As the candidate's supervisor I have approved this thesis for submission.

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ABSTRACT

Ensuring the persistence of populations of endangered species requires an understanding of, and response to, the causes of population declines. Species occurring in small populations are vulnerable to stochastic problems that are environmental, demographic, or genetic in nature, and can reduce survival as much as the threats of habitat degradation. Critically endangered black rhinoceros, *Diceros bicornis,* populations have declined throughout Africa since 1960, but, more recently, numbers are increasing at a continental level, but remain lower than three generations ago. The south-central black rhinoceros, *Diceros bicornis minor* is considered critically endangered and are found primarily in protected areas. To ensure the persistence of the species, management efforts have focussed on live-harvesting and translocation of individuals from certain sub-populations to populate additional reserves, whilst monitoring involved collecting demographic data (births, deaths, density, and sex and age structure) that could be used to improve conservation management of this species.

This study was initiated to determine population estimates, growth rate, and fecundity over time, as well as sex and age structure and age-specific probabilities of survival, using 18 years (1990–2008) of long-term sightings data from Ithala Game Reserve, KwaZulu-Natal, South Africa. I also wanted to determine if mortality occurrences were associated with social or environmental factors, or as a result of management interventions. There was no significant difference in the sex ratios at birth, although the proportion of females in the population was 0.58. There was strong evidence for density-dependent regulation, with density in conception year a key driver of population performance (birth rate). The population does not appear to be at ecological carrying capacity; however, social effects are delaying conception.

The model analyses showed that social interactions carried more weight than environmental factors on mortality, with a strong association between mortality and intensity of use, as well as mortality and management removals from the population. The mechanism of density dependence in Ithala Game Reserve is through mortality that is associated with increased social interactions, rather than from resource limitations.

To mitigate density-dependent social effects, my study recommends an adaptive management strategy of pre-selecting individuals with known information on their social behaviour and context, before removal from the reserve, so as to maintain stability in the social organization of the population. In the absence of restoring linkages between populations of black rhinoceros, the translocation of black rhinoceros is a primary tool to mimic how meta-population dynamics would play out across the landscape. However, careful monitoring to enhance understanding of social factors, particularly black rhinoceros male behaviour, should be intensified to allow strategic translocation of individuals in such a way that negative density dependent effects are mitigated.

PREFACE

The work described in this dissertation was carried out in Ithala Game Reserve, KwaZulu-Natal Province, South Africa, through the School of Life Sciences, University of KwaZulu-Natal, Durban, under the supervision of Professor Rob Slotow and Dr Sam Ferreira.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use have been made of the work of others it is duly acknowledged in the text.

[redacted]

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DECLARATION 1 – PLAGIARISM

I, Catherine Caroline Greaver, declare that

1. The research reported in this thesis is my original research.

2. This thesis has not been submitted for any degree or examination at any other university.

3. This thesis does not contain other person's data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other researchers.

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DECLARATION 2 – PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis (include publications in preparation, submitted, *in press* and published and give details of the contributions of each author to the experimental work and writing of each publication).

Publication 1
Greaver, C., Ferreira, S. & Slotow, R. (2013). Density-dependent regulation of the critically endangered black rhinoceros population in Ithala Game Reserve, South Africa. *Austral Ecology 39, 437–447.*

Publication 2
Greaver, C., Ferreira, S., Slotow, R. & Simms, C. (will be submitted for publication). Social interactions and management removals contribute to black rhinoceros, *Diceros bicornis*, mortalities in Ithala Game Reserve, South Africa.

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General Introduction

Populations are the fundamental unit of conservation (Coates *et al.*, 2018) and the primary goal of management (Anderson *et al.*, 2002) and policy directives to provide meaningful protection to small populations, or populations facing the imminent threat of extinction (Croteau & Mott, 2011). Many plant and animal species with highly specialized habitat requirements (Shipley *et al.*, 2009; Ainsworth & Drake, 2020), often naturally occur in small populations that are scattered over the landscape (Lacy, 2000). It is therefore important to understand the dynamics of populations (White *et al.*, 2007), and in particular the parameters that determine whether such populations are likely either to go extinct or to persist for extended periods (Griffen & Drake, 2008).

The most fundamental population demographic parameter is the number of individuals within a population (Lebreton *et al.*, 1992). A population is a group of individuals of the same species interacting within the same space (Tarsi & Tuff, 2012). The health and behaviour of the population is determined by the way the individuals interact with each other and with their surrounding environment (Snider & Brimlow, 2013). The population status can be determined by measuring principal determinants of population growth, such as size (Rai, 2003), density (Woolley *et al.*, 2009), fecundity (Knipe *et al.*, 2013), mortality (Law *et al.*, 2013), sex ratio (Mysterud *et al.*, 2000), and age structure (Mackey *et al.*, 2006).

Large populations are more likely to maintain genetic material, and, thus, generally have higher genetic diversity (Wright, 2005). Small populations are more vulnerable to extinction (Kani, 2011), and, therefore, the small-population paradigm deals with the effect of smallness on the persistence of a population (Caughley, 1994). Once the population becomes too small, processes that disproportionately influence the population are demographic stochasticity (the inevitable sampling variability in births and deaths - Braumann, 2010), genetic drift (the change in the gene pool of a small population - Kliman *et al.*, 2008), and inbreeding depression (the reduced biological fitness in a given population as a result of inbreeding, or breeding of related individuals - Charlesworth & Willis, 2009).

The genetic and demographic effects are magnified by environmental stochasticity e.g., annual variation in food (Pekkonen *et al.*, 2013), catastrophic events e.g., epidemics, floods (Lande, 1993), and interactions with other species, for example, competitors (Ferry *et al.*, 2016), predators (FitzGibbon & Lazarus, 1995), and diseases (Jolles *et al.*, 2006). These demographic, genetic, and environmental effects not only provide standardized methods for comparing populations and evaluating extinction risk (Caughley, 1994), but offer insight into the mechanisms regulating population declines (Di Fonzo *et al.*, 2016).

1.1 Population regulation

1.1.1 Density-dependent processes

Population regulation is an important process and arises as a result of potentially stabilizing density-dependent processes (Murdoch, 1994). In population ecology, density-dependent processes occur when population growth rates are regulated by the density of a population, for example, elephants, *Loxodonta africana* (Chamaillé-Jammes *et al.*, 2008), lions *Panthera leo,* (Trinkel *et al.*, 2010), and black rhinoceroses, *Diceros bicornis* (Greaver *et al.*, 2013). Most density-dependent factors, which are biological in nature (biotic) (Donkin, 2000), include predation (Plotz & Linklater, 2009), diseases (Jolles *et al.*, 2006), interspecific (Ferry *et al.*, 2016), and intraspecific competition (Breed *et al.*, 2013). Competition, for instance, is a fundamental force shaping population size and structure as a result of limited availability of resources (Gilad, 2008). Usually, the more dense a population is, the greater its mortality rate (Edwards & Edwards, 2011). For example, during intra- and interspecific competition, the reproductive rates of the individuals will usually be lower (Eberhardt, 2002), reducing their population’s rate of growth.

1.1.2 Density-independent processes

Density-independent regulation can be through factors that affect birth and death rates, such as abiotic factors (Reid *et al.,* 2007) for instance weather, natural disasters (Edwards & Edwards, 2011), pollution, and environmental factors (Freeman *et al.,* 2014b), such as severe weather and fire conditions (Strydom & Midzi, 2019). The abiotic factors are typically physical or chemical in nature, and influence the mortality of a population regardless of its density (Edwards & Edwards, 2011).

1.1.3 Mortality

Mortality is the measure of individual deaths in a population, and is measured in rates (Caughley, 1966), usually expressed as the number of individuals or the proportion of the population that dies over a given period (Tarsi & Tuff, 2012). Mortality rates are important for understanding mechanisms that affect the dynamics of wildlife populations, which is essential to manage populations effectively (Caughley, 1966; Raithel *et al.,* 2007). Understanding the factors that control the mortality rates of species in their natural environment is important for understanding the structure, population dynamics, and ecosystems (McCoy & Gillooly, 2008). To visualize mortality and fecundity within a population, conservationists create life tables (Wang *et al.*, 2017) to display age-specific statistical summaries of a population's survival patterns (Tarsi & Tuff, 2012). These statistical methods provide information about the mortality conditions (most notably the life expectancy) in the population.

1.1.4 Sociality & social issues

Social organization is defined by the size and composition of social groups and patterns of intergroup dispersal (Altizer *et al.*, 2003). Sociality in mammals is constrained by ecological (Kappeler *et al.*, 2013), evolutionary (Jones & Safi, 2011), and genetic (Charlesworth & Willis, 2009) factors. Variation in measures of fitness (i.e. survival and reproduction) has been linked to various aspects of sociality in animals, and variability in individual health and condition has been recognized as a key mediator of these relationships (Kappeler, 2015).

1.1.5 Dispersal and space use

To understand population dynamics, we must gain a thorough understanding of dispersal (Tesson & Edelaar, 2013) with an emphasis on space use of a population as well as habitat configuration (Dupré & Ehrlén, 2002) within which the population is found. The distribution of animals in space at one moment in time is the direct response of individuals to features of the environment, and to the presence or absence of other individuals of the species (Patton & Jones, 2008).

Dispersal is the movement of an animal from its home range to where it will potentially breed (Croteau, 2010). Adaptive dispersal (Duckworth, 2008) occurs in a population that is not dependent on density, where the drive for dispersal is low because adequate resources are available within the established range. Once the population density reaches a certain point it becomes beneficial to leave the established range in search of new habitat. This non-adaptive dispersal (Stenseth, 1983) occurs when animals are forced from established home ranges (Debeffe *et al.*, 2012) by social factors (Kappeler *et al.*, 2013) inherent in high density populations. For example dispersal of young males reduces competition for resources. The space use of a species or group (Williams & Lindell, 2019) is of great concern to managers because it provides valuable insight into the specific needs of an animal (Kernohan *et al.,* 2001). This information can be used in planning and conservation efforts (Williams & Lindell, 2019) to assist in the recovery of threatened and endangered species.

1.1.6 Management of populations

To ensure the continued survival of small populations, it is fundamental to understand the dynamics (White *et al.,* 2007), the causes of mortality (Law *et al*., 2013) and how natural selection shapes the life history of species (Sinclair, 2003). These concepts are important for wildlife managers to understand when making decisions affecting wildlife. Depending on the management objectives, direct manipulation of the animal population, such as removals of animals (Seddon *et al.,* 2014) to increase the growth and breeding success within a local population (Morgan, 2010), or translocation between reserves to achieve desired management results, such as genetic integrity (Milner *et al.,* 2006), is used to manage a population.

An increasing number of wildlife species are endangered because of overharvesting (Packer *et al.,* 2009), habitat destruction, pollution, poaching (le Roex & Ferreira, 2020), or a combination of these factors, and are increasingly managed within fenced sanctuaries (Western, 1989). Overharvesting, for instance, can occur as a result of poorly-regulated legal harvest (e.g. sport hunting; Packer *et al.,* 2009), subsistence removals (e.g. bush-meat snaring; Rogan *et al.,* 2017), population control strategies (e.g. culling; Rushton *et al.,* 2006), and illegal killing for profit (e.g. ivory poaching; Wittemyer *et al.,* 2014). Monitoring population declines is an especially important step in tackling biodiversity loss (Di Fonzo *et al.,* 2016), as severe population reductions act as a prelude to species extinction (Ceballos & Ehrlich, 2002; Collen *et al.,* 2009). Re-introductions are commonly used as a potentially powerful tool for ecological restoration and endangered species recovery (Van Wieren, 2006), to secure areas with suitable habitat within their former range (Adcock *et al.,* 1998). The ability to link certain factors with specific decline dynamics in an animal population is useful for management purposes, as it provides decision-makers with potential triggers upon which to base their conservation actions (Di Fonzo *et al.,* 2016).

1.2 Conservation of rhino species

1.2.1 Importance of conserving rhino species

Rhinoceroses, hereafter referred to as rhino, are considered an “umbrella species” (Foose *et al.,* 1995), and have a large impact on the ecosystems they live in (Owen-Smith, 1988). Efforts to protect ‘umbrella’ species such as rhino can also have positive effects on the conservation of other wildlife species (Caro, 2003). Some large animals influence their surroundings more than others. Elephants for instance are known as ecosystem engineers that affect the woody components of ecosystems, such as treefall rates, tree height (e.g. Asner & Levick, 2012) and woody species composition (O’Connor *et al.*, 2007). The white rhino, *Ceratotherium simum*, crops or ‘mows’ grasslands short (Owen-Smith, 1988) and hippopotamus, *Hippopotamus amphibius*, is known to create grazing lawns (Lock, 1972). Black rhinos, *Diceros bicornis*, function as ecosystem engineers by opening up thick understorey and, thereby, increasing landscape heterogeneity (Knight *et al.,* 2013). Removing rhinos from the ecosystem may thus lead to trophic cascades (Everatt *et al.,* 2016).

Black rhinos are presently listed as Critically Endangered at a global level (Emslie, 2020) whilst the white rhino is listed as Near Threatened, with one of its two subspecies, the Northern white rhino, listed as Critically Endangered and on the brink of extinction (IUCN, 2013). The world had an estimated 29 324 rhinos comprising five species made up of nine subspecies living in 14 countries by the end of 2015 (Emslie *et al.*, 2016). Approximately 85% of the global rhino population of ~29,000 is found in protected areas in Africa; ~20,000 are white rhinos and ~5,000 are black rhinos (Emslie *et al.*, 2016). Since 1960, the worldwide population of black rhino has declined by an estimated 98% (Adcock & Emslie, 2016).

Iconic animals, such as rhinos, are major attractions for tourists to South Africa (Lubbe *et al.*, 2017) and one of the 'Big Five' that functions as a flagship species (Home *et al.*, 2009), which forms the foundation of the wildlife tourism experience (Lubbe *et al.*, 2017). The conservation of these rare and charismatic animals also attracts donor as well as state support (Knight *et al*., 2013).

1.2.2 Threats to rhino conservation

The illegal demand for rhino horn and the subsequent poaching this generates continue to pose a serious threat to rhino populations worldwide (Amin *et al.*, 2006). Rhino horn is thought to be one of the most highly valued commodities on the planet (Hübschle, 2016a), and has been used in traditional medicines and as handles for ceremonial daggers (Emslie & Brooks, 1999), or as ornamentals related to status in the Far East (Biggs *et al.*, 2013). Poaching, extensive hunting (Emslie & Brooks, 1999), as well as loss of habitat by clearance of land for agriculture (Adcock & Emslie, 2016), have led to a rapid decline and near extinction. Rhinos, like other charismatic megaherbivores, require large areas to support viable populations (Amin *et al.*, 2006). However, wild black rhino populations are limited to protected areas which are often enclosed and limit migration (Landman & Kerley, 2013) or on private/community game farms or reserves (Emslie, 2012). The distribution of the black rhinos in particular, in South Africa is fragmented (Knight *et al.*, 2013).

1.2.3 Management and monitoring of rhinos

Decisions taken by conservationists concerning how to manage threatened species are essential to reducing extinction risk (Norris, 2004). Securing rhinos for instance through continued monitoring is a key factor that determines poaching rates elsewhere in Africa – more intensely monitored rhinos have lower poaching risks. This combination of protection and biological management (Guevara & Laborde, 2008), (translocations to keep established subpopulations productive whilst creating additional new subpopulations with the potential for growth) resulted in a rapid increase in numbers (Adcock & Emslie, 2016).

1.3 Black rhinos

Black rhinos are icons for international conservation (Freeman *et al.*, 2014b). They are elusive creatures that captivates many people as a charismatic reminder of prehistoric times (Hutchins & Kreger, 2006), and, in recent years, as an iconic species for conservation efforts (Janssens & Trouwborst, 2018). The black rhino is also commonly known as the "prehensile-lipped rhino" or "hooked-lip rhino" because the upper lip is adapted to browsing on herbs and shrubs (Hutchins & Kreger, 2006). They have a non-ruminant digestive system (Owen-Smith, 1988). Black rhinos are distinguished from white rhinos by a shorter head, a longer neck, smaller, rounded ears which has hairy fringes (Skinner & Chimimba, 2005), and a back which lacks the nuchal hump found in white rhinos (Milliken *et al*., 2009). The ears of rhino swivel independently and their elongated shape allows them to detect sounds in a wide arc (Dinerstein, 2011). The black rhino carries its head higher than the white rhino (Skinner & Chimimba, 2005). Black rhinos are smaller than white rhinos, and attain shoulder heights of up to 1.65 m (Owen-Smith, 1988) and can weigh as much as 1 000 kg (Skinner & Chimimba, 2005).

The horns of the black rhino are composed of a mass of tubular filaments which are similar to hair (Skinner & Chimimba, 2005). The horns grow from the skin and are not attached to the bone under the skin (Skinner & Chimimba, 2005). Black rhino skin is very thick and rough to the touch with sparse hairs that cannot be seen from a distance (Skinner & Smithers, 1990). Black rhinos suffer from skin lesions caused by filaria parasite *Stephanofilaria dinniki* (Kock & Kock, 1990). These lesions appear as black, blood-encrusted areas that ulcerate and haemorrhage (Skinner & Chimimba, 2005). The lesions appear on the skin behind the shoulders and may also appear on the chest, neck and forelegs (Skinner & Chimimba, 2005). Both flies and ticks are associated with the transmission of the parasite (Mutinda *et al.,* 2012). The lesions are not related to the health of the individual animal, as they have also been noted to occur on healthy animals (Skinner & Smithers, 1990).

Black rhinos have three toes on each foot, with broad, stout nails which mark clearly in the spoor (Skinner & Smithers, 1990); the front feet are larger than the back feet as it bears most of the animal's weight (particularly the shoulders, neck and head). The cushioned pads on the soles of the feet are rounded at the back and lack the indentation characteristic of the white rhino (Skinner & Smithers, 1990), which also assists with distinguishing spoor between the two species.

1.3.1 Taxonomy and distribution

Rhinos are considered biologically successful as a lineage because of their evolutionary persistence, and their widespread distribution (Dinerstein, 2011). The black rhino belongs to the Rhinocerotidae family, subfamily Dicerotinae (Owen-Smith, 1988). The three surviving sub-species of black rhino, *Diceros bicornis bicornis, D. b. michaeli* and *D. b. minor* occurred in much larger numbers over much of their former range - an estimated 100 000 in 1960 (Emslie *et al*. 2009). Until recently, the International Union for the Conservation of Nature and Natural Resources (IUCN) recognised four subspecies of black rhinos in Africa, but the recent extinction of the north-western black rhino, *D. b. longipes,* has, unfortunately, brought the number to three subspecies (Emslie, 2012).

The subspecies of black rhino are recognised by where they occur on the African continent (Fig. 1.1); the eastern *D. b. michaeli* (mainly in Kenya and Northern Tanzania with a small population in Addo Elephant National Park, South Africa, originating from Kenya), the south-western *D. b. bicornis* (mainly occurring in the Namibian desert areas), and the south-central *D. b. minor* (the bushveld group extending from KwaZulu-Natal, through Zimbabwe and Zambia into Tanzania) (Skinner & Smithers, 1990). The African Rhino Workshop, held in Cincinnati, October 1986, recommended that management programmes should attempt to maintain the integrity of these conservation units, i.e. they should not be allowed to interbreed (Brooks, 1989).

All populations of black rhinos are listed in Appendix I of the Convention on International Trade in Endangered Species and Wild Fauna and Flora (CITES). This study focuses on the south-central black rhino, *D. b. minor* subspecies, which occurs in Ithala Game Reserve, South Africa (the study area), and is listed as Critically Endangered on the IUCN Red List of Threatened Animals (Emslie, 2012).

1.3.2 Habitat, home range and behaviour

Black rhinos occur in a wide variety of habitats, from desert areas in Namibia, to wetter forested areas (Emslie, 2012). Black rhinos are selective in their use of habitat (Tatman *et al.,* 2000). Habitat selection is based on both the abiotic and biotic characteristics of a habitat (Warrick & Cypher, 1998). Abiotic factors include water availability, altitude, gradient, cover, and climate of an area (Reid *et al.,* 2007). Biotic factors include the distribution of food and the presence of competitors (Donkin, 2000). Black rhinos do not like steep areas, but will use these areas if it harbours good food or water, or if these resources lie beyond the steep areas (Brooks & Adcock, 1997). Another important habitat feature affecting area use appears to be absence of human disturbance (Tatman *et al.,* 2000)

The optimum habitat appears to be thick scrub and bushland, often with some woodland, which supports the highest densities (1.4 rhino/km^2, Goddard, 1970; 1.6 rhino/km^2, Conway & Goodman, 1989), and also nutrient-rich soils and in succulent valley bushveld areas (Emslie, 2012). The black rhino requires habitat that provides adequate shrubs and young trees up to 4 m height, including well developed woodland or thickets (Skinner & Smithers, 1990). Open grassland appears the least favourable habitat, supporting densities as low as 0.04 rhino/km^2 (Goddard, 1970).

Animals concentrate their movements within home ranges rather than wandering aimlessly (Spencer, 2012). Black rhinos, in particular, occupy a well-defined home range (Reid, 2004), although there may be considerable overlap of individual ranges (Tatman *et al.*, 2000). The daily activity of black rhinos is independent of environment (Ritchie, 1963), and entails travelling between feeding areas, to and from water, resting, and other maintenance behaviours such as drinking, wallowing, grooming, and social interactions (Owen-Smith, 1988; Hutchins & Kreger, 2006). Other comfort behaviours include scratching or rubbing the body against trees or other vegetation, which removes dead skin (Hutchins & Kreger, 2006). During the hottest parts of the day, black rhinos spend more time resting at bedding sites within their home ranges (Santymire *et al.*, 2012), under the shade of thickets or woodland (Skinner & Chimimba, 2005). Wallowing appears to be important in thermoregulation, repelling biting insects and external parasites, and protecting the skin from dehydration and sun (Hutchins & Kreger, 2006; Dinerstein, 2011).

Rhinos are known to frequently defecate in dung piles or middens (Hillman-Smith & Groves, 1994), and this habitual behaviour indicates an important role in intraspecific communication (Tatman *et al.*, 2000). The presence of fresh dung on the piles is thought to indicate to other rhinos “who” was in the area and “when” (Hillman-Smith & Groves, 1994). They also rely on vocalizations, urine, and scent to communicate with conspecifics (Dinerstein, 2011; Linklater *et al.*, 2013). Dinerstein (2011) highlights that body language is often the least common form of communication, because black rhinos possess acute senses of hearing and smell, but relatively poor eyesight. However, at close quarters it can be quite important in influencing outcomes of hostile encounters between males (Dinerstein, 2011).

1.3.3 Diet

Black rhinos are browsers mainly feeding on herbs, woody shrubs, and small trees (Hillman-Smith & Grove, 1994; Hutchins & Kreger, 2006). They obtain the majority of their food items from smaller plants (< 2.5m) (Kotze & Zacharias, 1993), and have a maximum reach of 1.5 m (Owen-Smith, 1988). Some grass is taken up, and succulent plants are often selected in the dry season (Mukinya, 1973). Kotze & Zacharias (1993) found *Vachellia nilotica, V. karroo*, and *Dichrostachys cinerea* contributed most to the black rhino diet in Ithala Game Reserve, South Africa, with *Cassine transvaalensis, Rhus guenzii*, and *V. gerrardii* the most preferred species. At Hluhluwe iMfolozi Park, South Africa, *V. gerrardii*, *V.senegalia*, and *V. borleae* make up the bulk of the black rhino diet (Skinner & Chimimba, 2005). In Augrabies Falls National Park, South Africa, species like *V. karroo* have preference values <1, but these species occur close to water, where they are encountered by rhinos feeding on their way to and from drinking water (Buk & Knight, 2012).

In most reserves, stem succulents like *Euphorbia* spp. are an important food source during the dry season (Skinner & Chimimba, 2005), whilst young *Spirostachys africana* trees form the dominant food item in the black rhino summer diet (Skinner & Chimimba, 2005). Black rhinos have been observed to select charred twigs after a burn (Hillman-Smith & Grove, 1994). Black rhinos prefer browsing on burnt trees because fire alters the smell and taste of twigs by denaturing the chemicals that inhibit digestion, and decreasing the physical defences used by the plants (Emslie & Adcock, 1994).

The degree of utilization of the different vegetation types by black rhinos in Ithala Game Reserve, South Africa, varied from no utilization in *Combretum apiculatum* sparse woodland to high in bottomland/scree slope forest, moist forest and *V. nilotica-V. karroo woodland* (Kotze & Zacharias, 1993). This suggests that black rhinos obtained more browse from the forest component of the moist forest *V. nilotica-V. karroo* woodland mosaic than from the open/sparse woodland component (Kotze & Zacharias, 1993). Kotze & Zacharias (1993), during a browse assessment, also observed that a large proportion of black rhino browsing occurred at forest margins.

1.3.4 Territorial and reproductive behaviour

Territorial behaviour may be defined as site dependent display behaviour, resulting in conspicuousness and avoidance of other similarly behaving individuals (Reid, 2004). It is indicated by the aversion of competing conspecifics from an area occupied by an individual, through explicit defence or advertisement (Adcock, 1994). The key difference between a home range and a territory is that territories rarely overlap to any extent (Eltringham, 1979).

Black rhinos primarily have a solitary lifestyle (Shrader & Owen-Smith, 2002), and adult males have strong territorial behaviour (Adcock, 1994). Territorial behaviour is of relevance to rhino population management because it sets a limit to the number of competing rhinos (mainly males) that can co-exist in a given reserve (Adcock, 1994). Black rhino males will sometimes display an aggressive ritual toward a potential rival through spraying repeatedly, scraping, trampling, and bashing bushes with their heads (Dinerstein, 2011).

All rhino species are polygamous and polyandrous, with both male and female seeking multiple mating partners (Owen-Smith, 2004). Rhino courtship can be prolonged and aggressive. During courtship the male rhino engage in mate guarding behaviour, following the female until she comes into full oestrus, and will tolerate close approach and physical contact with a male (Hutchins & Kreger, 2006). The pro-oestrus lasts six to seven days and is characterised by frequent tail–erecting by the female (Skinner & Chimimba, 2005). A female rhino may repeatedly drive the male away with mock charges and other defensive behaviours, until she is receptive (Hutchins & Kreger, 2006). Copulation occurs between two and seven times, with each copulation event lasting between 12 and 43 min (Skinner & Chimimba, 2005). The number of ejaculations per copulation event range from two in 2 min to nine in 43 min (Skinner & Chimimba, 2005).

Black rhinos have a 15-month gestation period, and age at first calving ranges from 6 to 9 years old (Alibhai *et al.*, 2001). Only one calf is born (Hillman-Smith & Grove, 1994). The calf is able to walk and suckle within 3 h of birth (Skinner & Chimimba, 2005). The intercalving interval (ICI), which is defined as the frequency distribution of observed intervals between calves (Adcock *et al.*, 1998), is usually 30 months (Owen-Smith, 1988).

1.4 History of black rhino conservation in South Africa

In South Africa, by 1930, only two relic-breeding black rhino populations remained in iMfolozi and uMkhuze Game Reserves (Emslie *et al.*, 2009). In an attempt to address the recovery of the critically endangered black rhino population in South Africa, (Brooks, 1989) compiled the conservation plan for the black rhinos in South Africa. Brooks & Adcock, (1997), updated the plan. The Rhino and Elephant Foundation and the Game Rangers Association (GRA) of South Africa, jointly convened a workshop in Skukuza, Kruger National Park, South Africa in 1988. The workshop highlighted the necessity for black rhino agencies to standardised monitoring and management according to the South African National Plan for black rhinos (De Graaff & Rautenbach, 1989).

Since 1995, when black rhino numbers at a continental level dropped to a low 2408 animals (Emslie, 2008), the population numbers increased, based on continental population estimates (revised every two years by range state updates), to about 6000 animals remaining globally (Emslie *et al.*, 2016). This continued increase in black rhino numbers on the continent resulted from the creation of new populations, and the increase in rhino range (Emslie *et al.*, 2009). A variety of conservation approaches, including increased investment in conservation programmes such as intensive rhino monitoring and law enforcement (Emslie, 2012), resulted in the stabilisation and partial recovery of populations in a number of countries.

A rating exercise was undertaken by the African Rhino Specialist Group in 1992, where it was agreed that the most relevant parameters on which to judge the conservation value of populations were population size, the significance of the population in conserving the relevant subspecies, and the likelihood of protection measures being effective. Two importance categories were recognised, namely “Key” [critically important] and “Important” [extremely valuable], and Ithala Game Reserve, hereafter Ithala, South Africa, was listed as containing a key black rhino population. Ithala’s black rhino population is important from a genetic point of view because of the large founder population size of 34. According to Brooks and Adcock (1997), populations with more than 20 founders will have reduced negative effects of genetic drift and inbreeding due to fitness and heterozygosity.

Ezemvelo KwaZulu Natal Wildlife (EKZNW) is mindful of its critical role in the conservation of the black rhino, and is guided by the biodiversity management plan for the black rhino in South Africa (Knight *et al.*, 2013), as well as the provincial strategy for the management of black rhino in

KwaZulu-Natal (Conway & Goodman, 2013). The strategic goals in the provincial plan are to increase the number of black rhinos in the province to at least 740 individuals by the end of 2022, to achieve an average of 0.25 births per adult female per annum (between 2013 and 2022), and to achieve a growth rate of 5% per annum over any 3-year cycle (Conway & Goodman, 2013).

One of the actions required to achieve these goals is to live remove individuals from populations that are greater than 70% of the estimated ecological carrying capacity, at a minimum rate of 5% up to a maximum of 8% per annum over any 3-year cycle (Conway & Goodman, 2013). The key constraint, however, is that there is little understanding of the drivers of black rhino dynamics. The species often does well after initial introduction, but subsequently has performance constraints (Brett, 1998). The performance of individual black rhino after translocation and release varies greatly (Adcock *et al.*, 1998). The mechanisms of these are either resource limitations, or social constraints. There is still much to learn about the details of black rhino social organization and behaviour, but this should be considered a key component when developing wildlife-management and conservation strategies (Hutchins & Kreger, 2006).

1.5 Black rhino monitoring through individual identification in Ithala Game Reserve

The entire adult black rhino population is individually marked and recognisable through unique ear notch patterns (Fig. 1.2), ear tears, or horn configurations (Brooks, 1989). Black rhinos at Ithala are routinely immobilized during notching operations, where small sections (usually in a small 'v' shape) is clipped from a rhino's ear or holes punched through the ear pinnae, to generate unique number combinations (Brooks, 1989) at different locations on the rhino’s ears. It is important that black rhinos within the same reserve receive a unique ear notch pattern (Brooks & Adcock, 1997). This allows the animal to be easily identified and monitored in the field. Each black rhino receives an individual number code, derived from the number of notches or holes cut in the ears, for instance the notching pattern in Fig. 1.3 illustrates number codes of 15 and 31 respectively.

In addition to notching, the staff at Ithala found that naming the rhinos helped maintain interest and motivation among staff. Calves were marked prior to them becoming independent from their mothers, but usually when they were between three and four years old. Until then, they were recognised through their association with individually marked females. This enabled the management staff to account for every individual in the population based on sightings alone.

Age classes were assigned to rhinos based on horn development and size of calves (Fig. 1.4) relative to adults (Adcock & Emslie, 2003). The sex of black rhinos in the field is determined by observing the external genitalia on the backside or underside area. If the individual's tales are lifted the vulva of the female and the flap of skin of the male can be noted (Adcock & Emslie, 2003).

1.6 Rationale for this study

The protected area where this study was conducted is Ithala Game Reserve in northern KwaZulu-Natal, South Africa, which contains an important donor black rhino population that forms part of the African Rhino Conservation Action Plan (Emslie & Brooks, 1999), and for the Black Rhino Range Expansion Programme (WWF, 2012). A black rhino population under suitable conditions (i.e. appropriate vegetation/habitat, adequate water supply, and rainfall) should have a growth rate of approximately 9% per year (du Toit, 2006), but should achieve at least a minimum of 5% per annum (du Toit, 2006; Goodman, 2013). As a donor population, Ithala management must ensure that these targets are achieved, but also be mindful that removals from the donor population must be such that they do not reduce the population's productivity (Emslie & du Toit, 2006), or that the species does not become locally extinct (du Toit, 2006). The population should be maintained at a level below which density dependent effects (Hrabar & du Toit, 2005) would occur. Consequently, it is important to understand the factors which can affect the population productivity (Hrabar & du Toit, 2005).

The main aim of my study was to evaluate whether the selective harvesting technique used by Ithala management is optimal for population persistence, by evaluating whether there are density-dependent effects or social interactions constraining the growth of the population, and to suggest possible alternative strategies to increase population performance. I also investigated the concerns raised by Ithala management regarding the effect of repeated removals on the populations' performance.

I expect an eruptive population growth rate, but assume that there are some density dependence effects limiting vital rates of the population. Vital rates such as the age at sexual maturity, conception rate, gestation length, and intercalving interval all influence fecundity, growth potential, and generational time (Festa-Bianchet *et al.*, 1998; Gaillard *et al.*, 2000). I hypothesize that social effects as a result of density may be constraining or regulating the Ithala black rhino population dynamics, through effects on survival.

1.7 Overview and main objectives of the thesis

The thesis is structured as introductory material (Chapters 1), followed by two data chapters structured as papers for peer-review publication (Chapters 2 and 3), and a concluding discussion (Chapter 4). To prevent repetition, I present a full list of references cited in this thesis. Chapter 2 aims to evaluate if density and growth of the Ithala black rhino population are indirectly driven by periodic translocations from the population. Chapter 3 aims to evaluate the influence of environmental, social, or management drivers, on mortality of black rhinos.

For me to evaluate the predictions above I set up eight specific objectives to:

(i) Determine the population size, birth and growth rate for each year;

(ii) Assess the influence of a range of factors on birth rate, including rainfall, population density, sex and age structure;

(iii) Determine the age-specific probabilities of survival of the population;

(iv) Assess if there are any density-dependent effects constraining the population growth;

(v) Create a density map representing high use areas within the reserve of all black rhinos;

(vi) Map the different individual distribution or occurrence areas of male and female black rhinos;

(vii) Compare the distribution of overlapping black rhino occurrence areas over the entire study period, to determine a correlation between probability of encounter and mortality;

(viii) Determine if a mortality occurrence was associated with (a) social factors (density, overlap of distribution areas), (b) environmental factors (distance to water, slope, Enhanced Vegetation Index (EVI), or (c) management intervention through live removal of black rhino individuals from the reserve.

Finally, in Chapter 4, I discuss possible management recommendations which could assist with ensuring the persistence of the Ithala black rhino population.

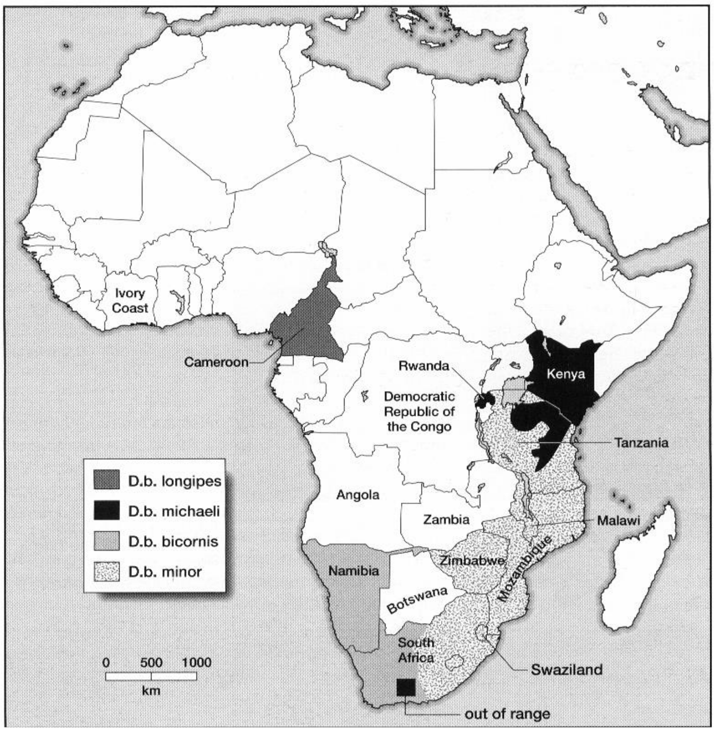

Fig. 1.1 Distribution of the four black rhino subspecies in 1999, Adapted from Emslie and Brooks (1999). *Diceros bicornis longipes* has since been listed as extinct in 2011 (Emslie, 2012)

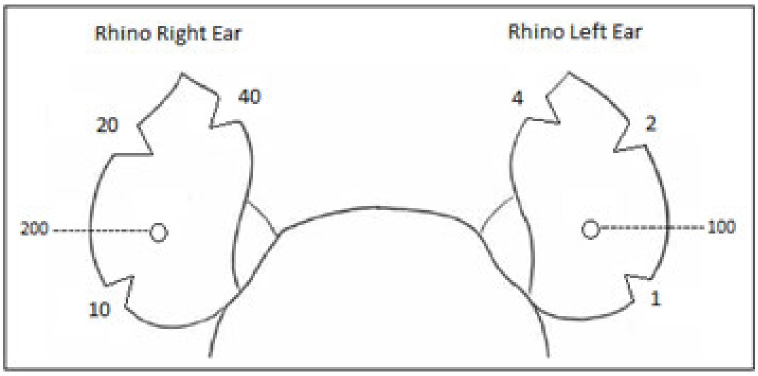

Fig. 1.2 Picture of black rhino ears showing the location and numbering sequence for notches (modified from Brooks, 1989).

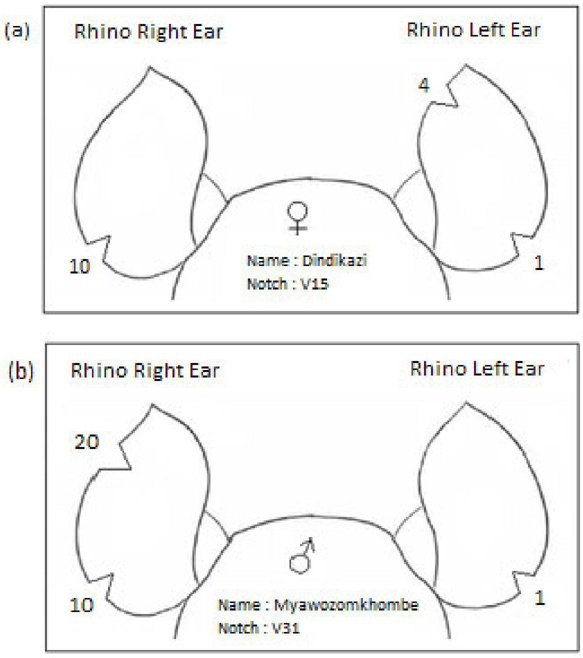

Fig. 1.3 Illustrates the "V" notch sequence for black rhino at Ithala for (a) female named "Dindikazi" who has notch number 15 and (b) male named "Nyawozomkhombe" with notch number 31.

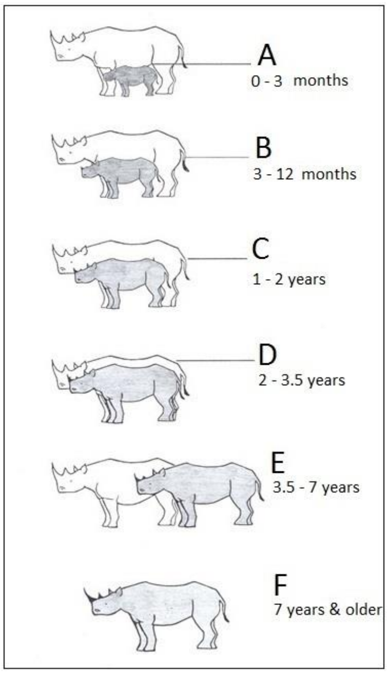

Fig. 1.4 Standardised black rhino age classes used in Ithala Game Reserve

CHAPTER 2

Density-dependent regulation of the critically endangered black rhinoceros population in Ithala Game Reserve

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Abstract

Ensuring the persistence of populations of endangered species requires an understanding of, and response to, the causes of population declines. Species occurring in small populations are vulnerable to stochastic problems that are environmental, demographic, or genetic in nature and can reduce survival as much as the deterministic threats of habitat degradation. Critically endangered black rhinoceros, *Diceros bicornis,* populations declined throughout Africa since 1960, with numbers steadily increasing at a continental level, but remaining lower than three generations ago. However, size, demographics, trends, and factors affecting these, are poorly known. We used 18 years (1990–2008) of long-term sightings data from Ithala Game Reserve, KwaZulu-Natal, South Africa, to determine population estimates, growth rate and fecundity over time, as well as sex and age structure and age-specific probabilities of survival. Calf survivorship between the ages of 0 and 1 year was 74% for females and 94% for males. Age-specific survivorship for both sexes was significantly higher from yearling to subadult age-classes (1–6 years) than for adults (7–30 years). The most frequent cause of mortality was attributed to unknown causes while fighting injuries was recorded as the second most common cause of mortality, particularly among subadult and adult males. There was no significant difference in the sex ratios at birth, although the proportion of females in the population was 0.58. There was strong evidence for density-dependent regulation, with density in conception year a key driver of population performance (birth rate). The population does not appear to be at ecological carrying capacity; however, social effects are delaying conception. To mitigate density-dependent social effects, we recommend an adaptive management strategy of pre-selecting individuals for removal from the reserve, so as to maintain stability in the social organization of the population.

Keywords: birth rate, *Diceros bicornis*, Ithala Game Reserve, population estimates, survivorship.

2.1 Introduction

Persistence of species occurring in small populations is often at risk from unpredictable changes in birth and death rates (Akçakaya, 2002), random variations in sex ratios (Mysterud *et al*., 2000), environmental fluctuations (Benton & Grant, 1999), and random genetic processes (Shaffer, 1981). Small populations are more vulnerable to an extinction vortex when stochastic (Lande, 1993) events exacerbate each other at low population sizes (Caughley, 1994). For instance, a rise in the frequency of mating between close relatives leads to reduced heterozygosity (Harmon & Braude, 2010) that results in reduced fecundity (Lande, 1988) and increased mortality (Saether & Heim, 1993). This causes the population to become smaller yet. These events and the loss of evolutionary adaptability of the species to environmental changes (Lande, 1988), may ultimately result in its extinction (Gilpin & Soule, 1986).

The recovery or persistence of small populations (Stacey & Taper, 1992), and hence typically rare species (Caughley, 1994) cannot occur without considering factors affecting the adaptability (Willi

& Hoffmann, 2008), demography (Nilsson & Ericson, 1997) and genetic traits (Ashley *et al.*, 1990) of populations. This remains challenging because stochastic (Akçakaya, 2002) rather than deterministic (Benton & Grant, 1999) drivers often influence demographics and their effects remain uncertain.

Intensive management often attempts to overcome stochasticity by translocating rare and endangered species (Van Houtan *et al.*, 2009) to establish self-sustaining populations that require minimal long-term management (IUCN, 1998). The critically endangered black rhinoceros, *Diceros bicornis*, (Emslie, 2012), hereafter referred to as black rhino, is a case example where translocations into, and then subsequently out from, new populations, form part of key tactical strategies aimed at improving and maintaining regional black rhino population growth (Brett & Adcock, 2002).

However, a trade-off exists in establishing a balance between removals from source populations and introductions into new founder populations. This trade-off can be risky when exploiting relatively small populations to found new populations (Swart *et al.*, 1990). A range of species recovery programmes (Griffith *et al*., 1989) and conservation strategies exist for threatened species. However, conservationists seldom assess the success of strategies using robust information (Gusset *et al*., 2008). Erratic variance in growth (Caughley, 1994), biased sex ratios (Berkeley & Linklater, 2010), environmental changes (Schroder *et al*., 2005), restricted dispersal (Rachlow & Berger, 1998), disease effects (Jolles *et al.*, 2006), and genetic problems, such as inbreeding depression (Gakahu, 1989), may weaken the ability of the population to recruit to a safe number again (Caughley, 1994).

Ideally, removals from the source population should be such that they do not reduce that population's productivity (Emslie & du Toit, 2006), and should maintain the population at a level below which density dependent effects (Hrabar & du Toit, 2005) would occur. Conversely, it may take some time for newly established populations to develop as future source populations. Founder effects and genetic drift can reduce the genetic diversity of the introduced population, which may reduce the potential for the introduced population to adapt (Kliber & Eckert, 2005) to the new environment.

In order to evaluate some of the potential constraints in small, managed, black rhino populations, we examine Ithala Game Reserve in northern KwaZulu- Natal, South Africa, an important donor population that forms part of the African Rhino Conservation Action Plan (Emslie & Brooks, 1999).

Our aim was to evaluate whether the selective harvesting technique used up to now is optimal, by evaluating whether there are density-dependent effects constraining the growth of the population. More specifically, the objectives were to: (i) Determine the population size and growth rate for each year; (ii) Calculate the birth rate for each year; (iii) Assess the influence of a range of factors on birth rate, including rainfall, population density, sex and age structure; (iv) Determine the age-specific probabilities of survival of the population; and (v) Assess if there are any density-dependent effects constraining the population growth. Through identification of these, or other key constraints on productivity, we may provide guidelines as to which variables the population is most sensitive to and hence how management can manipulate those for most effective persistence and translocations.

2.2. Methods

Study area

Ithala Game Reserve (hereafter referred to as Ithala) is 297 km² and situated in northern KwaZulu-Natal, South Africa (27°30’S, 31°25’E) (Fig. 2.1). Elevation ranges from 350 m.a.s.l. on the Pongola River, which forms the northern boundary, to 1550 m.a.s.l. on the southern escarpment plateau. Long-term mean annual rainfall is 791 mm, falling mainly during the summer (October to March). Summers are warm to hot (daily average of 18 – 30 °C), with winters being warm to mild (15 – 25

°C) (Porter, 1983). Frosts do not occur, but low (near freezing) temperatures occur during cold windy spells on winter nights.

Five tributaries of the Pongola River flow through the reserve, resulting in topography varying from undulating grassland to cliff faces (Wiseman *et al.*, 2004). Factors such as slope and abundance of paths, which affect the accessibility of a given area, have an important influence on the degree to which certain areas of the reserve are utilized by black rhino (Kotze & Zacharias, 1993). Sourveld vegetation occurs on steeper slopes, with sweetveld on dolerite ridge tops (Brooks & Adcock 1997). *Acacia karroo* and *Acacia nilotica* woodland exists primarily on old croplands (Kotze & Zacharias 1993). Prior to proclamation as a game reserve in 1973 (KwaZulu-Natal Nature Conservation Management Act, 1997), the land was used for agricultural purposes (Wiseman *et al.*, 2004). Since proclamation as a reserve, various browsers and mixed feeders were introduced (Wiseman *et al.*, 2004).

Ithala black rhino monitoring history

The introduction of 34 black rhino into Ithala took place between 1973 and 1985. This formed part of the efforts of the 'Natal Parks Board' (now Ezemvelo KZN Wildlife) directed at expanding the donor rhino populations of Hluhluwe iMfolozi Park and Mkhuze Game Reserve to other potential rhino reserves in KwaZulu-Natal (Henwood, 1989).

The entire adult black rhino population was individually marked and recognisable through unique ear notch patterns, ear tears or horn configurations (Brooks, 1989). Calves were marked prior to them becoming independent from their mothers, but usually when they were between three and four years old. Until then, they were recognized through their association with individually marked females.

This enabled the management staff to account for every individual in the population based on sightings alone.

Sightings from daily field ranger patrols in the reserve formed part of the intensive monitoring programme. Field rangers patrolled various areas of the reserve on a daily basis and recorded particulars of each rhino in their field data booklets. They reported the sightings information to the section rangers who maintained files on the life history of each animal. At monthly reserve meetings, a summary of the rhino sightings of the month were presented to the reserve manager and any changes to the population were discussed and updated. Sighting records were captured in the Animal Population Management Database (maintained by Ithala research staff) including information such as birth date (if known), sightings, mortalities, translocations and calving history (if it is female).

Age-classes were assigned to rhinos based on horn development and size of calves relative to adults (following Hitchins, 1970; refined by Emslie *et al.*, 1995). Data of the introductions to the Ithala black rhino population (*n* = 34) from 1973 to 1985 included the sex and ages of introduced individuals (females: *n* = 17; males: *n* = 16; unknown sex: *n* = 1). Historical paper records were filed (G. Root, pers. comm., 2008), and in later years imported to the Animal Population Management Database. There have been no further introductions to the population since 1985. In 1990, the start of the study period, the black rhino population consisted of 35 adults (males: *n* = 16; females: *n* = 19), nine subadults (males: *n* = 6; females: *n* = 3), one yearling (males: *n* = 1; females: *n* = 0) and one juvenile (males: *n* = 1; females: *n* = 0). During 11 January 1991 to 7 October 2008, a total of 39 black rhino (males: *n* = 23; females: *n* = 16) were successfully removed from Ithala.

The total population in 2008 consisted of 23 adults (males: *n* = 8; females: *n* = 15), nine subadults (males: *n* = 6; females: *n* = 3), eight yearlings (males: *n* = 2; females: *n* = 6), and three juveniles (males: *n* = 2; females: *n* = 1).

Data analysis

Prior to 1990, historical records were incomplete – search effort was low and inconsistent. We collated 7363 sighting records from 1990 to 2008, but after removal of incomplete sightings and duplicate entries, our cleaned dataset totalled 7046 sightings of 123 identifiable individuals. The sightings records contained detailed information of births, calves that became independent of their mothers, known mortalities, one dead and several live removals.

We estimated population size using the minimum number alive per year (White *et al.*, 1982). This was facilitated by the process of tracking an individual's life history. We calculated historical annual population growth rates $r = \ln(N_{t+1}) - \ln(N_t - N_{r,t\rightarrow t+1})$ where N_{t+1} is the population estimate for the subsequent year; Nt the population estimate for the current year and $N_{r,t\rightarrow t+1}$ the number of rhino removed during the current year (adapted from Caughley, 1977).

We obtained detailed records of mother–calf relationships with accurate age estimates of offspring since 1990. Age at sexual maturity was the mean age at which females in the population gave birth for the first time. We used the weighted average function to calculate the average calving interval (average number of years between consecutive births for each rhino female) from the inter-calf intervals of all females ($n = 16$) with more than one calf. We determined the mean birth rate as the number of calves born in the year, divided by the number of adult females (≥7 years old) at the end of that year.

We used the chi-squared function to test for disparities in the sex ratios. To determine the peak birth events we used the detailed records of mother–calf relationships (1990–2008) which details the spread of birth dates in the population per annum. We used a model selection approach (Johnson &

Omland, 2004) to assess influences on birth rates, and included the effect of rainfall and population density on birth rate.

We obtained rainfall records from the Thalu field office at Ithala, and used the monthly rainfall data to distinguish between wet and dry seasons. This enabled us to determine if the variability in birth rate was associated with population density, rainfall, or both. Rainfall in this case served as an indicator of resource quality (Bourgarel *et al.*, 2002).

We ran separate models for each of the peak birth months of March, April, May and July and also combined these representing alternative hypotheses for the effects on birth rate as follows: (i) R_{15}: Rainfall 15 months before the birth event; (ii) R_{27}: Rainfall 27 months before the birth event; (iii) D_c: Population density in the conception year; and (iv) D_b: Population density in the birth year. We then used Akaike's Information Criterion for small sample sizes (AIC_c) to rank models for each peak birth month from the most- to the least-supported model, given the data. We calculated the difference between the lowest-observed AIC value and the value for the current model (AIC_i), and Akaike weights (w_i) as measures of model support (Johnson & Omland 2004) where the estimated best model had an $\Delta AIC_c = 0$.

The ages of rhino born on the reserve, especially since 1992, are known within 1–4 weeks. We used Analyses of Variance (ANOVA) to determine any significant variability in the sex and age structure of the black rhino population at Ithala for each year. Four age-classes were distinguished, namely: juvenile (<1 year), yearling (1–2 years), sub-adult (2 to <7 years), and adult (≥7 years).

We then explored age- and sex-specific probabilities of survival by constructing a life table (Caughley, 1977) of every age-class, the number of deaths, the survivors remaining and the rate of mortality where: (i)The age at the beginning of an interval, symbolized x; (ii) f_x is the number of animals aged x in the population; (iii) l_x gives the probability at birth of an individual to survive to any age x and is termed 'survivorship' or simply 'survival'; (iv) Mortality (d_x) is the probability of dying during the age interval x, $x + 1$.This is the frequency of mortality calculated as the difference between two consecutive values of l_x with use of the following formula: $d_\mathrm{x} = l_\mathrm{x} - l_{x+1}$; (v) We used the ratio d_x/l_x to estimate the age-specific mortality rate q_x; and (vi) p_x is the survival rate of a proportion of animals alive at age x that survive to age $x + 1$.

The proportion of individuals in age-classes affects the demographic parameters (Chung, 1994). A life table articulates the patterns of changing mortality rates with age, which is a concise summary of certain vital statistics of a population (Deevey, 1947).

We used a two-tailed *t*-test to initially compare survivorship (the probability at birth of an individual to survive to any age x), and survival rate (the proportion of animals alive at age x that survive to age $x + 1$), of males and females of all age-classes in the population. Given that we used the mean and standard deviation, we applied the norm inverse function to extract random values from the sex-specific survival distribution.

To ascertain the fraction of individuals that survive to reproductive maturity, we used a two-tailed *t*-test assuming unequal variances to compare survival rate of only the juvenile to subadult males and females. To determine if survival of adults affects the fitness of the population, we used a two-tailed *t*-test assuming unequal variances to compare survival rate of only adult males and females.

2.3 Results

Since introductions started during 1973, there was a steady increase in population size, with the highest estimate (n = 53) reached in 1997. The observed population estimates (Fig. 2.2a) began to stabilize primarily because of the inception of the harvesting strategy in 1998, when 11 black rhino were removed from the population, the largest annual translocation operation from Ithala to date.

Population growth rates, corrected for the effects of removals and introductions, were negatively associated with population density ($F_{1,16}$ = 13.76, P = 0.01, r^2 = 0.46) (Fig. 2.2b). The average growth rate was 4.9% from 1990 to 2008. The mean birth rate (Fig. 2.2c) over the study period was 0.12, but this increased significantly over time ($F_{1,17}$ = 8.23, P = 0.01, r^2 = 0.33). The estimated age at first calving for the Ithala black rhino females was 6.5 ± SE 0.42 years (n = 18), with an average inter-calving interval of 3.2 ± SE 0.04 years (n = 61).

There was no significant difference in the sex ratio at birth ($X^2_{0.54,1}$ = 0.362, P = 0.55). Population density in the conception year D_c was consistently included as a variable in the most likely model explaining variation in birth rates (Table 2.1). Births were mostly explained by population density at conception, and the lag effect from rainfall on birth rate, particularly where we observed peaks in births (Fig. 2.3) as a secondary variable.

Ithala black rhino have produced 59 females. Of these, 22 have become reproductive and calved successfully while the remaining 37 consisted of non-reproductive females known to have died (n = 12), been translocated (n = 11), or were still too young (in 2008, n = 14) to reproduce. The female population (in 2008, n = 25) consisted of 15 reproductive females of seven years and older, while the male population (in 2008, n = 18) had eight sexually mature males (Fig. 2.4).

There was a significant change in the sex and age structure of the population over time, with a significant decrease in both male ($F_{1,\ 17}$ = 40.6, P = 0.01), and female ($F_{1,\ 17}$ = 12.8, P = 0.01) individuals >7 years over time (Fig. 2.5).

Forty-eight black rhino mortalities were recorded from 1990 to 2008 (Fig. 2.6), with juveniles (<1 year) (n = 8), yearlings (1–2 years) (n = 4), sub-adults (2 to <7 years) (n = 14), and adults (≥7 years) (n = 22) dying. The most frequent cause of death for adults were recorded as ‘unknown’ (n = 11) and old age (n = 5), while juvenile mortalities were mostly attributed to exposure or cold (n = 3). Fighting injuries were a common cause of death for sub-adult to adult males (n = 5) and females (n = 1). A fighting injury was also recorded for a female (n = 1) in the yearling age-class. Cause of death was established through post mortems by the wildlife veterinarian where possible, and in some cases the injuries were so severe that mortality could only be attributed as fighting injuries.

Analysis of age-specific survivorship (l_x) for males and females (Fig. 2.7) indicated a significantly higher survivorship from yearling to sub-adult age-class (1–6 years) (t = −3.53, d.f. = 5, P = 0.01) than for adults (7–30 years) (t = 5.31, d.f. = 33, P = 7.279). The mean sex-specific survival (Table 4.2) was significantly different for females (87%) than males (95%) in the 0–1 year age-class (t = −2.70, d.f. = 20, P = 0.01). However, in the 5–6-year-old age-class, although not significantly different, subadult males, had lower survival (92%) than females (100%) (t = 5.37, d.f. = 19, P = 3.43)

2.4 Discussion

The Ithala black rhino population is relatively young, with the older individuals all <30 years. Although there were records of animals dying from old age, these were very few and we could not determine natural senescence, but would expect lower senescence mortality than in a population with an older age structure (Mackey *et al.,* 2006). One would therefore expect an eruptive population growth rate (Caughley, 1994), which should continue in the short and medium-term while the population converges to stable-state distribution (Slotow *et al*., 2008).

However, the growth rate was relatively low at <5%, with a density-related effect that is constraining conception. The birth rate was driven by population density at conception, and rainfall as a secondary variable. At Ithala, reducing the density increased population growth rate by releasing vital rates from density-dependent limitations, thereby maximizing reproductive potential (Slotow *et al.,* 2005). The population is not acting in an eruptive manner because of the density-dependence through either resource limitation or social effects.

Density-dependence because of resource depletion should first decrease juvenile survival, then decrease reproductive rates, and finally decrease adult survival (Eberhardt, 2002). The demographic consequences of density-dependence include depressed female conception, increased interval between births, changes in sex ratios at birth, decreased juvenile survival, and changes in age-specific mortality (Mysterud *et al.,* 2000; Wittemyer *et al.*, 2007; van Aarde *et al.,* 2008; Bonenfant *et al.,* 2009).

Reproductive performance is also density dependent (Albon *et al.,* 1983).The age at first calving increases under conditions of resource limitations (e.g. Owen-Smith, 1990) because the onset of puberty is dependent on body mass (Hamilton & Blaxter, 1980). Black rhino have a 15-month gestation period and the average age at first calving has been reported as 6–9 years of age (Alibhai *et al.,* 2001; Okita-Ouma, 2004). In Ithala, the average age at first calving was 6.5 years, which is towards the lower end of the scale for this species. This implies that age at first calving is not a constraint on growth, and implies that resources are not the key constraint.

Although changes in sex ratios at birth have been attributed to density-dependence (Mysterud *et al.*, 2000), we found no significant difference in the sex ratios at birth. Selective removals favouring males for translocation by Ithala management (males n = 23; females *n* = 16) and higher mortalities in male (*n* = 23) than female (*n* = 14) sexes, therefore account for the significant decrease in male individuals over time. Small populations with high proportions of sexually mature females enhance reproductive potential (Slotow *et al*., 2005).

Lengthened inter-calving intervals (Laws *et al.*, 1975) are also demographic consequences of density dependence, with high densities resulting in an increase in the time between calves (Rachlow & Berger, 1998). The average inter-calving interval of 3.2 years (38 months) for the Ithala population may be compared with the 3.16 years (38 months) reported by Okita-Ouma (2004), but is shorter than the 3.35 years (40.3 months) reported by Alibhai *et al.*, (2001). The shorter interval between successive calves, along with the young age of first reproduction, implies that the density-dependent constraint is unlikely to be a resource limitation.

In the Ithala population, the cause of mortality for all age-classes was mostly recorded as ‘unknown’ where it could not be determined what the animals had died from or the carcasses were too old in order to carry out post mortems. However, in keeping with Emslie and du Toit (2006) our data indicated that fighting injuries were the second most common cause of mortality, particularly among sub-adult to adult males, possibly because of young dispersing males encountering older or territorial males more frequently. Adult males tend to be solitary and aggressive (Kock *et al.,* 1999), and the heightened competition between males competing for territories and mating possibilities (FitzGibbon & Lazarus, 1995) increases mortality rates.

Variability in juvenile survival is more sensitive to density-dependence (Gaillard *et al.,* 2000). The data from this study indicated a major effect on the suckling calves (0–1 year) (*n* = 12), but once suckling discontinued and the calves were past a certain age, that is, 1 year, they tended to perform well. The cause of mortalities of juveniles was attributed mostly to exposure or cold, rather than malnutrition. Once individuals reached adulthood, survival was high.

Even so, the results suggest that there might be disruption of the social system or social carrying capacity that constrains the Ithala population size. The effects of social interactions and how they influence demographic processes (Ishibashi *et al.,* 1998) are well known. Social interactions include intense competition among males (Archie *et al.,* 2007) for space to establish territories and, in accordance with Reid *et al.,* (2007), an imbalanced social structure might cause a reduction in productivity because more energy is exhausted in maintaining home ranges, rather than in reproduction. Sizes of home ranges are also strongly influenced by social interactions (Lent & Fike, 2003).

Black rhino in particular require protracted social interactions in order to breed (Emslie & du Toit, 2006), and are selective in their choice of habitat (Reid *et al.,* 2007). However, the spatial restrictions in smaller reserves (Rachlow & Berger, 1998) such as Ithala impose higher population densities and force high rates of association upon black rhinos (Linklater & Swaisgood, 2008). Increased social pressure along with territorial behaviour leads to increased fighting and higher levels of mortality (Adcock, 1994; Adcock *et al.,* 1998; Linklater *et al.,* 2010). The mechanism of density dependence is thus through mortality that is associated with increased social interactions rather than resource limitations. However, the challenge remains the maintenance of maximum reproductive performance while keeping the Ithala black rhino population size viable (Rai, 2003) to evade stochastic drivers which influence demographics.

In order to maximize the black rhino population performance, the rhino strategy for Ithala follows the guidelines and principles set in the conservation plan for black rhino (Brooks & Adcock, 1997), which requires a minimum acceptable population growth rate of 5% (Goodman, 2001).The plan prescribes a set harvesting rate of at least 5% per annum over time but not more than 8% (Emslie, 2001). In keeping with Brooks and Adcock (1997), the Ithala black rhino population is maintained at its estimated Maximum Productivity Carrying Capacity (MPCC) (Okita-Ouma *et al.*, 2008), that is, 75% of the Ecological Carrying Capacity (ECC), in order to maintain the population growth.

The appropriateness of using the carrying capacity concept in particular is not only challenged by our data, but also by other authors (O'Connor *et al.*, 2007; Morgan *et al.*, 2009). Decision-making around elephant numbers for instance, have moved away from single, constant maximum density-based approach to one using indicators from the environment (Slotow *et al.*, 2008). Given the age at first reproduction and inter-calving data, it does not appear that the Ithala population is at ecological carrying capacity, but that social effects are primarily disrupting the conception of females and affecting survival rates of some age-classes.

This is the likely explanation of how density dependence is limiting the population, despite the fact that it is young and should be eruptive. This also clarifies why the population is performing below the optimum growth rate, and is at the bottom-end of the desired 5–8% growth rate. It implies that management has to think carefully about how to manage the social factors (Lent & Fike, 2003) that are causing density dependence in a source population such as Ithala and this may improve the strategic and tactical planning for endangered species protection (Belovsky *et al.*, 1994).

The findings of our analysis have important implications for black rhino population management at Ithala. It highlights that the density and growth of the Ithala black rhino population are indirectly driven by periodic translocations from the population. Currently this option may ensure the persistence (Rai, 2003) of the Ithala population by impeding social interactions and injuries, particularly among males. Nonetheless, careful monitoring to enhance understanding of social factors (Van Dyk & Slotow, 2003) particularly black rhino male behaviour should be intensified in order to allow strategic translocation of individuals in such a way that the density dependent effects are mitigated.

Our study highlights the challenges associated with managing small populations, especially in the context of many threatened large mammal species that have social systems that may be unintentionally impacted by management interventions. We emphasize that, in this context, it is essential that detailed information of the focal population is known, and that management evaluates, including through scenarios, unintended risks of interventions to population persistence or growth. Any intervention would need to be nuanced in intensity across both space and time, based on this understanding, to mitigate risk and unintended consequences.

Table 2.1 The effect of rainfall and population density on birth rate in peak birth months March, April, May, and July.

Model	n	K	Fstat	r^2	ΔAIC_c	W_i	n	K	Fstat	r^2	ΔAIC_c	W_i
		March Births							April Births			
R15	10	1	0.3	0.036	8.682	0.009	5	1	0.086	0.028	0.334	0.225
R27	10	1	2.373	0.229	7.713	0.015	5	1	0.599	0.167	**0**	**0.266**
Dc	10	1	2.373	0.52	5.651	0.042	5	1	0.279	0.085	0.202	0.24
Db	10	1	0.056	0.007	8.811	0.009	5	1	0.018	0.006	0.383	0.22
R_{15} x D_c	10	2	4.621	0.569	8.401	0.011	5	2	0.208	0.172	6.652	0.01
R_{15} x D_b	10	2	0.134	0.037	11.89	0.002	5	2	0.218	0.179	6.635	0.01
R_{27} x D_c	10	2	4.702	0.573	8.358	0.011	5	2	1.305	0.566	5.248	0.019
R_{27} x D_b	10	2	1.408	0.287	10.59	0.004	5	2	0.355	0.262	6.403	0.011
R_{15} x D_c + D_b	10	3	84.14	0.977	**0**	**0.705**	5	3	0.995	69.67	15.45	1E-04
R_{27} x D_c + D_b	10	3	41.03	0.954	3.014	0.156	5	3	1.998	0.857	22.84	3E-06
R_{15} x R_{27} x D_c + D_b	10	4	54.33	0.978	5.862	0.038	5§	4				
		May Births							July Births			
R15	6	1	0.053	0.013	1.331	0.202	9	1	0.006	9E-04	2.463	0.11
R27	6	1	9E-06	2E-06	1.365	0.199	9	1	1.619	0.188	1.654	0.164
Dc	6	1	2.754	0.408	**0**	**0.393**	9	1	6.159	0.468	**0**	**0.376**
Db	6	1	0.079	0.019	1.314	0.204	9	1	0.198	0.027	2.358	0.116
R_{15} x D_c	6	2	1.585	0.514	13.53	5E-04	9	2	3.186	0.515	3.067	0.081
R_{15} x D_b	6	2	0.093	0.058	13.54	5E-04	9	2	0.086	0.028	5.785	0.021
R_{27} x D_c	6	2	1.529	0.505	13.53	5E-04	9	2	2.783	0.481	3.33	0.071
R_{27} x D_b	6	2	0.044	0.028	13.54	5E-04	9	2	0.703	0.19	5.073	0.03
R_{15} x D_c + D_b	6	3	110.5	0.994	16.53	1E-04	9	3	3.534	0.68	6.248	0.017
R_{27} x D_c + D_b	6	3	80.78	0.992	16.53	1E-04	9	3	3.355	0.668	6.385	0.015
R_{15} x R_{27} x D_c + D_b	6	4	41.44	0.994	20.2	2E-05	9	4	2.123	0.68	13.44	5E-04

§Too few parameters for the sample size. The number of parameters (K) in each model includes the intercept and each explanatory variable: R_{15} (Rainfall 15 months before the birth event); R_{27} (Rainfall 27 months before the birth event); D_c (Density in the conception year); D_b (Density in the birth year). Models with a lower ΔAIC_c and a greater Akaike weight (W_i,) have more support. Values for the model with the most support are in bold. AIC, Akaike's Information Criterion

Table 2.2 Sex specific survival for the Ithala black rhino population.

Age in years	Females (SD)	Males (SD)
0 - 1	87% (0.18)	95% (0.02)
2 - 4	96% (0.04)	94% (0.06)
5 - 6	100% (0)	92% (0.12)
Adults	97% (0.07)	94% (0.11)

Numbers in brackets are standard deviations (SD) of the mean

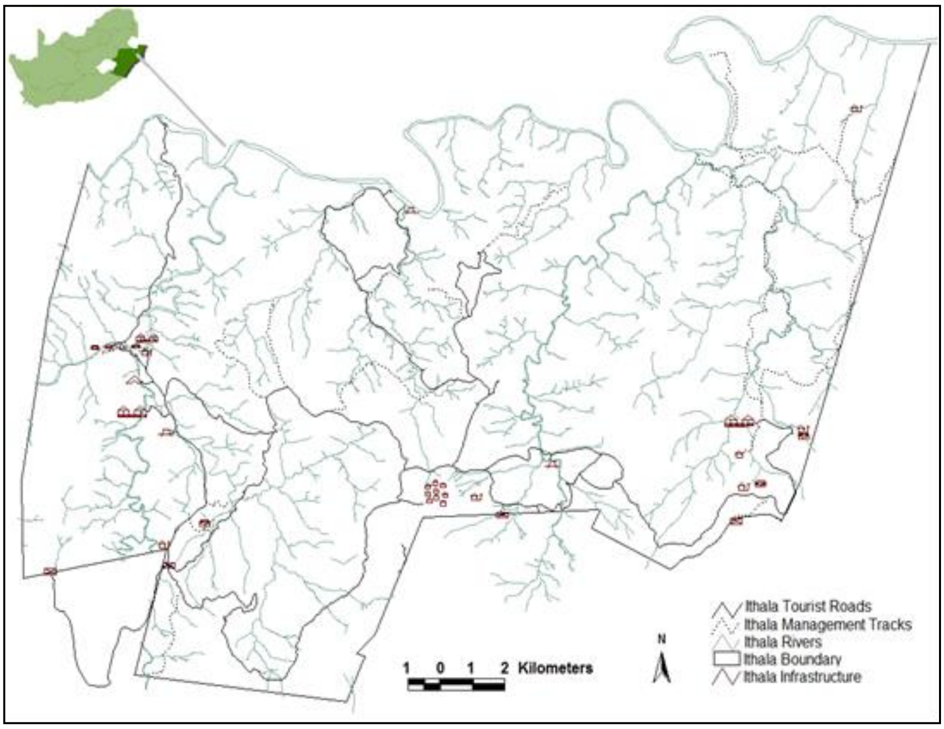

Fig. 2.1 The locality of Ithala Game Reserve within the KwaZulu-Natal Province of South Africa, and the multitude of rivers and streams throughout the reserve.

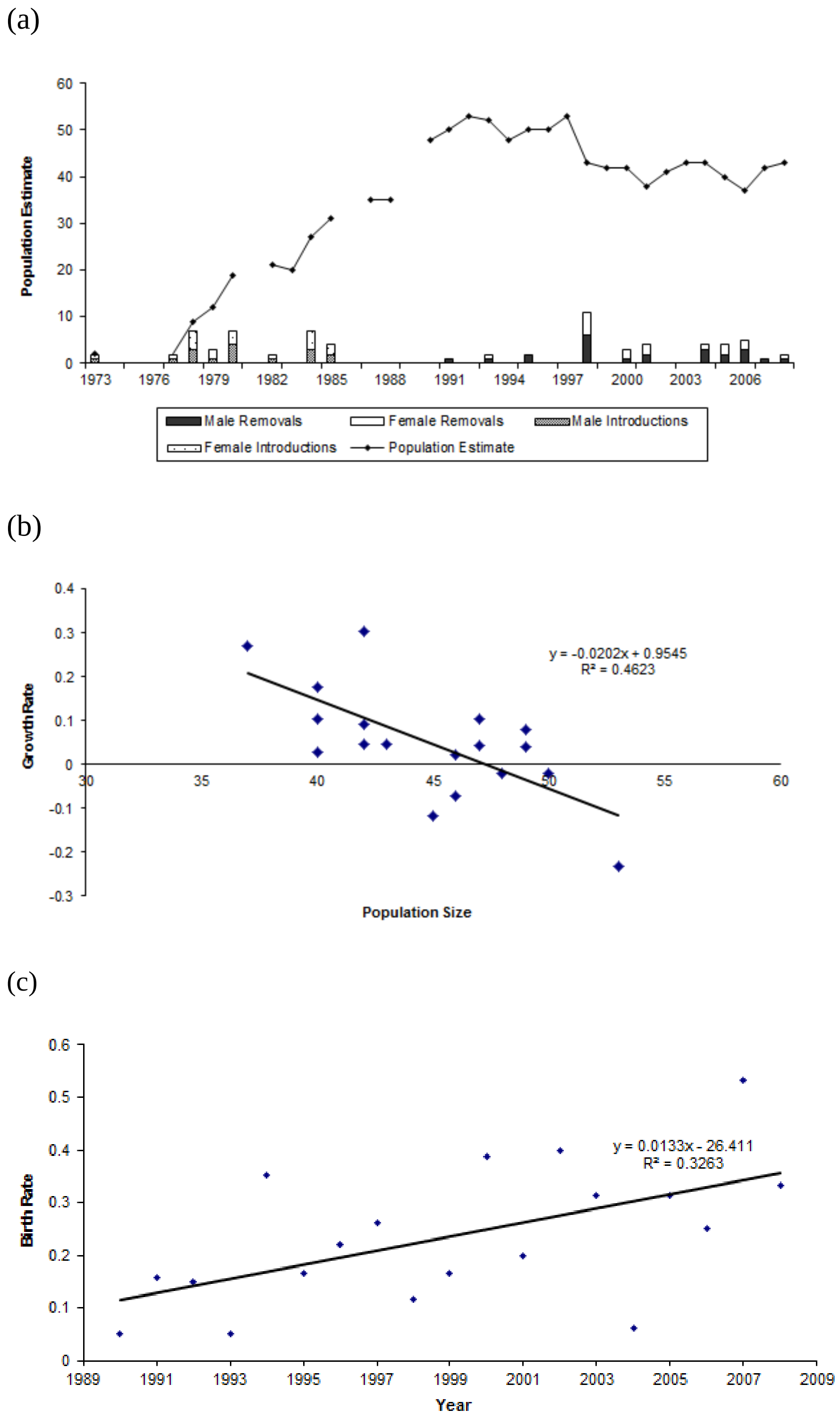

Fig. 2.2 Black rhino population (a) observed estimates since the introduction in Ithala in 1973 (b) growth rates (c) birth rates from 1990 to 2008. Ithala black rhino population birth rates from 1990 to 2008.

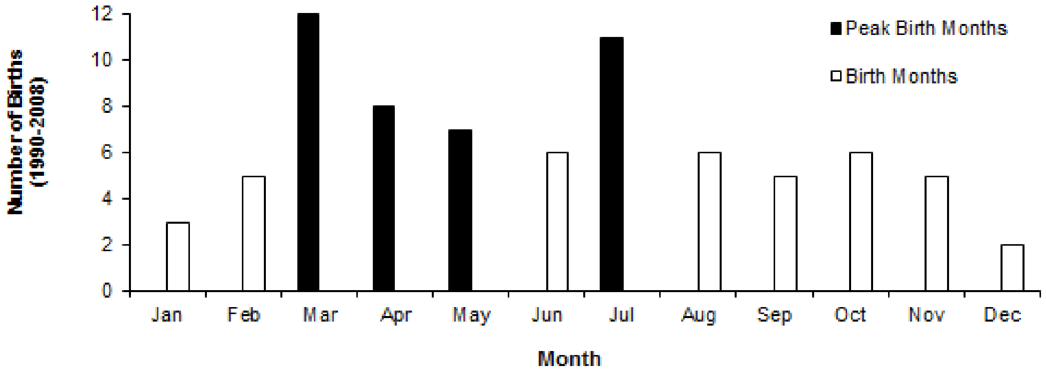

Fig. 2.3 The number of births per month indicating the peak birth months of March, April, May and July.

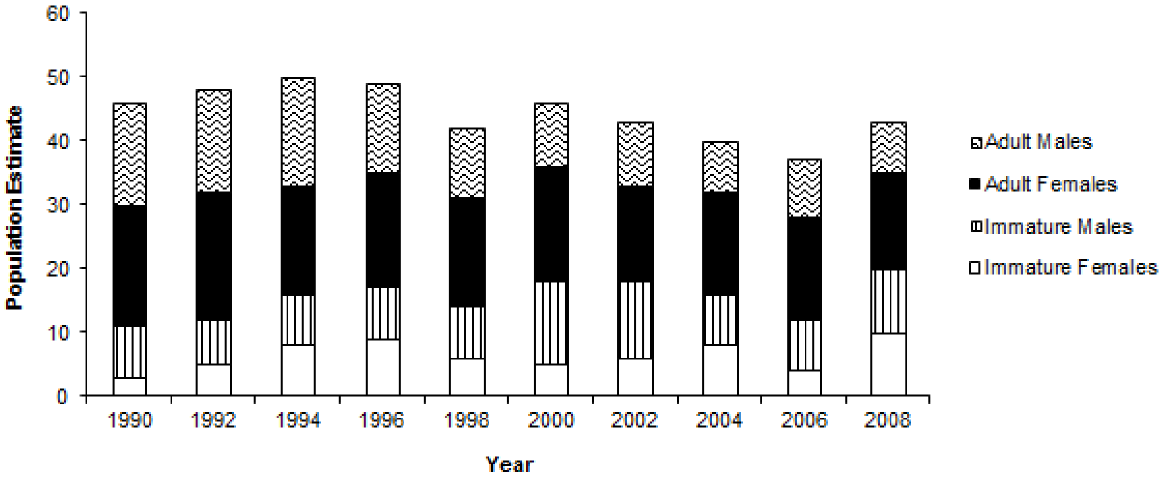

Fig. 2.4 The number of reproductive and non-reproductive black rhino females and males from 1990 to 2008.

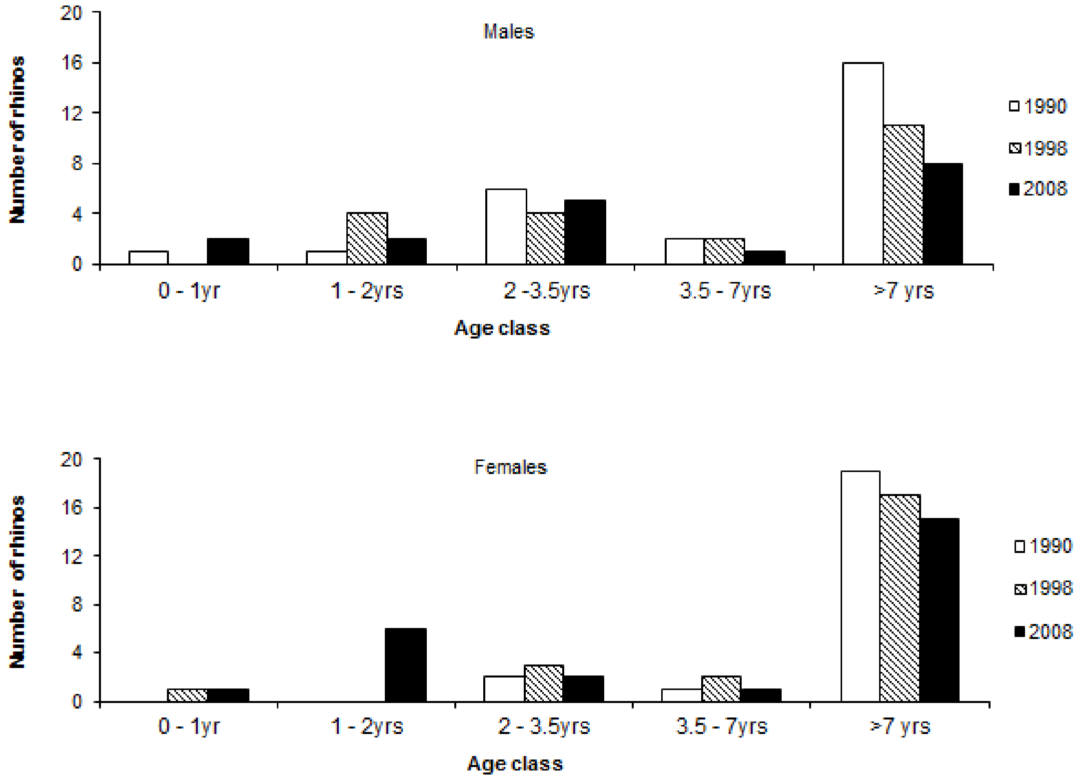

Fig. 2.5 Sex and age structure of the population for the years 1990, 1998 and 2008 respectively indicating a decline in the number of adult males and females.

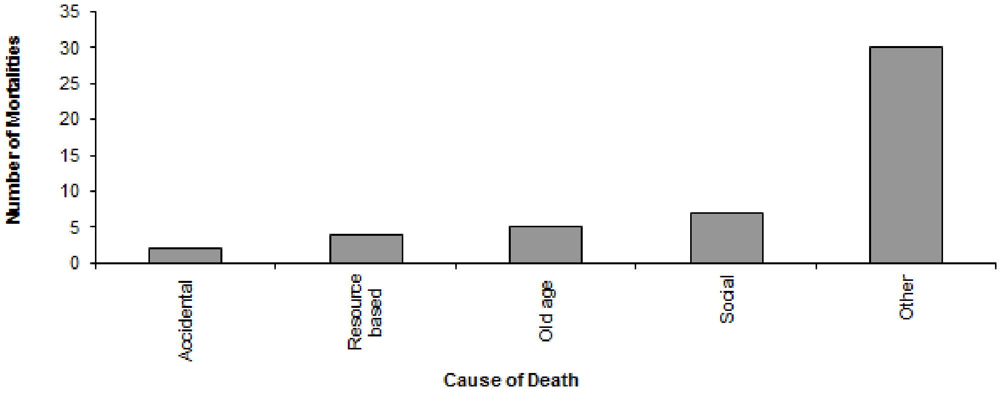

Fig. 2.6 The number of black rhino mortalities recorded in Ithala from 1990 to 2008.

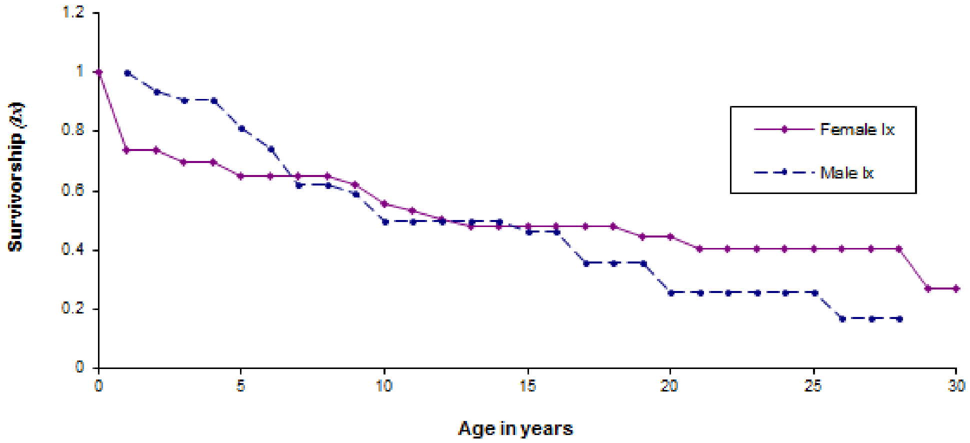

Fig. 2.7 Survivorship curves for males and females in the Ithala black rhino population.

CHAPTER 3

Social interactions and management removals contribute to black rhinoceros, *Diceros bicornis* mortalities in Ithala Game Reserve, South Africa

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Abstract

One of the key conservation challenges is how authorities can focus efforts to save a threatened animal population. Authorities commonly use reintroduction programs to achieve re-establishment and recovery of threatened species that require long-term management and monitoring. Success depends on multiple factors, some of which may be associated with life-history features of a species. We investigate whether social factors play a role in the incidences of mortalities of the critically endangered black rhinoceros (rhino), *Diceros bicornis,* in Ithala Game Reserve, South Africa. Our analysis makes use of demographic data on mortalities, sex, and age structure, as well as space use of black rhinos, between 1990 and 2008. Social interactions came out strongly as an explanatory factor for incidences of mortalities. Male and female areas of high density differed across the reserve. Observed mortalities of black rhino males and females increased with density, and were highest at > 4 or >5 overlaps with other rhino for males and females respectively. Apart from the strong association between mortality and black rhino intensity of use of an area, management removals unintentionally also contributed to mortalities. When supporting rhino meta-population conservation initiatives, removals of black rhinos for translocation should be more strategic; for example removal of young males and, on occasion, females, from areas of high density in Ithala Game Reserve. This approach maximises black rhino breeding performance, while minimising mortalities associated with increased density and undesirable social interactions.

Keywords:

Demographic data, density, threatened animal population, mortalities, monitoring, social interactions, reintroduction

Introduction

Endangered species may require intensive management of their populations. Planning for effective and efficient conservation interventions requires understanding of the population dynamics, and the factors and processes that affect these dynamics (Fowler, 1981; Berger & Cunningham, 1994; Van Houtan *et al.*, 2009). Depending on management objectives, the goal may be to increase, stabilize, or decrease population numbers. Authorities accomplish management objectives by manipulating the habitat, such as creation of waterholes (Ndlovu *et al.*, 2018) and controlled burning (Strydom & Midzi, 2019). Others may require direct manipulation of the animal population, such as removals of animals (Seddon *et al.*, 2014) to increase the growth and breeding success within a local population (Morgan, 2010), or translocation between reserves to achieve desired management results, such as genetic integrity (Milner *et al.*, 2006).

Conservation of threatened species has two main threads: a small-population paradigm (le Roex *et al.*, 2019) that attempts to understand how low levels of abundance influence population persistence (Mattsson *et al.*, 2008), and a declining population paradigm that attempts to understand how and why abundance reaches critically low levels, and to use such insights to design counteractive management (Caughley, 1994). Both paradigms are often important in saving endangered species from extinction (Asquith, 2001). Management initiatives (Scholte, 2011), however, may be ineffective when they fail to consider life history and behavioural strategies adequately (Knight, 2001).

Understanding the dynamics (Scholte, 2011) and the behaviour of animals (Jones & Safi, 2011) is important because behaviour affects species persistence through a wide variety of mechanisms (Reed, 2002). These mechanisms can include social disruption of breeding (Borg *et al.,* 2015), learned and socially facilitated foraging (Deygout *et al.,* 2010), translocation success (Linklater *et al.*, 2011), dispersal (Parvinen *et al.*, 2020), and settlement decisions (Reed, 2002).

The dynamics of populations depend on how individuals of a species respond to environmental factors (Freeman *et al.,* 2014b), individuals of its own species (Woolley *et al.*, 2009), and individuals of other species (Lipshutz, 2017), which can be summarized by population growth rate, a consequence of age-specific birth, death, immigration, and emigration rates (Eberthardt, 1985). Sex- and age structures reflect the outcome of how individuals respond to various factors (Rughetti, 2016). Eberhardt's framework (2002) predicts that, when density increase, or environmental conditions degrade, there will be a decrease in juvenile survival, then an increase in the age at first reproduction, followed by a decline in birth rates, and, finally, a decrease in the survival of adults. Density effects traditionally relate to resources (Łomnicki, 1978). Resource availability (Pekkonen *et al.,* 2013) per individual is reduced at high population densities, affecting mortality, fecundity, and age at maturity, i.e. resource-related density dependence (Both & Visser, 2003).

Mammals, however, show extreme variations in social complexity and behavioural flexibility (Kappeler *et al.*, 2013). Individual animals differ in their average level of behaviour, and in their responsiveness to environmental variation (Dingemanse *et al.,* 2010). Such behavioural adaptations (Kappeler *et al.,* 2013) could influence the consequences of resource related density-dependence. Because black rhinoceros, *Diceros bicornis,* hereafter black rhino, are browsers, mainly feeding on herbs and shrubs (Hutchins & Kreger, 2006), resources are normally not as restrictive – browse material, for instance, is not as sensitive to variation in rainfall as grass (Vetter, 2009; February *et al.,* 2013).

Black rhinos have a secretive nature (Freeman *et al.,* 2014a), and are fairly solitary and sedentary in their movements (Morgan, 2010). Adult black rhino males, in particular, are solitary and aggressive (Owen-Smith, 2004), and do not tolerate other males (Adcock, 1994), but permit overlap with females (Lent & Ficke, 2003) while forming consort relationships with oestrus females (Tatman *et al.,* 2000). Indeed, fighting was a common cause of mortalities in Ithala Game Reserve, South Africa (Greaver *et al.,* 2013). When densities increase, we expect an increase in black rhino activity where other rhinos are already active, and, thus, reflecting high potential for social interactions between individuals with potentially competing interests.

Animals concentrate their movements within home ranges (Buk & Knight, 2012), rather than wandering aimlessly (Spencer, 2012), and factors such as the presence of landscape patches that provide food, water, the availability of cover, and the absence of human disturbance, all influence home range size and location (Tatman *et al.,* 2000, Göttert *et al.,* 2010). Spatial specific behaviour within an individual's home range is a common pattern of space use (Borger *et al.,* 2008) for activities such as feeding, resting, and reproduction (Harestad & Bunnel, 1979). Space use varies between individual home range sizes, overlap fluctuates with other individuals' home ranges, and black rhinos shift home ranges over time (Tatman *et al.,* 2000, Göttert *et al.,* 2010). Factors such as steep slopes affect the accessibility of a given area, and have an important influence on the degree to which black rhinos use certain areas (Kotze & Zacharias, 1993). Black rhino population densities can also influence habitat selection and home range size (Shaw, 2011). Distance from roads and tourist activity could have a negative impact on black rhino range use (Buk & Knight, 2012). Home range size also depends on the sex and age of the individual black rhino (Skinner & Chimimba, 2005).

Established males tolerate sub-adult to young adults, which are at risk of being killed or injured if they are not suitably subordinate (Adcock, 1994). Competition for mating possibilities (FitzGibbon & Lazarus, 1995) is the main social pressure exerted on black rhino males, which, in turn, influences the location and size of the black rhino male home range (Owen-Smith, 1988). Males separate themselves spatially and temporally through olfactory communication; dung piles and urine spraying (Campbell-Palmer & Rosell, 2011) are commonly used olfactory signals, while scrapes and broken vegetation may offer visual evidence of the presence of other individuals (Linklater *et al.*, 2013). Females tend to have overlapping home ranges (Shrader & Owen-Smith, 2002), a strong social bond with their calves (Tatman *et al.*, 2000), and seem less prone to injury or fighting deaths related to high levels of social pressure (Adcock, 1994).

The above sociality patterns make some explicit predictions. Mortalities of black rhinos should increase as activity of individuals increase in areas where other rhinos already occur and are active. We expect that presence of more males will accentuate such mortality patterns. We predict that observed mortalities would occur more frequently than random when there is increased social interaction. For instance, males marking and defending territories (Freeman *et al.*, 2014a), would have an increased probability of encountering other males, with intraspecific fighting (Linklater *et al.*, 2011), and some fatal consequences, when there is more overlap with other males. For females, we expect a similar relationship, but of far less magnitude because, we presume, females are less aggressive than the males as adult females share their home range with their young (Buk, 2004), and overlap with home ranges of other females and males (Tatman *et al.*, 2000) .

We focus on the black rhino population of Ithala Game Reserve where density mediates population vital rates (Greaver *et al.*, 2013). We expect that density would play a key role in mortality. We used black rhino occurrence areas, and overlaps of these occurrence areas, as indicators of intensity of social interactions, based on sightings data recorded over an 18-year period (1990-2008) in Ithala Game Reserve. This allowed us to evaluate the influence of environmental, social (as a result of density or territoriality), or management drivers, on mortality of black rhino. Our specific objectives were to: (1) create a density map representing high use areas within the reserve of all black rhinos; (2) map the individual distribution or occurrence areas of male and female black rhinos; (3) compare the distribution of overlapping black rhino occurrence areas over the entire study period, to determine a correlation between probability of encounter and mortality; (4) determine if a mortality occurrence was associated with (a) social factors (density, overlap of distribution areas), (b) environmental factors (distance to water, slope, Enhanced Vegetation Index (EVI), or (c) management intervention through live removal of black rhino individuals from the reserve. Removals were conservation translocations for reintroduction or supplementation, which are the deliberate movement of organisms from one site to another where the primary objective is a conservation benefit (IUCN/SSC, 2013).

Methods

Ithala Game Reserve (hereafter referred to as Ithala), located in northern KwaZulu Natal, South Africa (27°30´S, 31°25´E) is 297 km² in size. Elevation ranges from 350 m.a.s.l. at the northern boundary along the Pongola River, to 1550 m.a.s.l. at the southern escarpment plateau. Long-term mean annual rainfall is 791 mm, falling mainly during the summer (October to March). Summers are warm to hot (daily average of 18 – 30 °C), with winters being warm to mild (15 – 25 °C) (Porter, 1983). Frosts do not occur, but low (near freezing) temperatures occur during cold windy spells on winter nights.

Five tributaries of the Pongola River flow through the reserve, resulting in topography varying from undulating grassland to cliff faces (Wiseman *et al.*, 2004). The reserve lies within the Savanna /Grassland biome, and hosts 26 different types of vegetation communities (Van Rooyen & Van Rooyen, 2008). Sourveld vegetation occurs on steeper slopes, with sweetveld dominating on dolerite ridge tops (Brooks & Adcock, 1997). *Vachellia karroo* and *V. nilotica* woodland exist primarily on old croplands (Kotze & Zacharias, 1993). Prior to proclamation as a game reserve in 1973, land-use was for agricultural purposes (Wiseman *et al.,* 2004). Since proclamation as a reserve, authorities introduced various browsers, grazers and mixed feeders (Wiseman *et al.,* 2004). The Reserve comprises two management sections namely Thalu (West) and Kwasambane (East).

Field data collection followed the guidelines of the SADC Regional Programme for Rhino Conservation (Adcock & Emslie, 2003). The entire adult black rhino population has recognisable and unique ear markings (Ngene *et al.,* 2011), ear tears, or horn configurations (Brooks, 1989). This enabled the management staff to account regularly for every individual in the population based on sightings alone. The sightings records contained detailed information collected by field rangers, who patrolled the reserve on a daily basis, and recorded particulars of each rhino in their field data booklets. They reported the sightings information to the section rangers, who maintained files on the life history of each animal.

We divided the reserve into 1 km^2 grids, and noted sightings as grid locations. During the study period, the formula used to estimate the position of the centre of the grid and converting it into latitude and longitude was standard on Ezemvelo KZN Wildlife (EKZNW) computers, using the Animal Population Management Database (APMD). For all the spatial analysis ArcGIS 10.2 (ESRI 2014. ArcGIS Desktop: Release 10.2. Redlands, CA: Environmental Systems Research Institute) was used. Field observers assigned all the rhino sightings within a 1 km^2 grid to the central point of that grid. Using the sum of all the rhino sightings in a block for the entire study period, a rhino density map was created. This map identifies areas that rhinos frequented in the reserve based on the 1 km^2 observation grid.

In terms of space use, we needed a measure of the intensity of social interactions. Territorial interactions would result in more intense social interactions. Rather than mapping individual home ranges per se, we created a black rhino occurrence map for the reserve. We combined the incidences of occurrence of individually identified black rhinos across the entire time series to indicate areas in the reserve most intensely utilised by black rhino. An occurrence map for each known individual resulted by creating a presence layer for each individual. By combining all these occurrence maps, the areas with the most overlap of individual occurrence maps are then rhino hotspots, where we assumed a higher potential for social interaction among individuals of the same or opposite sex. This provided a proxy index for the strength of social interactions. We used the same approach to identify areas favoured by female and male rhinos, and created female and male overlap maps. We also created occurrence areas over time, producing occurrence maps of all individuals sighted within a year, for each year of the study.

Identified occurrence edges, i.e. the outermost grid cells for each individual rhino occurrence map, equated roughly to the territory edges. We reasoned that more occurrence edges in an area could indicate a more disputed area between neighbouring individuals. The number of occurrence edges that occurred within a 500 m buffer area around a specific mortality point served as a proxy for the level of potential dispute. If there were no occurrence edges in a mortality point buffer area, the specific locality of that mortality was completely within the high use occurrence area of all the black rhinos utilising that area.

Because two types of resources are important for black rhinos, i.e. food and water (le Roex *et al.*, 2019), we used the average EVI value and Distance to Water, respectively, as proxies for these. The enhanced vegetation index (EVI) is a vegetation index derived from remotely sensed imagery that provides comparisons of vegetation greenness. It serves extensively as a proxy for biomass, with higher EVI values reflecting higher vegetation cover and/or higher vegetation greenness (Fraga *et al.*, 2014). The EVI dataset used for this analysis came from MODIS imagery collected and processed by NASA, and further cleaned and supplied by the Meraka Institute, CSIR (Pretoria). To create the Distance to Water layer, we used the Euclidean Distance tool and produced a continuous layer of the distance to the closest surface water source within the reserve (1:50 000 Topographical map series, National Geospatial Information, Mowbray, Cape Town, South Africa).

During the study period, rangers recorded 48 black rhino mortalities. Of the 48 mortality records, we could not link 15 to a location or grid reference. For the spatial analysis we could, therefore, only use the mortality data with location references (n=33). Due to the limited mortality data for this period, we could not evaluate data by year, and pooled information for the entire period. Our hypothesis is that these black rhino mortalities were a function of social conflict. We plotted each recorded mortality and extracted the underlying social, management and environmental values (Table 3.1) for the full time period. In addition, we selected control sites using the *Create Random Points* function to create 33 random localities. These localities reflect places of fake black rhino mortalities across the reserve.

If our predictions hold, the values of the social and environmental variables at these random points should be different compared to those at the observed black rhino mortality locations. The resulting 66-point layer (33 observed mortalities and 33 random mortalities) and associated extracted values of the participating environmental, management and social variables at each mortality location (see Table 1) allowed us to use Ordinary Least Squares (OLS) (Fischer & Getis, 2010) linear regression analysis to determine if a true mortality occurrence was associated with a specific variable.

For the OLS analysis, we used all model permutations ranging from models that included only one of the variables at a time; models that included a combination of the variables; to models that included all the variables. We then used Akaike's Information Criterion (AICc) to rank models for each variable from the most- to the least-supported model, given the data. We calculated the difference between the lowest-observed AIC value and the value for the current model (AICi), and Akaike weights (wi) as measures of model support (Johnson & Omland, 2004). We present the models that had ΔAICc < 2 in comparison with the estimated best model.

To evaluate whether males or females accentuate mortalities through social interactions, we conducted an additional simulation using the 33 random fake mortality locations (simulated mortalities) generated previously. We then extracted, for each simulated mortality location, the number of overlaps in male occurrence as well as female occurrence areas associated with that location. We could then calculate the number of simulated mortalities associated with one overlap, two overlaps, and so forth. This created a dataset that reflected the number of mortalities for observed overlaps as well as random overlaps, ranging from 1 to 13 overlaps derived from male occurrence areas and 1 to 9 overlaps derived from female occurrence areas.

We subtracted the randomly predicted number of simulated mortalities at a specific number of overlaps from the actual relevant observed mortalities, to generate a directed residual (observed minus simulated). A positive value means that there were more actual mortalities than randomly expected. We repeated this process five times to generate five sets of simulated data. We then used segmented regression (Snedecor & Cochran, 1980) to identify break-points in the residuals at increasing number of overlaps. The Chow test (Chow, 1960) enabled us to determine whether a break in segments at a specific overlap was significant. We present the stingiest signal of a break to indicate where the significant overlap was.

Results

Our dataset totalled 7003 sightings of 69 identifiable individuals (males: n = 36; females: n = 33). The annual number of sightings of all identifiable black rhinos had a maximum of 710 in 1995, with the fewest sightings recorded in 1991 (n = 19). The number of identifiable individuals sighted per year indicates higher number of females recorded from 1997 onwards (Fig. 3.1a).

Males and females did not have similar distribution in the game reserve (Fig. 3.2). Overlay of male (Fig. 3.2b) and female (Fig. 3.2c) occurrence areas identified areas dominated by male occurrence and other areas dominated by female occurrence, as well as areas with no strong bias for either sex (Fig. 3.2a).

Only four of the 681 candidate models (S1 Appendix) explained variation in mortalities sufficiently (Table 3.2). The year in which the mortality occurred was consistently included as a variable in most of the successful models. As we expected, density was included as an important variable, followed by management removals, and EVI.

Year is an arbitrary variable, but the most important biological variable was the density of black rhino. We recorded positive relationships between mortality and density, as well as between mortality and management removals from the population, but a weaker EVI influence once we accounted for the effects of year.

The residuals of observed versus random mortalities increased with increasing overlaps up to five overlaps for males and females, and then levelled off. Our best model for males (break point at five overlaps: $r^2 = 0.55$, $F_{3,62} = 19.48$, $p < 0.01$) explained more of the variation than that for females (break point at six overlaps: $r^2 = 0.31$, $F_{3,44} = 5.38$, $p < 0.01$). Note that observed mortalities of males were consistently less than randomly predicted when males shared <5 overlaps with other rhinos. For males, in 84.4% of the simulations, observed mortalities of black rhino males were higher or equal to the simulated mortalities when they shared > 4 overlaps with other black rhinos, irrespective of sex, in their occurrence area (Fig 3.4a). For females, in 60% of the simulations, observed mortalities were higher or equal to the simulated mortalities when they shared > 5 overlaps of other black rhinos in their occurrence area (Fig 3.4b).

Discussion

Fecundity reduces when densities increase (Bonenfant *et al.,* 2009), a typical response to resource restrictions (Law *et al.*, 2013). Eberhardt's (2002) framework predicts that impacts on survival schedules may also occur. Such impacts can be both through a resource limitation effect (le Roex *et al.*, 2019) or social effects (Reed, 2002). For black rhino, social interactions, however, as indicated by the results of density and overlaps in occurrence areas, carried more weight than environmental factors.

Black rhinos primarily have a solitary lifestyle (Shrader & Owen-Smith, 2002), and adult males have strong territorial behaviour (Adcock, 1994). Territorial behaviour is of relevance to rhino population management because it sets a limit to the number of competing rhino (mainly males) that can co-exist in a given reserve (Adcock, 2001). One can expect that at higher densities opportunities for interactions increase. The high overlaps in occurrence areas in our study supports an expectation that opportunities for interactions are high in Ithala.

Our existing understanding of black rhino social behaviour suggests that many of these interactions may be antagonistic, which could lead to injuries and mortalities (Patton & Jones, 2008). Sub-adult males, for instance, have a higher mortality rate than adults, because they are subject to social stress, especially when establishing home ranges (Swart *et al.*, 1990). In our study, the observed mortalities strongly associated with overlaps in occurrence areas suggesting that social factors play a key role in constraining or regulating black rhino dynamics, through effects on survival. Indeed, where cause of death was determined, fighting reflecting social factors was the largest cause (Greaver *et al.*, 2013).

Black rhino use olfactory communication via dung and urine (Linklater *et al.*, 2013), which have an important role in black rhino social, mating, and spatial relationships. Thus, conspecific scent might play a role in black rhino movements (Linklater *et al.*, 2013), for instance oestrous females urinate frequently (Hutchins & Kreger, 2006) to communicate their sexual status, whilst faecal markings advertise the dominance of adult males (Freeman *et al.*, 2014a). Female black rhino can also avoid overly aggressive males (Hutchins & Kreger, 2006). Black rhino females may thus employ social mechanisms to mitigate conflict, but these options diminish as density increase. Even so, our data highlight that mortalities increased with increasing number of overlaps in male occurrence areas, and levelled off at five overlaps.

Males black rhinos have social techniques to avoid conflict at low overlaps, but the choices (e.g. dominant male black rhinos scraping their faeces farther to advertise their size and territory to conspecifics - Freeman *et al.,* 2014a), become fewer at higher densities, because there may be limited options for altering behaviour (Hutchins & Kreger, 2006). The importance of behavioural changes to minimise risk has been demonstrated for subordinate carnivores (Vanak *et al.,* 2013), for instance, leopard *Panthera pardus* use fine-scaled avoidance behaviours and restricted resource acquisition when home ranges overlapped with the home range of lions *Panthera leo*. These behavioural mechanisms allows subordinate carnivores to coexist with dominant carnivores (Hayward & Slotow, 2009). Although the example is inter-specific, see also segregation of zebra *Equus quagga*, kudu *Tragelaphus strepsiceros* and giraffe *Giraffa camelopardalis,* from elephants *Loxodonta africana* at waterholes (Ferry *et al.*, 2016); a large, dominant elephant male in musth often suppresses musth in smaller elephant males (Taylor *et al.,* 2019), such behavioural adaptation is important within species, such as the case for black rhinos in Ithala.

Our results may provide some explanation for why mortalities associate positively with management interventions or removals. Hypothetically, a reduction in black rhino numbers and, thus, density should reduce mortalities if the mechanisms were entirely resource related. The mechanisms that black rhinos have to reduce conflict, specifically among males, may associate with familiarity of rhinos to each other. Disruption of the social familiarity mechanism may impose different drivers of black rhino mortalities other than resource restrictions. Indeed, black rhinos appear more prone to aggressive interaction with unfamiliar than familiar rhinos (Linklater & Swaisgood, 2008).

Removing rhinos that know each other, together, has better successes as part of re-introductions, compared to using unrelated or unfamiliar individuals to make up a source population for a newly established locality (Emslie *et al.*, 2009). It is likely that management disrupt the primary mechanisms, familiarity, of reduced conflict between adult males when they randomly target individuals for removals. Indiscriminate management may interfere with the behavioural adaptation of black rhinos to reduce conflict that can lead to deaths, as was speculated for the black rhino population in Hluhluwe–iMfolozi Park (Nhleko *et al.,* 2017). Note that rhino focused management interventions are not the only actions that can disrupt conflict coping mechanisms, and result in higher mortalities of black rhino. The introduction of orphan elephants to Pilanesberg Game Reserve, for instance, resulted in aggressive interactions between elephant and rhino, in some incidences even leading to fatalities of rhino (Slotow *et al.*, 2001; Slotow & van Dyk, 2001).

So what were the influences of environmental conditions, the remaining variable that was included in our models? In our case, the average EVI provides an index to resource availability, because we assume that resource availability links to underlying undetectable climatic conditions. Rainfall is the main driver of herbivore food production (Chamaillé-Jammes *et al.,* 2008), and variability in rainfall results in variability in productivity, most strongly expressed in grass production (Gherardi & Sala, 2015). Resource availability typically has a larger effect on the grass layer rather than the browse layer (Gherardi & Sala, 2015). Therefore, systems need to experience an extreme drought event that reduces browse productivity and biomass substantially.

Browsers should thus be more resilient than grazers should, as was the case for black rhino in comparison to white rhino *Ceratotherium simum* in Kruger National Park – black rhinos had no drought-related population consequences due to their browsing diet (Ferreira *et al.,* 2019). Given that black rhinos are browsers (Buk, 2004), and, during the study period, Ithala had a fairly consistent EVI value, availability of the necessary resources does not appear to be a constraint. In Ithala, environmental effects may, perhaps, manifest more strongly through acute events like an exceptional cold spell that could induce mortalities of calves or unhealthy individuals. In our data set, we noted three black rhino mortality events attributed to exceptional cold spells, in 2001 (n=2) and 2002 (n=1).

We have illustrated that the black rhino mortalities in Ithala were not primarily related to resources, but to social processes. Deaths result when opportunities for social antagonistic interactions, such as fighting, increase in areas with relatively high rhino occurrence. The implications are that management of black rhino populations does not only entail removal of specific individuals, but also requires improved information on the social behaviour of black rhino (Linklater & Hutcheson, 2010). The elusive nature of black rhinos makes monitoring populations costly and logistically difficult (Garnier *et al.*, 1998). Even so, detailed social information requires intensified monitoring especially in source populations targeted for restocking other areas. This will better inform management decisions.

Our analysis highlights the importance of understanding the black rhino social relationships and social behaviour when making management decisions. Like many territorial species, black rhinos communicate their physical state to others (Hutchings & White, 2000) by demarcating their habitat with behavioural or physical signs (Stoops & Roth, 2003) to deal with conflicts. Challenges arise when landscapes, isolation, and fences limit the evolved options that black rhinos have to deal with conflict.

In fragmented landscapes, species persist through meta-population (Knight *et al.*, 2013) dynamics by colonizing and decolonizing suitable habitat patches through dispersal processes (Parvinen *et al.*, 2020). In large mammals, dispersal for males are mostly innate (Dalerum *et al.*, 2007), while dispersal of individuals of both sexes are occasionally environmental driven (Owen-Smith, 2006). Our results suggest that, in the absence of restoring linkages between populations of black rhinos, conservation management could benefit from mimicking evolved dispersal dynamics (Parvinen *et al.*, 2020), by removing young black rhino males, and, occasionally, young females, from high-density areas. This will also minimise disruption of familiarity that has been build up among the older animals, which mitigates conflict escalations.

Table 3.1. The environmental (distance to water, EVI, slope), management (removals) and social (density, edges, overlaps) variables extracted for 1 km^2 grid cells with observed black rhino mortalities, in Ithala Game Reserve and for randomly generated points.

Variables	**Description**
Year	The year when the black rhino mortality occurred.
Environmental variables	
Distance to water	Euclidean distance to water from which the black rhino mortality occurred.
EVI value	Average EVI value for the year of the black rhino mortality, for the location at which the mortality occurred.
Slope	Slope value for the location at which the black rhino mortality occurred.
Management variable	
Removals	Number of black rhino removals from the 1 km^2 block in which the black rhino mortality occurred.
Social variables	
Density	Intensity of use based on the number of unique black rhino sightings for all observations made per grid cell during the entire study period
Edges	Number of individual occurrence area edges in the 1 km^2 block in which the black rhino mortality occurred.
Overlaps All	Total number of overlaps by all known black rhino individuals over the entire study period.
# Overlaps Female	Number of overlaps of female black rhino occurrence maps for the year the black rhino mortality occurred.
# Overlaps Male	Number of overlaps of male black rhino occurrence maps for the year the black rhino mortality occurred.
# Overlaps Year	Number overlaps of all known black rhino individual occurrence area maps for the year the black rhino mortality occurred.

Table 3.2 The four explanatory models which best describe the association between mortality occurrences with a set of variables (density, management removals, EVI and Year). See (Appendix 3.1) for full list of models.

Model	**N**	**K**	**Fstat**	**r2**	**AiCc**	**ΔAICc (Δi)**	**Model likelihood**	**Wi**
Year	66	1	5877902.0	0.99989	-652.05	0	1.000	0.072
Density-Year	66	2	2920987.7	0.99999	-650.41	1.634	0.442	0.032
Removals-Year	66	2	2915015.6	0.99999	-650.28	1.769	0.413	0.030
EVI-Year	66	2	2910125.6	0.99999	-650.17	1.880	0.391	0.028

(a)

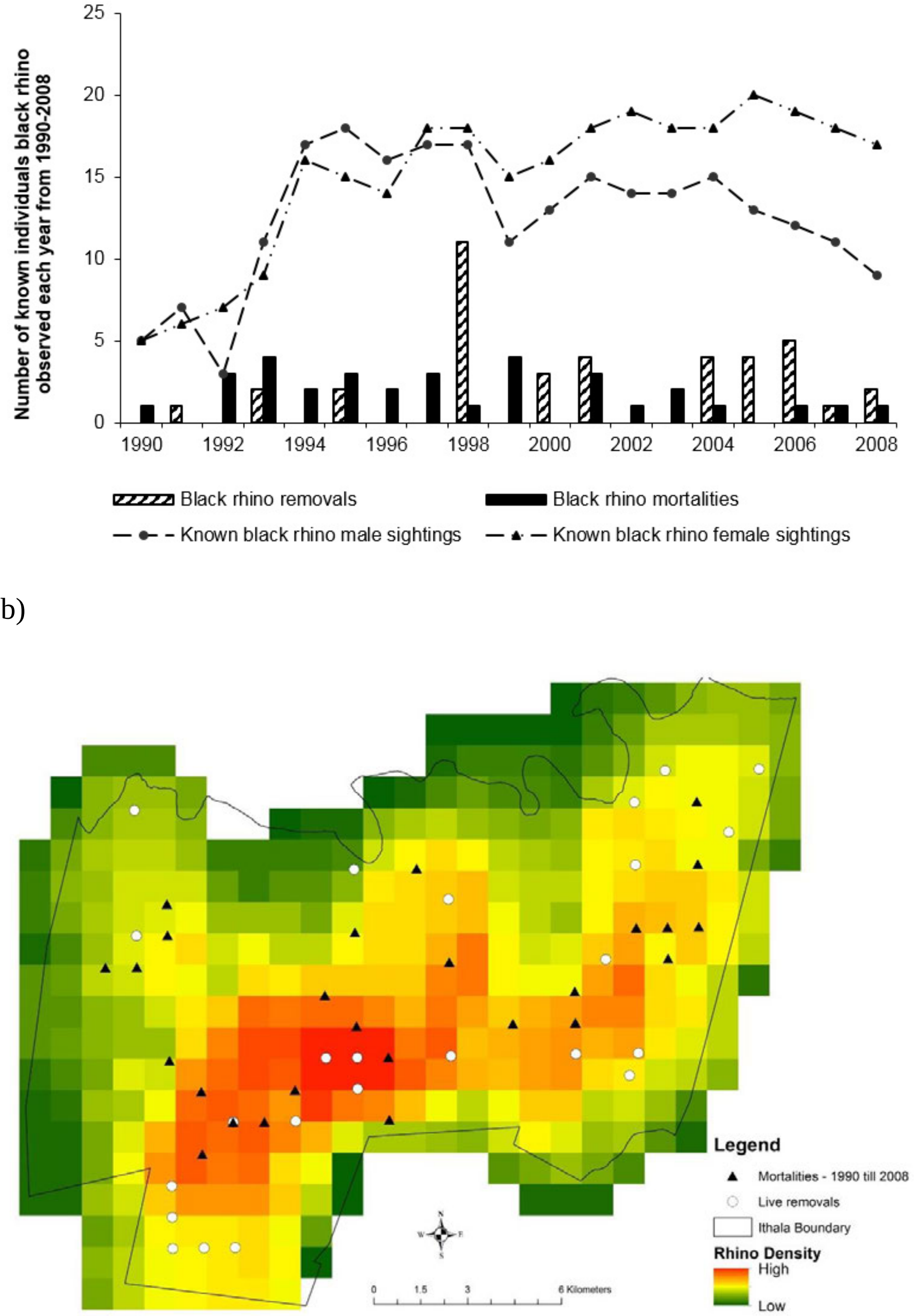

Fig. 3.1 (a) the number of identifiable black rhino from sightings in Ithala Game Reserve from 1990-2008, as well as mortalities and management removals (see Greaver, *et al*., 2013). (b) The black rhino live removal and mortality points in Ithala Game Reserve from 1990-2008, overlaid onto a map of rhino density (number of sightings in a grid cell over the study period).

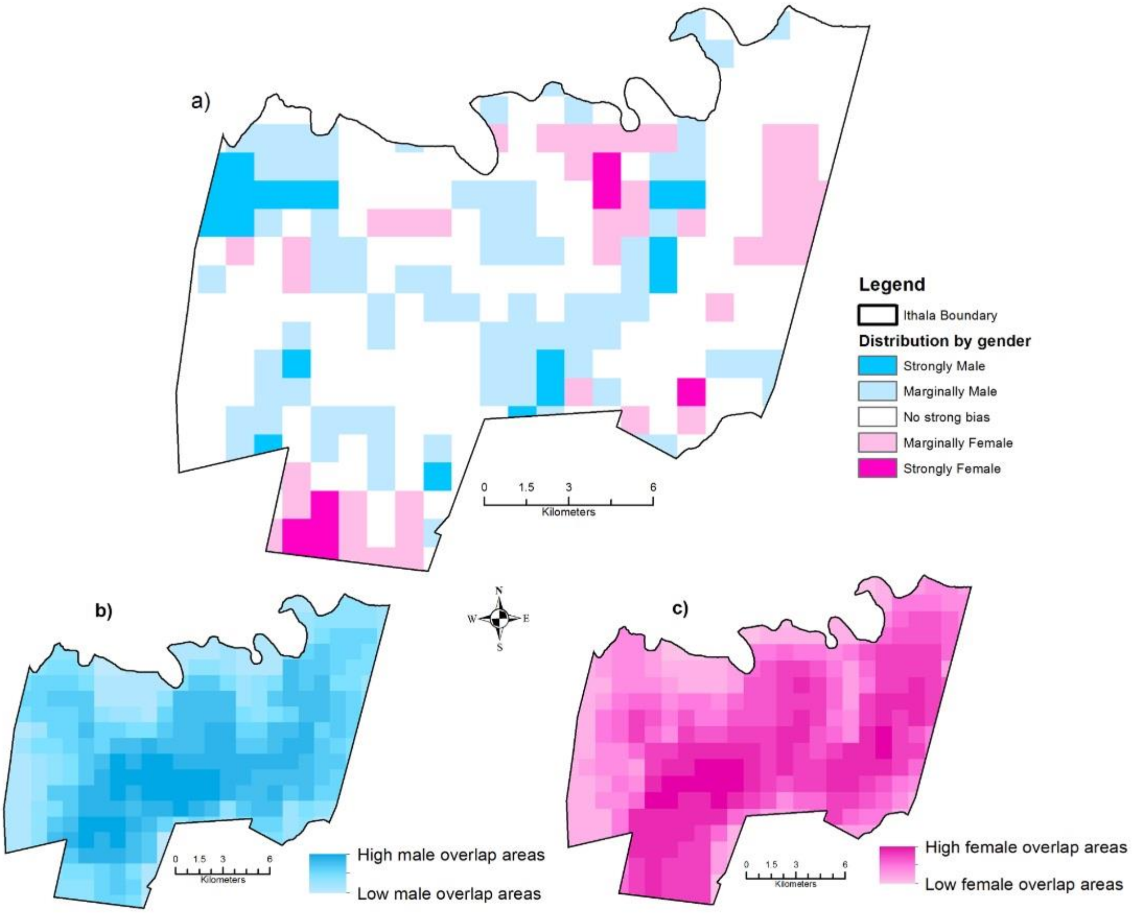

Fig. 3.2 Distribution of (a) all black rhino, (b) males, and (c) females, from 1990 – 2008. Grid cells (1 km^2) represent the presence of known individuals detected in a grid cell over the study period.

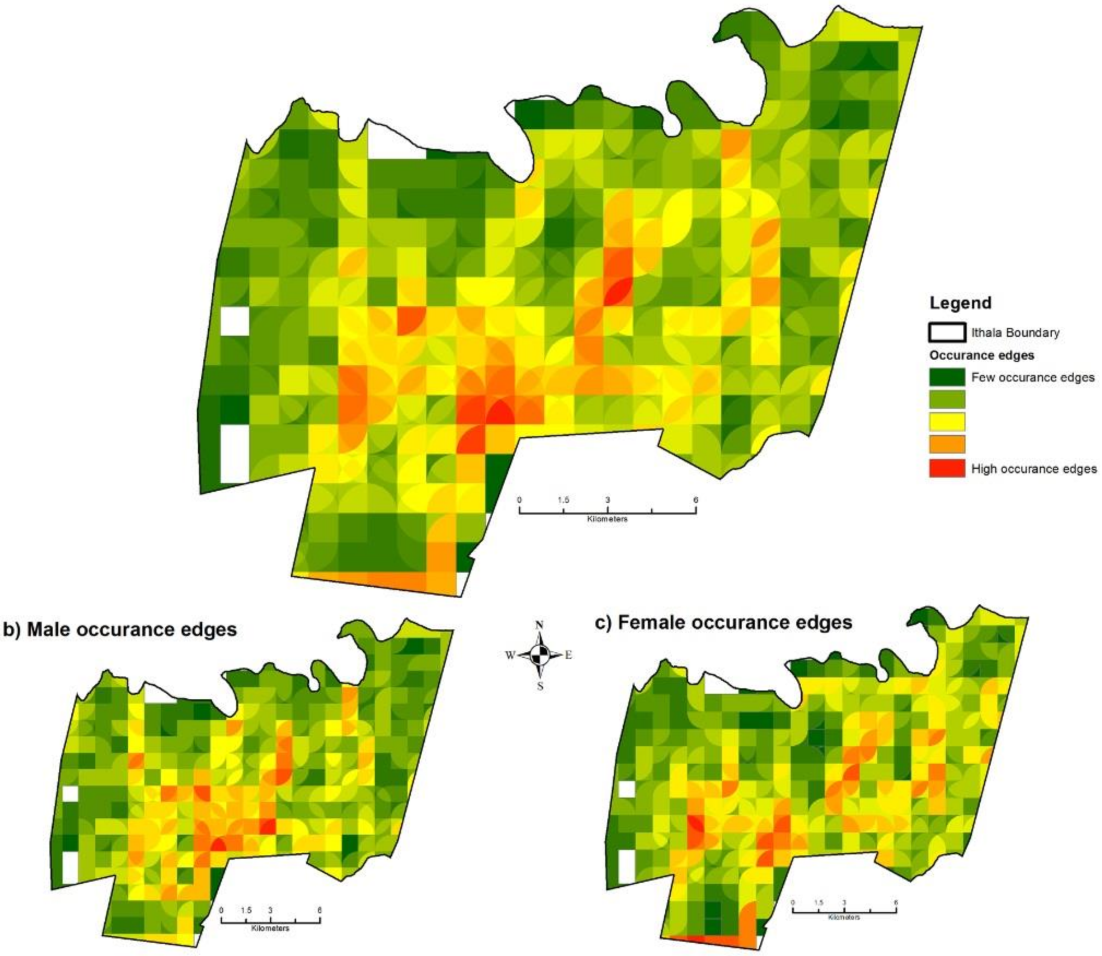

Fig. 3.3 Occurrence edge effects across Ithala Game Reserve from 1990 – 2008. The map represents the cumulative number of outermost grid cells (equating to the territory edges) summed across individual black rhino occurrence areas. High occurrence area edges could indicate a more disputed area between neighbouring individuals.

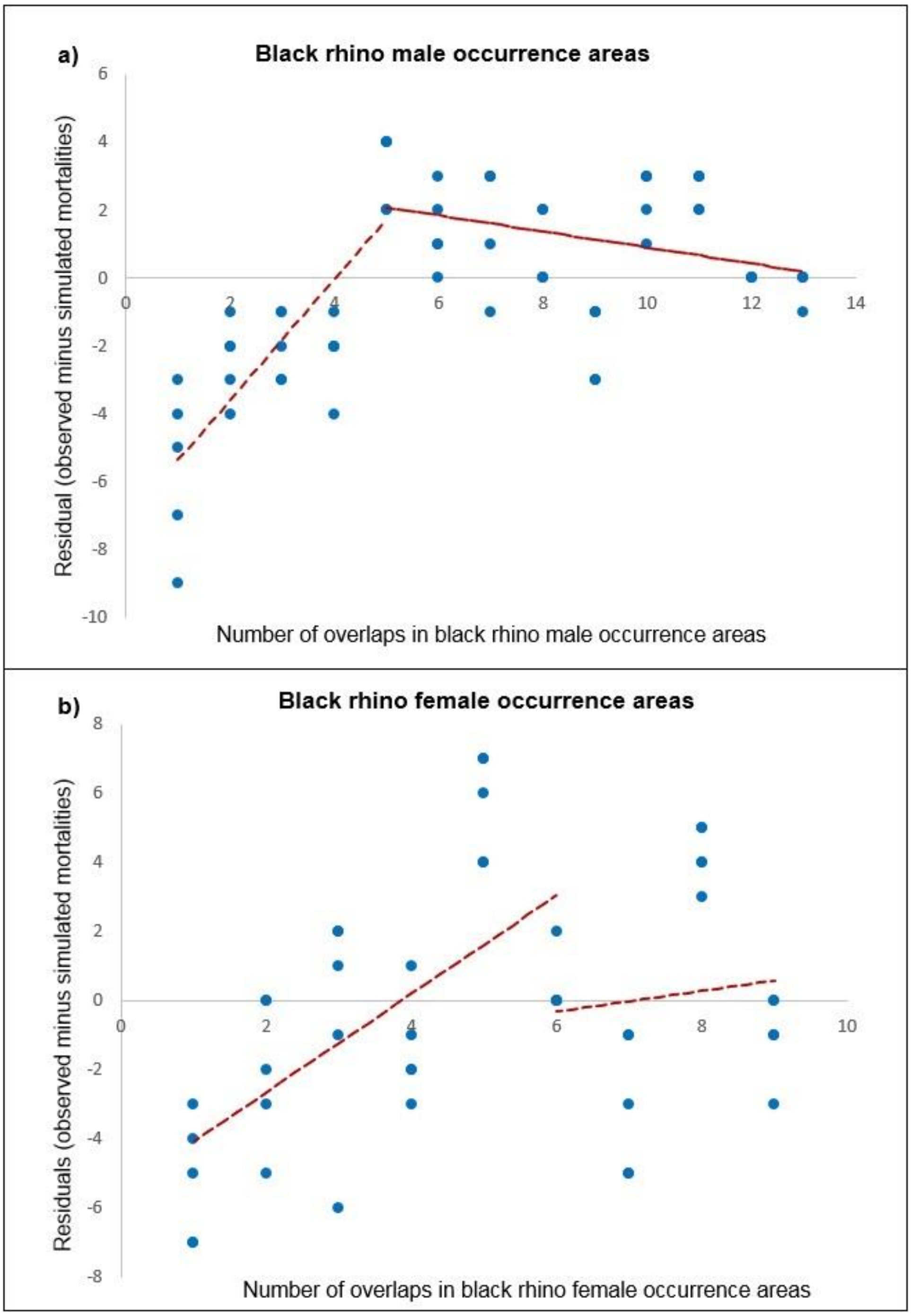

Fig. 3.4 The influence of the intensity of space use (number of overlaps in a grid cell) of male (a) and female (b) black rhino on the occurrence of mortalities. The number of observed mortalities compared to simulated mortalities increased strongly as the number of overlaps in male occurrence areas increased.

CHAPTER 4

Conclusions and management implications

Species generally respond to resources which can be affected by environmental conditions (Freeman *et al.,* 2014b), competition with other species (interspecific) (Ferry *et al.,* 2016), or competition within species (intraspecific) (Breed *et al.*, 2013). For animals, important resources include shelter, food, water and safety (Owen-Smith, 2002). If there are many resources and few individuals, the exponential growth may happen for a while (Snider & Brimlow, 2013). However, when the number of individuals increases, the resources needed to support exponential growth must eventually become inadequate, leading to a decline in population growth rate, with a density-dependence of population growth rate (e.g. wild reindeer, *Rangifer tarandus,* herds has density-dependent food limitation in winter; Skogland, 1985). If the form of density-dependence were constant and known, then the future population dynamics could, to some degree be predicted (Sibly & Hone, 2002).

When density increases or ecological conditions degrade, density-dependence or responses to environmental conditions are not necessarily linear (Sibly *et al.*, 2000). For convex non-linear density-dependence, effects on population growth only show up when the population is close to limiting factor values. This typically happens in large herbivore populations. The environmental effects at high population density may differ from its effects at low density in a similar way as that noted for density-dependence. The reason why this happens may associate with Eberhardt’s (2002) framework: At increasing densities or degrading ecological conditions resource depletion should first decrease juvenile survival, then decrease reproductive rates, and finally decrease adult survival. Should this framework materialise, it has implications for management of large herbivores.

All of the above impose particular challenges on the management of large herbivores because of the delayed responses or responses that are not detected easily. By the time density-dependence is detected on a numerical scale, a range of vital rates has already been affected. In this study, I explored some of the implications that may play out through environmental and density effects on vital rates of populations, as well as through social behaviour and spatial effects. I expect some implications for management because if density-dependence only materialise very late and the population is resource constraint (le Roex *et al.*, 2019), there are likely to be some other factors that are already playing a role in population dynamics (Saether, 1997).

As reported in Chapter 2, there was strong evidence for density-dependent regulation, with density in conception year a key driver of population performance. The population is not acting in an eruptive manner because of the density-dependence, through either resource limitation or social effects. Furthermore, the shorter interval between successive calves, along with the young age of first reproduction, implies that the density-dependent constraint is unlikely to be a resource limitation.

I could not refute my hypothesis that social effects as a result of density may be constraining or regulating the Ithala black rhino population dynamics. The mechanism of density-dependence in Ithala is through mortality that is associated with increased social interactions rather than resource limitations. This was reinforced in Chapter 3 where social interactions came out strongly as an explanatory factor for incidences of mortalities, but there was also a positive relationship between mortality and density. Apart from the strong association between mortality and black rhino intensity of use of an area, management removals also reflected as an explanatory variable for mortalities. This suggest that removals and translocations may unintentionally disrupt the social structure of a population, by leading to shifts in home ranges that create conflicts between individuals (Patton *et al.*, 2008).

The importance of stable dominance hierarchies among known individuals are essential to reduce the escalation of interactions to actual fighting, with potential mortality. Dominance hierarchies are often set and maintained by displays of aggression (Forkman & Haskell, 2004) and can greatly influence access to limited resources (Franz *et al*., 2015) and opportunities for mating (Sapolsky, 2005). Once individuals recognize the rank of a conspecific (Utne-Palm & Hart, 2000), or when the ranks are settled (Forkman & Haskell, 2004), the costly aggression may not be necessary, and, thereby, decreasing the risk of fatal injury. Therefore, behavioural studies should be effectively incorporated into planning for management removals and factored into management decisions.

Three broad conclusions can be drawn from my study; density in conception year is a key driver of population performance; social interactions is a strong explanatory factor for incidences of mortalities; and the density and growth of the Ithala black rhino population are indirectly driven by periodic translocations from the population. This study was initiated to determine the factors that may be affecting the reproductive performance of the black rhino population at Ithala. The population does not appear to be at ecological carrying capacity; however, social effects are delaying conception of females.

4.1 Management implications

Although up for revision, the South African Black Rhinoceros Biodiversity Management Plan (Knight *et al.,* 2013) has two strategic targets – at least 2800 south-central black rhinos and a sustained growth of 5% per annum by 2020. A key element is expanding the present black rhino distribution to have populations, albeit fragmented, across the species' previous range. South-central black rhinos were wide-spread across the south-eastern parts of Africa. The continental population declined and the distribution is now fragmented (Knight *et al.,* 2013). Individuals now occur in isolated protected areas across southern Africa (Githui, 2017). This reflects patches of suitable habitat embedded in a landscape of unsuitable habitat (Franklin & Lindenmayer, 2009). Such fragmentation influences the population dynamics of black rhinos, because resource gradients (Morgan, 2010), and how these vary, impacts on how species use landscapes (Campos *et al.*, 2013), and how vital rates respond.

Black rhinos may persist locally, and evolutionarily, if they can overcome the risks imposed by landscape fragmentation of suitable habitat (Adcock *et al.*, 1998). In such instances populations, albeit small, that occasionally interact with other populations, create a meta-population that has, as a whole, a higher chance of persistence than individual populations on their own. Meta-populations typically span landscapes that have patches of suitable habitat supporting local breeding populations, with vacant habitat patches that individuals can colonize (Hanski, 1999); suitable habitat vary on those patches resulting in different birth and death rates in asynchrony between patches; colonization and extinction of species on a patch takes place; and dispersal occurs between local populations occurring on patches (Hanski, 1999).

For large mammals, the time- and spatial-scale over which population dynamics play out, results in more lenient meta-population features. These focus on local breeding populations being discrete rather than inhabiting discrete habitat patches. This feature is very real for the black rhino populations in South Africa, such as the population which resides in Ithala. Secondly, local populations should have dissimilar growth rates, *i.e.* some local populations may increase while, at the same time, others decrease (Elmhagen & Angerbjörn, 2001).

Considering persistence of black rhinos as part of a meta-population, a key requirement is occasional dispersal between discrete populations. Biological dispersal is the movement of individuals from their birth site to their breeding site, as well as the movement from one breeding site to another

(Nathan, 2001). Dispersal, however, can be innate as well as environmentally driven (Howard, 1960). For black rhinos, males disperse innately as sub-adults looking for territories where they can eventually mate and breed. When such dispersal is constrained or prevented by features such as fences, then young males are likely to have higher mortality rates (Emslie & Brooks, 1999). Females disperse at much lower frequencies, but most likely in response to environmental driven factors like reduced food quality or increased negative social interactions as density increases. When dispersal is constrained, females may also experience higher mortality rates due to increased negative social interactions. An additional consequence is reduced reproductive output because of reduced body conditions associated with increased competition for food as densities increase (Rachlow & Berger, 1998). My study highlighted a combination of these factors playing out in Ithala.

If the landscapes had no constraints on dispersal, the above drivers may lead to occasional movement of individuals from one discrete population to another. The protected areas, including Ithala, where black rhinos occur are all fenced for a variety of reasons. Conservation managers cannot restore linkages across unsuitable habitat, but can mimic the process. The translocation as well as relocation of black rhinos are the primary tool to mimic how meta-population dynamics would play out across the landscape. The framework predicts that sub-adults will be the primary dispersers and that dispersal rate for males would be faster than females. Translocation and relocation should reflect this dynamic (Linklater & Swaisgood, 2008).

The above framework also provides some directives on how a species may colonize vacant habitat and establish new discrete populations. Because young males disperse innately, and, thus, more often, they will also colonize vacant habitats first, with females following much later at a slower rate (le Roex & Ferreira, 2020). Introducing black rhinos into new areas should thus mimic this process.

The mimicking of landscape-scale dispersal dynamics to enhance meta-population functioning and expanding rhino range, predicts maintenance, and even enhancement, of genetic integrity at a local discrete population scale. Apart from population responses, genetic integrity could thus serve as an indicator of the success of implementing management actions that seek to mimic meta-population dynamics.

My study highlighted some refinements required to help achieve aims of biological management for black rhino conservation that seek to maximise meta-population growth rates that aids species recovery. In addition, refining management processes that mimic dispersal dynamics that maintain persistence of black rhinos in fragmented landscapes contributes to ensuring genetic diversity is not lost, and, thereby, retaining the long-term evolutionary potential of black rhinos (Patton *et al.*, 2008). Specifically, live removal of young black rhino males, and, occasionally, young females, from high-density areas. This will minimise disruption of familiarity that has been build up among the older animals, which mitigates conflict escalations. Dispersal should also be studied in more detail. This could determine if the "buddy system" is important in reducing the high costs potentially associated with dispersal (Shrader & Owen-Smith, 2002).

Presence data obtained through direct observations of marked individual rhinos placed some limitations on my study. Understanding home range and habitat use of black rhinos and the impact on population performance at Ithala could improve through using tracking equipment such as GPS collars to track the movements of individual black rhinos (Morgan, 2010). This will improve movement analyses. By using tracking equipment, the number of sightings per individual black rhino will be significantly increased and this will allow for a more comprehensive assessment of space use, whilst also allowing for the collection of nocturnal spatial data for black rhinos (Morgan, 2010).

In addition, my EVI variable indicated a weaker influence of environmental factors on mortality once I accounted for the effects of year. It would be beneficial if research can be conducted on black rhino distribution in relation to plant community and diet selection. This will provide further information on the nutritional requirements of black rhino in Ithala Game Reserve.

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APPENDICES

Appendix 3.1. The full list of explanatory models which best describe the association between mortality occurrences with a set of variables (density, EVI, management removals and Year).

Model	n	K	Fstat	r2	AiCc	ΔAICc (Δi)	Model likelihood	Wi
Year	66	1	5877902.0	0.9999	-652.046	0.00000	1.00000	0.07192
Density-Year	66	2	2920987.7	1.0000	-650.412	1.63389	0.44178	0.03177
Removals-Year	66	2	2915015.6	1.0000	-650.277	1.76897	0.41293	0.02970
EVI-Year	66	2	2910125.6	1.0000	-650.166	1.87978	0.39067	0.02810
Year-Overlaps Females	66	2	2896804.9	1.0000	-649.863	2.18258	0.33578	0.02415
Slope-Year	66	2	2896661.0	1.0000	-649.860	2.18586	0.33523	0.02411
Year-Overlaps Males	66	2	2893921.1	1.0000	-649.797	2.24831	0.32493	0.02337
Distance to Water-Year	66	2	2893262.5	1.0000	-649.782	2.26333	0.32250	0.02319
Year-Overlaps All	66	2	2893036.1	1.0000	-649.777	2.26850	0.32166	0.02313
Year-Edge-Overlaps All	66	3	1950473.2	1.0000	-649.230	2.81554	0.24469	0.01760
Year-Edge-Overlaps Males	66	3	1944452.2	1.0000	-649.026	3.01959	0.22096	0.01589
Removals-Year-Edge	66	3	1939653.5	1.0000	-648.863	3.18267	0.20365	0.01465
Density-Removals-Year	66	3	1939644.1	1.0000	-648.863	3.18299	0.20362	0.01464
Slope-Year-Edge	66	3	1930181.7	1.0000	-648.540	3.50575	0.17328	0.01246
Year-Overlaps All-Overlaps Females	66	3	1925870.0	1.0000	-648.392	3.65335	0.16095	0.01158
Density-Year-Edge-Overlaps Females	66	4	1471489.3	1.0000	-648.268	3.77767	0.15125	0.01088
Density-EVI-Year	66	3	1920063.5	1.0000	-648.193	3.85263	0.14568	0.01048
Density-Distance to Water-Year	66	3	1918794.4	1.0000	-648.149	3.89627	0.14254	0.01025
Removals-Year-Overlaps Males	66	3	1917937.8	1.0000	-648.120	3.92574	0.14045	0.01010
EVI-Year-Edge-Overlaps Females	66	4	1468170.8	1.0000	-648.119	3.92668	0.14039	0.01010
Density-Slope-Year	66	3	1916566.8	1.0000	-648.073	3.97294	0.13718	0.00987
Removals-Year-Overlaps All	66	3	1914482.3	1.0000	-648.001	4.04476	0.13234	0.00952
Removals-Distance to Water-Year	66	3	1914027.6	1.0000	-647.985	4.06043	0.13131	0.00944
Year-Overlaps Females-Overlaps Males	66	3	1913671.5	1.0000	-647.973	4.07272	0.13050	0.00939
Removals-Year-Overlaps Females	66	3	1912800.3	1.0000	-647.943	4.10277	0.12856	0.00925
Density-Year-Edge-Overlaps All	66	4	1463568.9	1.0000	-647.912	4.13388	0.12657	0.00910
Slope-Year-Edge-Overlaps Females	66	4	1462739.0	1.0000	-647.874	4.17131	0.12423	0.00893
EVI-Distance to Water-Year	66	3	1910009.5	1.0000	-647.847	4.19913	0.12251	0.00881
EVI-Slope-Year	66	3	1909346.5	1.0000	-647.824	4.22205	0.12111	0.00871
Slope-Year-Overlaps Females	66	3	1905930.0	1.0000	-647.706	4.34025	0.11416	0.00821
EVI-Year-Edge-Overlaps All	66	4	1458404.6	1.0000	-647.679	4.36717	0.11264	0.00810
Year-Overlaps Males-Overlaps All	66	3	1903166.2	1.0000	-647.610	4.43602	0.10883	0.00783
Distance to Water-Year-Overlaps Females	66	3	1900773.3	1.0000	-647.527	4.51906	0.10440	0.00751
Slope-Year-Overlaps All	66	3	1900688.3	1.0000	-647.524	4.52201	0.10425	0.00750
Slope-Year-Overlaps Males	66	3	1900583.7	1.0000	-647.520	4.52564	0.10406	0.00748
Slope-Distance to Water-Year	66	3	1900566.4	1.0000	-647.520	4.52624	0.10403	0.00748
Density-Year-Edge-Overlaps Males	66	4	1453684.7	1.0000	-647.465	4.58111	0.10121	0.00728
Distance to Water-Year-Overlaps Males	66	3	1898770.7	1.0000	-647.457	4.58863	0.10083	0.00725
Distance to Water-Year-Overlaps All	66	3	1898226.2	1.0000	-647.438	4.60756	0.09988	0.00718
Slope-Year-Edge-Overlaps All	66	4	1452814.2	1.0000	-647.425	4.62065	0.09923	0.00714

Model	n	K	Fstat	r2	AiCc	ΔAICc (Δi)	Model likelihood	Wi
EVI-Year-Edge-Overlaps Males	66	4	1449057.7	1.0000	-647.254	4.79152	0.09110	0.00655
Density-EVI-Year-Overlaps Females	66	4	1448739.1	1.0000	-647.240	4.80603	0.09044	0.00650
Density-Year-Overlaps All-Overlaps Females	66	4	1448442.5	1.0000	-647.226	4.81955	0.08984	0.00646
Removals-Year-Edge-Overlaps Females	66	4	1447297.4	1.0000	-647.174	4.87175	0.08752	0.00629
Year-Overlaps All-Overlaps Females-Edge	66	4	1446983.6	1.0000	-647.160	4.88606	0.08690	0.00625
Distance to Water-Year-Edge-Overlaps Females	66	4	1445723.8	1.0000	-647.102	4.94354	0.08444	0.00607
Year-Edge-Overlaps Males-Overlaps Females	66	4	1445719.7	1.0000	-647.102	4.94373	0.08443	0.00607
Slope-Year-Edge-Overlaps Males	66	4	1443559.4	1.0000	-647.003	5.04243	0.08036	0.00578
Density-Year-Overlaps Females-Overlaps Males	66	4	1443272.2	1.0000	-646.990	5.05556	0.07984	0.00574
Removals-Year-Edge-Overlaps All	66	4	1440378.5	1.0000	-646.858	5.18802	0.07472	0.00537
Year-Overlaps Males-Overlaps All-Edge	66	4	1439503.5	1.0000	-646.818	5.22812	0.07324	0.00527
Distance to Water-Year-Edge-Overlaps All	66	4	1439289.8	1.0000	-646.808	5.23792	0.07288	0.00524
Removals-Year-Overlaps All-Overlaps Females	66	4	1438462.4	1.0000	-646.770	5.27587	0.07151	0.00514
Removals-Year-Edge-Overlaps Males	66	4	1436223.6	1.0000	-646.667	5.37867	0.06793	0.00489
EVI-Year-Overlaps All-Overlaps Females	66	4	1435486.8	1.0000	-646.633	5.41254	0.06679	0.00480
Distance to Water-Year-Edge-Overlaps Males	66	4	1434830.0	1.0000	-646.603	5.44274	0.06578	0.00473
Density-EVI-Year-Overlaps All	66	4	1432429.4	1.0000	-646.493	5.55326	0.06225	0.00448
Density-Removals-Slope-Year	66	4	1432333.4	1.0000	-646.488	5.55768	0.06211	0.00447
Year-Overlaps Females-Overlaps Males-Overlaps All	66	4	1432092.4	1.0000	-646.477	5.56879	0.06177	0.00444
Removals-Distance to Water-Edge	66	4	1431734.4	1.0000	-646.460	5.58529	0.06126	0.00441
Density-Year-Overlaps Males-Overlaps All	66	4	1430129.3	1.0000	-646.386	5.65932	0.05903	0.00425
Density-Slope-Year-Edge-Overlaps Females	66	5	1168753.3	1.0000	-646.377	5.66884	0.05875	0.00423
Density-EVI-Year-Edge-Overlaps Females	66	5	1168720.8	1.0000	-646.375	5.67068	0.05870	0.00422
Density-EVI-Year-Edge	66	4	1429130.5	1.0000	-646.340	5.70543	0.05769	0.00415
Removals-Year-Overlaps Females-Overlaps Males	66	4	1427786.8	1.0000	-646.278	5.76752	0.05592	0.00402
Slope-Year-Overlaps All-Overlaps Females	66	4	1426884.1	1.0000	-646.237	5.80925	0.05477	0.00394
EVI-Year-Overlaps Females-Overlaps Males	66	4	1426079.4	1.0000	-646.199	5.84649	0.05376	0.00387
Density-EVI-Year-Overlaps Males	66	4	1424803.5	1.0000	-646.140	5.90556	0.05219	0.00375
Slope-Distance to Water-Year-Edge	66	4	1424289.7	1.0000	-646.116	5.92937	0.05158	0.00371
EVI-Removals-Slope-Year	66	4	1422797.5	1.0000	-646.047	5.99855	0.04982	0.00358
Density-Distance to Water-Year-Edge-Overlaps Females	66	5	1162605.5	1.0000	-646.029	6.01693	0.04937	0.00355
EVI-Slope-Year-Edge-Overlaps Females	66	5	1162227.2	1.0000	-646.007	6.03841	0.04884	0.00351
Distance to Water-Year-Overlaps All-Overlaps Females	66	4	1421105.7	1.0000	-645.969	6.07707	0.04790	0.00345
Density-EVI-Year-Edge-Overlaps All	66	5	1160710.5	1.0000	-645.921	6.12459	0.04678	0.00336
Density-Slope-Year-Edge-Overlaps All	66	5	1160501.4	1.0000	-645.909	6.13648	0.04650	0.00334
Density-Removals-Year-Edge-Overlaps Females	66	5	1160320.9	1.0000	-645.899	6.14674	0.04626	0.00333
Removals-Year-Overlaps Males-Overlaps All	66	4	1419503.9	1.0000	-645.894	6.15151	0.04615	0.00332
Density-Year-Edge-Overlaps Males-Overlaps Females	66	5	1160027.2	1.0000	-645.882	6.16345	0.04588	0.00330
Slope-Year-Overlaps Females-Overlaps Males	66	4	1417172.5	1.0000	-645.786	6.25999	0.04372	0.00314
Density-EVI-Slope-Year	66	4	1416868.6	1.0000	-645.772	6.27415	0.04341	0.00312
Density-Year-Overlaps All-Overlaps Females-Edge	66	5	1157911.7	1.0000	-645.762	6.28392	0.04320	0.00311
Removals-Distance to Water-Year-Overlaps Males	66	4	1416419.8	1.0000	-645.751	6.29505	0.04296	0.00309
Density-Distance to Water-Year-Edge-Overlaps All	66	5	1157521.6	1.0000	-645.740	6.30616	0.04272	0.00307
Density-Slope-Distance to Water-Year	66	4	1415918.2	1.0000	-645.727	6.31843	0.04246	0.00305
EVI-Year-Overlaps Males-Overlaps All	66	4	1415367.5	1.0000	-645.702	6.34411	0.04192	0.00301
EVI-Year-Edge-Overlaps All-Overlaps Females	66	5	1155926.9	1.0000	-645.649	6.39715	0.04082	0.00294
EVI-Year-Overlaps All-Overlaps Females-Edge	66	5	1155926.9	1.0000	-645.649	6.39715	0.04082	0.00294

Model	**n**	**K**	**Fstat**	**r2**	**AiCc**	**ΔAICc (Δi)**	**Model likelihood**	**Wi**
EVI-Distance to Water-Year-Edge-Overlaps Females	66	5	1155827.2	1.0000	-645.643	6.40284	0.04070	0.00293
Removals-Distance to Water-Edge-Overlaps All	66	4	1413814.3	1.0000	-645.629	6.41657	0.04043	0.00291
EVI-Year-Edge-Overlaps Females-Overlaps Males	66	5	1155320.2	1.0000	-645.614	6.43180	0.04012	0.00289
Density-Year-Overlaps Females-Overlaps Males-Overlaps All	66	5	1155314.8	1.0000	-645.614	6.43211	0.04011	0.00288
Removals-Distance to Water-Year-Overlaps Females	66	4	1412583.4	1.0000	-645.572	6.47406	0.03928	0.00283
Distance to Water-Year-Overlaps Females-Overlaps Males	66	4	1412166.8	1.0000	-645.552	6.49353	0.03890	0.00280
Distance to Water-Year-Overlaps Females-Overlaps Males-Overlaps All	66	5	1412166.8	1.0000	-645.552	6.49353	0.03890	0.00280
EVI-Slope-Year-Edge-Overlaps All	66	5	1152849.6	1.0000	-645.473	6.57309	0.03738	0.00269
Density-Removals-Year-Edge-Overlaps All	66	5	1152366.3	1.0000	-645.445	6.60076	0.03687	0.00265
Density-EVI-Removals-Slope-Distance to Water	66	5	1409420.4	1.0000	-645.424	6.62201	0.03648	0.00262
EVI-Slope-Distance to Water-Year	66	4	1409420.4	1.0000	-645.424	6.62201	0.03648	0.00262
Density-Removals-Year-Overlaps All-Overlaps Females	66	5	1151944.8	1.0000	-645.421	6.62491	0.03643	0.00262
Density-Year-Overlaps Males-Overlaps All-Edge	66	5	1151662.1	1.0000	-645.405	6.64111	0.03613	0.00260
Slope-Year-Overlaps All-Overlaps Females-Edge	66	5	1151555.8	1.0000	-645.399	6.64720	0.03602	0.00259
Slope-Year-Edge-Overlaps Males-Overlaps Females	66	5	1151094.1	1.0000	-645.372	6.67367	0.03555	0.00256
Slope-Year-Overlaps Males-Overlaps All	66	4	1407336.7	1.0000	-645.326	6.71965	0.03474	0.00250
Density-EVI-Year-Edge-Overlaps Males	66	5	1149662.3	1.0000	-645.290	6.75581	0.03412	0.00245
Slope-Distance to Water-Year-Overlaps Females	66	4	1406528.9	1.0000	-645.288	6.75755	0.03409	0.00245
Density-Slope-Year-Edge-Overlaps Males	66	5	1148389.3	1.0000	-645.217	6.82893	0.03289	0.00237
EVI-Distance to Water-Year-Edge-Overlaps All	66	5	1148264.0	1.0000	-645.210	6.83613	0.03278	0.00236
EVI-Year-Edge-Overlaps Males-Overlaps All	66	5	1148236.3	1.0000	-645.208	6.83773	0.03275	0.00236
Density-Distance to Water-Year-Edge-Overlaps Males	66	5	1147914.3	1.0000	-645.190	6.85623	0.03245	0.00233
Density-Removals-Slope-Year-Overlaps Females	66	5	1147395.9	1.0000	-645.160	6.88605	0.03197	0.00230
Slope-Distance to Water-Year-Overlaps All	66	4	1402624.3	1.0000	-645.105	6.94102	0.03110	0.00224
Year-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	5	1146420.1	1.0000	-645.104	6.94220	0.03108	0.00224
Slope-Distance to Water-Year-Overlaps Males	66	4	1402518.6	1.0000	-645.100	6.94600	0.03102	0.00223
Density-Removals-Year-Overlaps Females-Overlaps Males	66	5	1145886.4	1.0000	-645.073	6.97293	0.03061	0.00220
Density-EVI-Year-Overlaps Females-Overlaps All	66	5	1145862.7	1.0000	-645.071	6.97430	0.03059	0.00220
Density-Distance to Water-Year-Overlaps All-Overlaps Females	66	5	1145475.3	1.0000	-645.049	6.99662	0.03025	0.00218
Density-Removals-Year-Edge-Overlaps Males	66	5	1144521.6	1.0000	-644.994	7.05159	0.02943	0.00212
Slope-Year-Overlaps Males-Overlaps All-Edge	66	5	1143748.9	1.0000	-644.950	7.09616	0.02878	0.00207
Density-Slope-Year-Overlaps All-Overlaps Females	66	5	1143399.9	1.0000	-644.929	7.11630	0.02849	0.00205
Density-Distance to Water-Year-Overlaps Females-Overlaps Males	66	5	1143265.3	1.0000	-644.922	7.12407	0.02838	0.00204
Slope-Distance to Water-Year-Edge-Overlaps All	66	5	1143205.0	1.0000	-644.918	7.12756	0.02833	0.00204
Slope-Distance to Water-Year-Edge-Overlaps Females	66	5	1143205.0	1.0000	-644.918	7.12756	0.02833	0.00204
EVI-Slope-Year-Edge-Overlaps Males	66	5	1142934.8	1.0000	-644.903	7.14315	0.02811	0.00202
Removals-Year-Overlaps All-Overlaps Females-Edge	66	5	1141738.8	1.0000	-644.834	7.21226	0.02716	0.00195
Density-EVI-Year-Overlaps Males-Overlaps Females	66	5	1141130.6	1.0000	-644.798	7.24742	0.02668	0.00192
Density-EVI-Slope-Year-Overlaps Females	66	5	1141100.8	1.0000	-644.797	7.24915	0.02666	0.00192
EVI-Distance to Water-Year-Edge-Overlaps Males	66	5	1140644.7	1.0000	-644.770	7.27553	0.02631	0.00189
Removals-Year-Edge-Overlaps Males-Overlaps Females	66	5	1139160.9	1.0000	-644.684	7.36144	0.02520	0.00181
Removals-Distance to Water-Edge-Overlaps Females	66	5	1138967.1	1.0000	-644.673	7.37267	0.02506	0.00180
Density-Slope-Year-Overlaps Females-Overlaps Males	66	5	1138772.3	1.0000	-644.662	7.38396	0.02492	0.00179
Distance to Water-Year-Overlaps All-Overlaps Females-Edge	66	5	1138610.2	1.0000	-644.652	7.39335	0.02481	0.00178
Removals-Year-Overlaps Females-Overlaps Males-Overlaps All	66	5	1138355.5	1.0000	-644.638	7.40812	0.02462	0.00177
EVI-Year-Overlaps All-Overlaps Females-Overlaps Males	66	5	1138088.6	1.0000	-644.622	7.42360	0.02443	0.00176
Distance to Water-Year-Edge-Overlaps Males-Overlaps Females	66	5	1137619.7	1.0000	-644.595	7.45079	0.02410	0.00173

Model	n	K	Fstat	r2	AiCc	ΔAICc (Δi)	Model likelihood	Wi
Slope-Distance to Water-Year-Edge-Overlaps Males	66	5	1135916.3	1.0000	-644.496	7.54969	0.02294	0.00165
Density-Removals-Year-Overlaps Males-Overlaps All	66	5	1135351.2	1.0000	-644.463	7.58253	0.02257	0.00162
Density-EVI-Removals-Distance to Water-Year	66	5	1134726.9	1.0000	-644.427	7.61883	0.02216	0.00159
Removals-Year-Overlaps Males-Overlaps All-Edge	66	5	1133997.8	1.0000	-644.385	7.66125	0.02170	0.00156
Removals-Distance to Water-Edge-Overlaps All	66	5	1133556.6	1.0000	-644.359	7.68694	0.02142	0.00154
Distance to Water-Year-Overlaps Males-Overlaps All-Edge	66	5	1132749.2	1.0000	-644.312	7.73396	0.02092	0.00150
Removals-Distance to Water-Edge-Overlaps All-Overlaps Females	66	5	1132447.2	1.0000	-644.294	7.75156	0.02074	0.00149
Density-Distance to Water-Year-Overlaps Males-Overlaps All	66	5	1132446.6	1.0000	-644.294	7.75160	0.02074	0.00149
Density-Removals-Slope-Distance to Water-Year	66	5	1132199.0	1.0000	-644.280	7.76603	0.02059	0.00148
Slope-Year-Overlaps Females-Overlaps Males-Overlaps All	66	5	1131763.3	1.0000	-644.254	7.79143	0.02033	0.00146
EVI-Slope-Year-Overlaps All-Overlaps Females	66	5	1130972.9	1.0000	-644.208	7.83754	0.01987	0.00143
Removals-Distance to Water-Edge-Overlaps Males	66	5	1130280.4	1.0000	-644.168	7.87797	0.01947	0.00140
EVI-Distance to Water-Year-Overlaps All-Overlaps Females	66	5	1129872.6	1.0000	-644.144	7.90178	0.01924	0.00138
Density-EVI-Slope-Year-Edge-Overlaps Females	66	6	962989.2	1.0000	-644.143	7.90258	0.01923	0.00138
Density-EVI-Year-Overlaps Males-Overlaps All	66	5	1129369.6	1.0000	-644.115	7.93117	0.01896	0.00136
Density-Removals-Slope-Year-Overlaps Males	66	5	1129195.0	1.0000	-644.104	7.94137	0.01886	0.00136
Density-EVI-Slope-Year-Overlaps All	66	5	1127384.1	1.0000	-643.998	8.04730	0.01789	0.00129
Density-Slope-Distance to Water-Year-Edge-Overlaps Females	66	6	960749.6	1.0000	-643.990	8.05625	0.01781	0.00128
Density-Slope-Year-Overlaps Males-Overlaps All	66	5	1126876.6	1.0000	-643.969	8.07702	0.01762	0.00127
Density-Year-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	6	960414.6	1.0000	-643.966	8.07927	0.01760	0.00127
Density-Removals-Slope-Year-Edge-Overlaps Females	66	6	960041.3	1.0000	-643.941	8.10493	0.01738	0.00125
Density-Slope-Year-Edge-Overlaps Males-Overlaps Females	66	6	959893.4	1.0000	-643.931	8.11510	0.01729	0.00124
Density-EVI-Year-Edge-Overlaps Males-Overlaps Females	66	6	959229.0	1.0000	-643.885	8.16080	0.01690	0.00122
Density-EVI-Slope-Year-Edge	66	5	1124629.4	1.0000	-643.837	8.20877	0.01650	0.00119
Removals-Distance to Water-Year-Overlaps Females-Overlaps Males	66	5	1124418.3	1.0000	-643.825	8.22115	0.01640	0.00118
Density-Slope-Year-Overlaps All-Overlaps Females-Edge	66	6	957805.5	1.0000	-643.787	8.25881	0.01609	0.00116
Density-EVI-Year-Overlaps Females-Overlaps All-Edge	66	6	957710.8	1.0000	-643.780	8.26533	0.01604	0.00115
EVI-Slope-Year-Overlaps Females-Overlaps Males	66	5	1123283.6	1.0000	-643.758	8.28779	0.01586	0.00114
Slope-Distance to Water-Year-Overlaps All-Overlaps Females	66	5	1122796.7	1.0000	-643.729	8.31641	0.01564	0.00112
EVI-Distance to Water-Year-Overlaps Females-Overlaps Males	66	5	1122754.4	1.0000	-643.727	8.31889	0.01562	0.00112
Density-Distance to Water-Year-Edge-Overlaps Males-Overlaps Females	66	6	955615.5	1.0000	-643.636	8.40989	0.01492	0.00107
Density-EVI-Slope-Year-Overlaps Males	66	5	1121166.3	1.0000	-643.633	8.41231	0.01490	0.00107
Density-EVI-Slope-Year-Edge-Overlaps All	66	6	955306.5	1.0000	-643.615	8.43123	0.01476	0.00106
Density-Slope-Distance to Water-Year-Edge-Overlaps All	66	7	955111.1	1.0000	-643.601	8.44474	0.01466	0.00105
Density-Removals-Year-Overlaps Females-Overlaps Males-Overlaps All	66	6	954210.3	1.0000	-643.539	8.50701	0.01421	0.00102
Density-EVI-Removals-Distance to Water-Year-Overlaps Females	66	6	953781.7	1.0000	-643.509	8.53666	0.01401	0.00101
EVI-Removals-Slope-Year-Edge-Overlaps Females	66	6	953469.2	1.0000	-643.487	8.55829	0.01385	0.00100
Density-Distance to Water-Year-Overlaps All-Overlaps Females-Edge	66	6	952987.8	1.0000	-643.454	8.59162	0.01363	0.00098
Removals-Distance to Water-Year-Overlaps Males-Overlaps All	66	5	1118076.8	1.0000	-643.451	8.59443	0.01361	0.00098
EVI-Slope-Year-Overlaps All-Overlaps Females-Edge	66	6	952720.8	1.0000	-643.436	8.61012	0.01350	0.00097
EVI-Slope-Distance to Water-Year-Edge-Overlaps Females	66	6	952607.7	1.0000	-643.428	8.61795	0.01345	0.00097
EVI-Slope-Year-Edge-Overlaps Males-Overlaps Females	66	6	952489.7	1.0000	-643.420	8.62612	0.01339	0.00096
Density-Removals-Slope-Year-Edge-Overlaps All	66	6	951453.6	1.0000	-643.348	8.69796	0.01292	0.00093
Density-Removals-Year-Edge-Overlaps Males-Overlaps Females	66	6	951396.7	1.0000	-643.344	8.70190	0.01289	0.00093
Density-Removals-Slope-Distance to Water-Year-Overlaps Females	66	6	951301.1	1.0000	-643.337	8.70854	0.01285	0.00092
Density-EVI-Year-Overlaps Males-Overlaps All-Edge	66	6	951224.4	1.0000	-643.332	8.71386	0.01282	0.00092
Density-Removals-Year-Overlaps All-Overlaps Females-Edge	66	6	951148.3	1.0000	-643.327	8.71914	0.01278	0.00092

Model	**n**	**K**	**Fstat**	**r2**	**AiCc**	**ΔAICc (Δi)**	**Model likelihood**	**Wi**
Density-Slope-Year-Overlaps Males-Overlaps All-Edge	66	6	951023.8	1.0000	-643.318	8.72778	0.01273	0.00092
Density-EVI-Year-Overlaps Males-Overlaps Females-Overlaps All	66	6	950981.2	1.0000	-643.315	8.73074	0.01271	0.00091
Density-Distance to Water-Year-Overlaps Females-Overlaps Males-Overlaps All	66	6	950848.8	1.0000	-643.306	8.73992	0.01265	0.00091
Slope-Distance to Water-Year-Overlaps Females-Overlaps Males	66	5	1115183.3	1.0000	-643.280	8.76545	0.01249	0.00090
Slope-Year-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	5	950310.9	1.0000	-643.268	8.77727	0.01242	0.00089
Density-Slope-Year-Overlaps Females-Overlaps Males-Overlaps All	66	6	949899.1	1.0000	-643.240	8.80588	0.01224	0.00088
EVI-Distance to Water-Year-Overlaps Males-Overlaps All	66	5	1114421.6	1.0000	-643.235	8.81055	0.01221	0.00088
EVI-Slope-Year-Overlaps Males-Overlaps All	66	5	1114176.2	1.0000	-643.221	8.82508	0.01212	0.00087
Density-Removals-Slope-Year-Overlaps All-Overlaps Females	66	6	948936.6	1.0000	-643.173	8.87279	0.01184	0.00085
Density-Distance to Water-Year-Overlaps Males-Overlaps All-Edge	66	6	948538.5	1.0000	-643.145	8.90048	0.01168	0.00084
EVI-Distance to Water-Year-Overlaps All-Overlaps Females-Edge	66	6	947588.0	1.0000	-643.079	8.96665	0.01130	0.00081
EVI-Distance to Water-Year-Edge-Overlaps Males-Overlaps Females	66	6	947176.9	1.0000	-643.050	8.99529	0.01114	0.00080
EVI-Slope-Year-Overlaps Males-Overlaps All-Edge	66	6	945455.2	1.0000	-642.930	9.11536	0.01049	0.00075
EVI-Slope-Distance to Water-Year-Edge-Overlaps All	66	6	945048.8	1.0000	-642.902	9.14374	0.01034	0.00074
EVI-Removals-Slope-Year-Edge-Overlaps All	66	6	945011.8	1.0000	-642.899	9.14633	0.01033	0.00074
Density-Removals-Year-Overlaps Males-Overlaps All-Edge	66	6	944347.2	1.0000	-642.853	9.19275	0.01009	0.00073
Slope-Distance to Water-Year-Overlaps Males-Overlaps All	66	5	1107499.1	1.0000	-642.824	9.22180	0.00994	0.00072
Distance to Water-Year-Overlaps Males-Overlaps All	66	4	1107499.1	1.0000	-642.824	9.22180	0.00994	0.00072
Density-EVI-Slope-Year-Edge-Overlaps Males	66	6	943871.9	1.0000	-642.820	9.22598	0.00992	0.00071
Density-Slope-Distance to Water-Year-Edge-Overlaps Males	66	6	943719.1	1.0000	-642.809	9.23667	0.00987	0.00071
Slope-Distance to Water-Year-Overlaps All-Overlaps Females-Edge	66	6	943647.8	1.0000	-642.804	9.24165	0.00984	0.00071
Slope-Distance to Water-Year-Edge-Overlaps Males-Overlaps Females	66	6	943260.2	1.0000	-642.777	9.26877	0.00971	0.00070
Density-Removals-Slope-Year-Overlaps Females-Overlaps Males	66	6	943207.2	1.0000	-642.773	9.27248	0.00969	0.00070
Density-Removals-Slope-Year-Edge-Overlaps Males	66	6	941568.4	1.0000	-642.659	9.38725	0.00915	0.00066
EVI-Distance to Water-Year-Overlaps Males-Overlaps All-Edge	66	6	941496.8	1.0000	-642.653	9.39227	0.00913	0.00066
Density-Slope-Distance to Water-Year-Overlaps All-Overlaps Females	66	6	941244.1	1.0000	-642.636	9.40999	0.00905	0.00065
Removals-Year-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	6	941195.7	1.0000	-642.632	9.41338	0.00903	0.00065
Density-EVI-Removals-Distance to Water-Year-Overlaps All	66	6	941116.1	1.0000	-642.627	9.41896	0.00901	0.00065
Density-EVI-Slope-Year-Overlaps Females-Overlaps All	66	6	940226.5	1.0000	-642.564	9.48138	0.00873	0.00063
EVI-Removals-Slope-Year-Overlaps All-Overlaps Females	66	6	940041.5	1.0000	-642.551	9.49437	0.00868	0.00062
Distance to Water-Year-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	6	939534.5	1.0000	-642.516	9.52997	0.00852	0.00061
Density-Slope-Distance to Water-Year-Overlaps Females-Overlaps Males	66	6	938992.3	1.0000	-642.478	9.56807	0.00836	0.00060
Density-Removals-Slope-Distance to Water-Year-Overlaps All	66	6	938662.6	1.0000	-642.455	9.59125	0.00827	0.00059
Slope-Distance to Water-Year-Overlaps Males-Overlaps All-Edge	66	6	937245.7	1.0000	-642.355	9.69095	0.00786	0.00057
EVI-Removals-Slope-Year-Edge-Overlaps Males	66	6	937184.2	1.0000	-642.350	9.69528	0.00785	0.00056
EVI-Slope-Distance to Water-Year-Edge-Overlaps Males	66	6	936775.8	1.0000	-642.322	9.72404	0.00773	0.00056
Density-EVI-Slope-Year-Overlaps Males-Overlaps Females	66	6	936121.4	1.0000	-642.276	9.77017	0.00756	0.00054
Removals-Distance to Water-Edge-Overlaps All-Overlaps Females	66	6	935715.9	1.0000	-642.247	9.79876	0.00745	0.00054
Removals-Distance to Water-Edge-Overlaps All-Overlaps Females-Edge	66	5	935715.9	1.0000	-642.247	9.79876	0.00745	0.00054
Density-EVI-Removals-Distance to Water-Year-Overlaps Males	66	6	934055.6	1.0000	-642.130	9.91597	0.00703	0.00051
EVI-Slope-Year-Overlaps Females-Overlaps Males-Overlaps All	66	6	933922.5	1.0000	-642.120	9.92538	0.00699	0.00050
Removals-Distance to Water-Edge-Overlaps Males-Overlaps Females	66	6	933599.5	1.0000	-642.098	9.94821	0.00691	0.00050
Removals-Distance to Water-Overlaps All-Overlaps Females-Overlaps Males	66	6	932926.2	1.0000	-642.050	9.99582	0.00675	0.00049
Removals-Distance to Water-Year-Overlaps Females-Overlaps Males-Overlaps All	66	6	932926.2	1.0000	-642.050	9.99582	0.00675	0.00049
Density-Removals-Slope-Year-Overlaps Males-Overlaps All	66	6	932838.0	1.0000	-642.044	10.00207	0.00673	0.00048
EVI-Distance to Water-Year-Overlaps Females-Overlaps Males-Overlaps All	66	6	932629.6	1.0000	-642.029	10.01681	0.00668	0.00048
EVI-Removals-Slope-Year-Overlaps Males-Overlaps Females	66	6	932437.7	1.0000	-642.015	10.03039	0.00664	0.00048

Model	n	K	Fstat	r2	AiCc	ΔAICc (Δi)	Model likelihood	Wi
Density-EVI-Removals-Distance to Water-Year-Edge	66	6	932318.5	1.0000	-642.007	10.03883	0.00661	0.00048
Density-Removals-Slope-Distance to Water-Year-Overlaps Males	66	6	931984.4	1.0000	-641.983	10.06248	0.00653	0.00047
Density-Slope-Year-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	7	816858.0	1.0000	-641.895	10.15046	0.00625	0.00045
Density-EVI-Year-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	7	815799.7	1.0000	-641.810	10.23602	0.00599	0.00043
Removals-Distance to Water-Year-Overlaps Males-Overlaps All-Edge	66	6	929416.4	1.0000	-641.801	10.24459	0.00596	0.00043
Density-Slope-Distance to Water-Year-Overlaps Males-Overlaps All	66	6	928998.7	1.0000	-641.772	10.27425	0.00587	0.00042
Slope-Distance to Water-Year-Overlaps Females-Overlaps Males-Overlaps All	66	6	927566.3	1.0000	-641.670	10.37610	0.00558	0.00040
EVI-Slope-Distance to Water-Year-Overlaps All-Overlaps Females	66	6	926945.3	1.0000	-641.625	10.42030	0.00546	0.00039
Density-Removals-Slope-Distance to Water-Year-Edge-Overlaps Females	66	7	813414.8	1.0000	-641.617	10.42924	0.00544	0.00039
Density-EVI-Slope-Year-Overlaps Females-Overlaps Males-Edge	66	7	813018.3	1.0000	-641.584	10.46142	0.00535	0.00038
Density-EVI-Slope-Year-Overlaps All-Overlaps Males	66	6	925822.3	1.0000	-641.545	10.50031	0.00525	0.00038
Density-Distance to Water-Year-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	7	812349.7	1.0000	-641.530	10.51572	0.00521	0.00037
Density-Slope-Distance to Water-Year-Edge-Overlaps Males-Overlaps Females	66	7	812312.1	1.0000	-641.527	10.51877	0.00520	0.00037
Density-EVI-Slope-Year-Overlaps Females-Overlaps All-Edge	66	7	811471.4	1.0000	-641.459	10.58711	0.00502	0.00036
EVI-Removals-Slope-Year-Overlaps Males-Overlaps All	66	6	924176.0	1.0000	-641.428	10.61777	0.00495	0.00036
Density-Removals-Year-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	7	810329.9	1.0000	-641.366	10.68003	0.00480	0.00034
Density-Slope-Distance to Water-Year-Overlaps All-Overlaps Females-Edge	66	7	809896.9	1.0000	-641.330	10.71530	0.00471	0.00034
Density-Removals-Slope-Year-Edge-Overlaps Males-Overlaps Females	66	7	809586.3	1.0000	-641.305	10.74061	0.00465	0.00033
Density-Removals-Slope-Year-Overlaps All-Overlaps Females-Edge	66	7	809119.4	1.0000	-641.267	10.77869	0.00456	0.00033
Density-Removals-Slope-Year-Overlaps Females-Overlaps Males-Overlaps All	66	7	808192.1	1.0000	-641.191	10.85437	0.00440	0.00032
EVI-Slope-Year-Edge-Overlaps Females-Overlaps All-Overlaps Males	66	7	808187.7	1.0000	-641.191	10.85474	0.00439	0.00032
EVI-Slope-Distance to Water-Year-Overlaps Females-Overlaps Males	66	6	920861.8	1.0000	-641.191	10.85488	0.00439	0.00032
Density-Removals-Slope-Distance to Water-Year-Edge-Overlaps All	66	7	806104.5	1.0000	-641.021	11.02507	0.00404	0.00029
Density-Removals-Slope-Distance to Water-Year-Overlaps All	66	7	806077.6	1.0000	-641.018	11.02728	0.00403	0.00029
Density-EVI-Slope-Year-Overlaps All-Overlaps Males-Edge	66	6	805120.7	1.0000	-640.940	11.10567	0.00388	0.00028
Density-Slope-Year-EVI-Overlaps Males-Overlaps All-Edge	66	7	805120.7	1.0000	-640.940	11.10567	0.00388	0.00028
Density-Slope-Distance to Water-Year-Overlaps Males-Overlaps All-Edge	66	7	804809.3	1.0000	-640.915	11.13120	0.00383	0.00028
EVI-Removals-Slope-Year-Overlaps All-Overlaps Females-Edge	66	7	804609.9	1.0000	-640.898	11.14755	0.00380	0.00027
Density-Slope-Distance to Water-Year-Overlaps Females-Overlaps Males-Overlaps All	66	7	803555.9	1.0000	-640.812	11.23407	0.00364	0.00026
EVI-Removals-Slope-Year-Edge-Overlaps Males-Overlaps Females	66	7	803432.8	1.0000	-640.802	11.24418	0.00362	0.00026
EVI-Distance to Water-Year-Edge-Overlaps Females-Overlaps All-Overlaps Males	66	7	803421.6	1.0000	-640.801	11.24510	0.00362	0.00026
EVI-Slope-Distance to Water-Year-Overlaps All-Overlaps Females-Edge	66	7	802933.1	1.0000	-640.761	11.28524	0.00354	0.00025
EVI-Slope-Distance to Water-Year-Overlaps All-Overlaps Females-Edge	66	7	802933.1	1.0000	-640.761	11.28524	0.00354	0.00025
EVI-Slope-Distance to Water-Year-Edge-Overlaps Males-Overlaps Females	66	7	802782.2	1.0000	-640.748	11.29764	0.00352	0.00025
Density-Removals-Slope-Distance to Water-Year-Overlaps Females-Overlaps Males	66	7	802714.3	1.0000	-640.743	11.30323	0.00351	0.00025
Density-EVI-Slope-Year-Overlaps Males-Overlaps Females-Overlaps All	66	7	802586.3	1.0000	-640.732	11.31375	0.00349	0.00025
Density-Removals-Slope-Year-Overlaps Males-Overlaps All-Edge	66	7	801905.0	1.0000	-640.676	11.36980	0.00340	0.00024
EVI-Slope-Distance to Water-Year-Overlaps Males-Overlaps All	66	6	913514.0	1.0000	-640.662	11.38362	0.00337	0.00024
Slope-Distance to Water-Year-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	7	800904.0	1.0000	-640.594	11.45224	0.00326	0.00023
EVI-Removals-Slope-Year-Overlaps Males-Overlaps All-Edge	66	7	797290.4	1.0000	-640.295	11.75070	0.00281	0.00020
EVI-Slope-Distance to Water-Year-Overlaps Males-Overlaps All-Edge	66	7	796975.5	1.0000	-640.269	11.77677	0.00277	0.00020
EVI-Removals-Slope-Year-Overlaps Females-Overlaps Males-Overlaps All	66	7	796501.3	1.0000	-640.230	11.81605	0.00272	0.00020
Density-Removals-Slope-Distance to Water-Year-Edge-Overlaps Males	66	7	796327.7	1.0000	-640.215	11.83044	0.00270	0.00019
Density-Removals-Slope-Distance to Water-Year-Overlaps Males-Overlaps All	66	7	793689.6	1.0000	-639.996	12.04944	0.00242	0.00017
Removals-Distance to Water-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	6	793065.7	1.0000	-639.944	12.10135	0.00236	0.00017
Removals-Distance to Water-Overlaps All-Overlaps Females-Overlaps Males-Edge	66	7	793065.7	1.0000	-639.944	12.10135	0.00236	0.00017
EVI-Slope-Distance to Water-Year-Overlaps Females-Overlaps Males-Overlaps All	66	7	786941.8	1.0000	-639.433	12.61295	0.00182	0.00013

Model	n	K	Fstat	r2	AiCc	ΔAICc (Δi)	Model likelihood	Wi
Density-EVI-Slope-Year-Edge-Overlaps Females-Overlaps All-Overlaps Males	66	8	705578.7	1.0000	-639.405	12.64074	0.00180	0.00013
Density-Slope-Distance to Water-Year-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	8	704552.4	1.0000	-639.309	12.73681	0.00171	0.00012
Density-Removals-Slope-Year-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	8	703421.6	1.0000	-639.203	12.84283	0.00163	0.00012
Density-EVI-Removals-Distance to Water-Edge-Overlaps Males-Overlaps Females	66	7	700922.7	1.0000	-638.968	13.07771	0.00145	0.00010
Density-EVI-Removals-Distance to Water-Year-Edge-Overlaps Males-Overlaps Females	66	8	700922.7	1.0000	-638.968	13.07771	0.00145	0.00010
Density-EVI-Removals-Distance to Water-Year-Overlaps Females-Overlaps Males-Overlaps All	66	8	700808.5	1.0000	-638.957	13.08846	0.00144	0.00010
Density-EVI-Removals-Distance to Water-Year-Overlaps All-Overlaps Females-Edge	66	8	700434.7	1.0000	-638.922	13.12367	0.00141	0.00010
Density-Removals-Slope-Distance to Water-Year-Edge-Overlaps Males-Overlaps Females	66	8	700172.8	1.0000	-638.897	13.14836	0.00140	0.00010
Density-Removals-Slope-Distance to Water-Year-Overlaps Females-Overlaps Males-Overlaps All	66	8	699793.5	1.0000	-638.862	13.18412	0.00137	0.00010
Density-Removals-Slope-Distance to Water-Year-Overlaps All-Overlaps Females-Edge	66	8	699517.8	1.0000	-638.836	13.21013	0.00135	0.00010
EVI-Removals-Slope-Year-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	8	696022.9	1.0000	-638.505	13.54069	0.00115	0.00008
EVI-Slope-Distance to Water-Year-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	8	694979.6	1.0000	-638.406	13.63970	0.00109	0.00008
Density-EVI-Removals-Distance to Water-Year-Overlaps Males-Over All-Edge	66	8	694685.5	1.0000	-638.378	13.66763	0.00108	0.00008
Density-Removals-Slope-Distance to Water-Year-Overlaps Males-Overlaps All-Edge	66	8	693412.1	1.0000	-638.257	13.78873	0.00101	0.00007
Density-EVI-Removals-Distance to Water-Year-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	9	617077.4	1.0000	-636.612	15.43336	0.00045	0.00003
Density-Removals-Slope-Distance to Water-Year-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	8	616984.8	1.0000	-636.603	15.44326	0.00044	0.00003
Removals-Overlaps All-Overlaps Females-Edge	66	4	10.8	0.4140	73.960	726.00551	0.00000	0.00000
Removals-Distance to Water-Edge-Overlaps Females-Overlaps All	66	5	9.0	0.4288	74.778	726.82372	0.00000	0.00000
Density-Removals-Overlaps All-Overlaps Females-Edge	66	5	8.9	0.4249	75.220	727.26538	0.00000	0.00000
EVI-Removals-Overlaps All-Overlaps Females-Edge	66	5	8.7	0.4204	75.733	727.77921	0.00000	0.00000
Removals-Slope-Edge-Overlaps Females-Overlaps All	66	5	8.7	0.4204	75.738	727.78339	0.00000	0.00000
Distance to Water-Overlaps All-Overlaps Females-Edge	66	4	9.8	0.3916	76.429	728.47464	0.00000	0.00000
Removals-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	5	8.48	0.4140	76.467	728.51229	0.00000	0.00000
Density-Removals-Distance to Water-Overlaps All-Overlaps Females-Edge	66	6	7.47	0.4317	77.039	729.08448	0.00000	0.00000
Density-Removals-Slope-Overlaps All-Overlaps Females-Edge	66	6	7.42	0.4299	77.238	729.28413	0.00000	0.00000
Removals-Distance to Water-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	6	7.39	0.4292	77.323	729.36922	0.00000	0.00000
Density-EVI-Removals-Overlaps All-Overlaps Females-Edge	66	6	7.36	0.4282	77.439	729.48451	0.00000	0.00000
Overlaps All-Overlaps Females-Edge	66	3	11.56	0.3588	77.474	729.51990	0.00000	0.00000
Removals-Edge-Overlaps Females	66	4	9.41	0.3816	77.503	729.54832	0.00000	0.00000
Density-Removals-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	6	7.28	0.4254	77.756	729.80217	0.00000	0.00000
EVI-Slope-Removals-Overlaps All-Overlaps Females-Edge	66	6	7.24	0.4240	77.918	729.96363	0.00000	0.00000
Slope-Distance to Water-Overlaps All-Overlaps Females-Edge	66	5	7.970977	0.3991	78.117	730.16262	0.00000	0.00000
EVI-Removals-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	6	7.13	0.4204	78.329	730.37439	0.00000	0.00000
Removals-Slope-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	6	7.13	0.4204	78.332	730.37786	0.00000	0.00000
Density-Overlaps All-Overlaps Females-Edge	66	4	9.09	0.3734	78.374	730.41963	0.00000	0.00000
EVI-Distance to Water-Overlaps Females-Overlaps All-Edge	66	5	7.88	0.3964	78.411	730.45650	0.00000	0.00000
Distance to Water-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	5	7.808826	0.3942	78.655	730.70068	0.00000	0.00000
Density-Distance to Water-Overlaps All-Overlaps Females-Edge	66	5	7.78	0.3932	78.760	730.80537	0.00000	0.00000
Removals-Distance to Water-Edge-Overlaps Females-Overlaps Males	66	5	7.77	0.3929	78.797	730.84273	0.00000	0.00000
EVI-Overlaps All-Overlaps Females-Edge	66	4	8.92	0.3691	78.825	730.87032	0.00000	0.00000
Density-Removals-Edge-Overlaps Males-Overlaps Females	66	5	7.71	0.3911	78.989	731.03450	0.00000	0.00000
Density-Removals-Slope-Distance to Water-Overlaps All-Overlaps Females-Edge	66	7	6.44	0.4374	79.051	731.09695	0.00000	0.00000
EVI-Removals-Edge-Overlaps Males-Overlaps Females	66	5	7.68	0.3902	79.095	731.14040	0.00000	0.00000
Slope-Overlaps All-Overlaps Females-Edge	66	4	8.809617	0.3662	79.135	731.18091	0.00000	0.00000
Removals-Slope-Edge-Overlaps Males-Overlaps Females	66	5	7.65	0.3894	79.180	731.22583	0.00000	0.00000
Density-EVI-Removals-Distance to Water-Overlaps All-Overlaps Females-Edge	66	7	6.36	0.4344	79.411	731.45663	0.00000	0.00000
Removals-Edge-Overlaps Males	66	3	10.61	0.3392	79.465	731.51047	0.00000	0.00000

Model	**n**	**K**	**Fstat**	**r2**	**AiCc**	**ΔAICc (Δi)**	**Model likelihood**	**Wi**
Density-Removals-Distance to Water-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	7	6.31	0.4325	79.633	731.67867	0.00000	0.00000
Density-EVI-Removals-Slope-Overlaps All-Overlaps Females-Edge	66	7	6.29	0.4315	79.744	731.79017	0.00000	0.00000
Overlaps Males-Overlaps All-Overlaps Females-Edge	66	4	8.57	0.3597	79.803	731.84853	0.00000	0.00000
Density-Removals-Slope-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	7	6.26	0.4304	79.872	731.91741	0.00000	0.00000
Density-EVI-Removals-Edge-Overlaps Males-Overlaps Females-Overlaps All	66	7	6.21	0.4286	80.085	732.13097	0.00000	0.00000
Distance to Water-Edge-Overlaps Males-Overlaps Females	66	4	8.44082	0.3563	80.155	732.20042	0.00000	0.00000
Density-Slope-Overlaps All-Overlaps Females-Edge	66	5	7.32	0.3790	80.292	732.33767	0.00000	0.00000
Density-EVI-Overlaps All-Overlaps Females-Edge	66	5	7.32	0.3790	80.294	732.33941	0.00000	0.00000
Density-EVI-Distance to Water-Edge-Overlaps All- Overlaps Females	66	6	7.32	0.3790	80.294	732.33941	0.00000	0.00000
Slope-Distance to Water-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	6	6.603502	0.4018	80.423	732.46925	0.00000	0.00000
EVI-Slope-Distance to Water-Overlaps All-Overlaps Females-Edge	66	6	6.59	0.4013	80.475	732.52104	0.00000	0.00000
Removals-Distance to Water-Edge-Overlaps Males	66	4	8.289555	0.3522	80.577	732.62318	0.00000	0.00000
Density-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	5	7.24	0.3762	80.583	732.62911	0.00000	0.00000
Overlaps Males-Overlaps Females-Edge	66	3	10.08	0.3278	80.588	732.63370	0.00000	0.00000
EVI-Slope-Removals-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	7	6.10	0.4240	80.606	732.65131	0.00000	0.00000
Density-Slope-Distance to Water-Overlaps All-Overlaps Females-Edge	66	6	6.56	0.4001	80.607	732.65276	0.00000	0.00000
Density-Removals-Slope-Edge-Overlaps Males-Overlaps Females	66	6	6.49	0.3974	80.899	732.94522	0.00000	0.00000
EVI-Slope-Overlaps All-Overlaps Females-Edge	66	5	7.13	0.3727	80.961	733.00670	0.00000	0.00000
Density-Distance to Water-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	6	6.46	0.3965	80.996	733.04156	0.00000	0.00000
Density-EVI-Removals-Edge-Overlaps Males-Overlaps Females	66	6	6.45	0.3962	81.038	733.08328	0.00000	0.00000
Density-Removals-Distance to Water-Edge-Overlaps Males-Overlaps Females	66	6	6.44	0.3959	81.064	733.10948	0.00000	0.00000
Removals-Distance to Water-Edge-Overlaps Males-Overlaps All	66	5	7.065553	0.3706	81.179	733.22481	0.00000	0.00000
EVI-Slope-Removals-Edge-Overlaps Males-Overlaps Females	66	6	6.40	0.3943	81.241	733.28666	0.00000	0.00000
EVI-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	5	7.04	0.3699	81.251	733.29712	0.00000	0.00000
Slope-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	5	6.960313	0.3671	81.544	733.59013	0.00000	0.00000
Density-Overlaps Males-Edge-Overlaps Females	66	4	7.92	0.3419	81.609	733.65512	0.00000	0.00000
Density-Removals-Edge-Overlaps Males	66	4	7.92	0.3419	81.617	733.66325	0.00000	0.00000
EVI-Removals-Overlaps Males-Overlaps All-Edge	66	5	6.93	0.3660	81.659	733.70486	0.00000	0.00000
Density-Removals-Overlaps Males-Overlaps All-Edge	66	5	6.93	0.3659	81.665	733.71092	0.00000	0.00000
EVI-Removals-Edge-Overlaps Males	66	4	7.90	0.3413	81.673	733.71885	0.00000	0.00000
Density-EVI-Removals-Slope-Distance to Water-Overlaps All-Overlaps Females-Edge	66	8	5.56	0.4385	81.713	733.75871	0.00000	0.00000
Slope-Distance to Water-Edge-Overlaps Males-Overlaps Females	66	5	6.906769	0.3653	81.731	733.77678	0.00000	0.00000
Density-Removals-Slope-Distance to Water-Edge-Overlaps Females-Overlaps Males-Overlaps all	66	8	5.56	0.4382	81.746	733.79166	0.00000	0.00000
EVI-Edge-Overlaps Males-Overlaps Females	66	4	7.87	0.3405	81.757	733.80265	0.00000	0.00000
Distance to Water-Edge-Overlaps Males	66	3	9.529866	0.3156	81.777	733.82270	0.00000	0.00000
Removals-Slope-Edge-Overlaps Males	66	4	7.85	0.3400	81.808	733.85417	0.00000	0.00000
Removals-Slope-Edge-Overlaps All-Overlaps Males	66	5	6.88	0.3645	81.819	733.86434	0.00000	0.00000
Density-EVI-Removals-Distance to Water-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	8	5.49	0.4350	82.124	734.16998	0.00000	0.00000
Slope-Edge-Overlaps Males-Overlaps Females	66	4	7.736011	0.3366	82.148	734.19374	0.00000	0.00000
Overlaps Males-Edge	66	2	12.51	0.2843	82.387	734.43264	0.00000	0.00000
Distance to Water-Overlaps Males-Overlaps All-Edge	66	4	7.636021	0.3337	82.436	734.48147	0.00000	0.00000
Density-Distance to Water-Edge-Overlaps Males-Overlaps Females	66	5	6.70	0.3584	82.447	734.49234	0.00000	0.00000
Density-EVI-Removals-Slope-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	8	5.42	0.4319	82.487	734.53274	0.00000	0.00000
Density-EVI-Removals-Slope-Edge-Overlaps Males-Overlaps Females	66	7	5.42	0.4319	82.487	734.53274	0.00000	0.00000
Density-EVI-Slope-Overlaps All-Overlaps Females-Edge	66	6	6.08	0.3822	82.547	734.59273	0.00000	0.00000
Density-Slope-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	6	6.07	0.3817	82.598	734.64421	0.00000	0.00000
Density-EVI-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	6	6.06	0.3813	82.646	734.69176	0.00000	0.00000

Model	**n**	**K**	**Fstat**	**r2**	**AiCc**	**ΔAICc (Δi)**	**Model likelihood**	**Wi**
Overlaps Males-Overlaps All-Edge	66	3	9.09	0.3055	82.744	734.79000	0.00000	0.00000
EVI-Slope-Distance to Water-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	7	5.61	0.4037	82.899	734.94491	0.00000	0.00000
Density-Slope-Distance to Water-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	7	5.60	0.4033	82.945	734.99041	0.00000	0.00000
Density-Removals-Slope-Distance to Water-Edge-Overlaps Males-Overlaps Females	66	7	5.59	0.4030	82.976	735.02153	0.00000	0.00000
Density-Removals-Distance to Water-Edge-Overlaps Males	66	5	6.52	0.3522	83.084	735.13003	0.00000	0.00000
Density-EVI-Slope-Distance to Water-Overlaps All-Overlaps Females-Edge	66	7	5.57	0.4019	83.100	735.14553	0.00000	0.00000
Density-EVI-Edge-Overlaps Males-Overlaps Females	66	5	6.44	0.3493	83.375	735.42103	0.00000	0.00000
Density-EVI-Distance to Water-Edge-Overlaps Males-Overlaps Females	66	6	6.44	0.3493	83.375	735.42103	0.00000	0.00000
Density-Slope-Edge-Overlaps Females	66	5	6.43	0.3488	83.427	735.47313	0.00000	0.00000
EVI-Slope-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	6	5.86	0.3735	83.471	735.51703	0.00000	0.00000
Density-Removals-Distance to Water-Overlaps Males-Overlaps All-Edge	66	6	5.82	0.3718	83.643	735.68840	0.00000	0.00000
Density-EVI-Removals-Overlaps Males-Overlaps All-Edge	66	6	5.77	0.3699	83.852	735.89773	0.00000	0.00000
EVI-Slope-Edge-Overlaps Males-Overlaps Females	66	5	6.31	0.3446	83.853	735.89831	0.00000	0.00000
Density-Removals-Slope-Overlaps Males-Overlaps All-Edge	66	6	5.77	0.3698	83.855	735.90041	0.00000	0.00000
EVI-Slope-Distance to Water-Edge-Overlaps Males-Overlaps Females	66	6	5.74	0.3687	83.975	736.02030	0.00000	0.00000
EVI-Slope-Removals-Overlaps Males-Overlaps All-Edge	66	6	5.74	0.3684	84.001	736.04657	0.00000	0.00000
EVI-Distance to Water-Edge-Overlaps Males	66	4	7.08	0.3169	84.071	736.11667	0.00000	0.00000
Slope-Distance to Water-Edge-Overlaps Males	66	4	7.075501	0.3169	84.072	736.11805	0.00000	0.00000
Density-Removals-Slope-Edge-Overlaps Males	66	5	6.25	0.3423	84.080	736.12618	0.00000	0.00000
EVI-Slope-Removals-Edge-Overlaps Males	66	5	6.22	0.3415	84.161	736.20662	0.00000	0.00000
Density-Overlaps Males-Edge-Overlaps All	66	4	7.04	0.3157	84.187	736.23274	0.00000	0.00000
Density-Slope-Distance to Water-Edge-Overlaps Males-Overlaps Females	66	6	5.69	0.3666	84.195	736.24077	0.00000	0.00000
Density-Distance to Water-Edge-Overlaps Males	66	4	7.03	0.3156	84.196	736.24223	0.00000	0.00000
EVI-Overlaps Males-Overlaps All-Edge	66	4	7.03	0.3156	84.199	736.24503	0.00000	0.00000
Density-Edge-Overlaps Males	66	3	8.42	0.2896	84.239	736.28511	0.00000	0.00000
Density-Overlaps Males-Edge	66	3	8.42	0.2896	84.239	736.28511	0.00000	0.00000
EVI-Edge-Overlaps Males	66	3	8.38	0.2886	84.328	736.37376	0.00000	0.00000
Slope-Distance to Water-Overlaps Males-Overlaps All-Edge	66	5	6.165522	0.3394	84.371	736.41642	0.00000	0.00000
EVI-Distance to Water-Overlaps Males-Overlaps All-Edge	66	5	6.14	0.3386	84.452	736.49810	0.00000	0.00000
Density-EVI-Removals-Slope-Distance to Water-Edge-Overlaps Females-Overlaps Males-Overlaps All	66	9	4.87	0.4392	84.524	736.57017	0.00000	0.00000
Slope-Overlaps Males-Overlaps All-Edge	66	4	6.89011	0.3112	84.623	736.66840	0.00000	0.00000
Slope-Edge-Overlaps Males	66	3	8.252167	0.2854	84.630	736.67615	0.00000	0.00000
Density-Distance to Water-Overlaps Males-Overlaps All-Edge	66	5	6.03	0.3343	84.876	736.92169	0.00000	0.00000
Density-EVI-Slope-Edge-Overlaps Males-Overlaps Females-Overlaps All	66	7	5.18	0.3845	84.987	737.03304	0.00000	0.00000
Density-EVI-Removals-Slope-Distance to Water-Edge-Overlaps Males-Overlaps Females	66	8	4.85	0.4050	85.534	737.58021	0.00000	0.00000
Density-EVI-Slope-Distance to Water-Overlaps Males-Overlaps Females-Overlaps All-Edge	66	8	4.84	0.4047	85.571	737.61680	0.00000	0.00000
Density-Removals-Slope-Distance to Water-Edge-Overlaps Males	66	6	5.37	0.3531	85.579	737.62468	0.00000	0.00000
Density-EVI-Slope-Edge-Overlaps Males-Overlaps Females	66	6	5.37	0.3531	85.583	737.62895	0.00000	0.00000
Density-Removals-Slope-Distance to Water-Overlaps Males-Overlaps All-Edge	66	7	5.00	0.3764	85.854	737.89995	0.00000	0.00000
Density-EVI-Removals-Distance to Water-Overlaps Males-Overlaps All-Edge	66	7	4.97	0.3752	85.982	738.02791	0.00000	0.00000
Density-EVI-Edge-Overlaps Males-Overlaps All	66	5	5.69	0.3218	86.109	738.15514	0.00000	0.00000
Density-EVI-Overlaps Males-Overlaps All-Edge	66	5	5.69	0.3218	86.109	738.15514	0.00000	0.00000
Density-Slope-Overlaps Males-Overlaps All-Edge	66	5	5.65	0.3201	86.276	738.32192	0.00000	0.00000
Density-EVI-Removals-Slope-Overlaps Males-Overlaps All-Edge	66	7	4.91	0.3721	86.305	738.35059	0.00000	0.00000
Density-EVI-Edge-Overlaps Males	66	4	6.28	0.2918	86.453	738.49917	0.00000	0.00000
EVI-Slope-Overlaps Males-Overlaps All-Edge	66	5	5.60	0.3180	86.474	738.51929	0.00000	0.00000
EVI-Slope-Distance to Water-Edge-Overlaps Males	66	5	5.58	0.3176	86.514	738.56013	0.00000	0.00000

Model	**n**	**K**	**Fstat**	**r2**	**AiCc**	**ΔAICc (Δi)**	**Model likelihood**	**Wi**
Density-EVI-Distance to Water-Edge-Overlaps Males	66	5	5.57	0.3172	86.555	738.60057	0.00000	0.00000
Density-Slope-Distance to Water-Edge-Overlaps Males	66	5	5.57	0.3171	86.563	738.60890	0.00000	0.00000
Density-EVI-Slope-Distance to Water-Overlaps Males-Overlaps Females-Edge	66	7	4.85	0.3694	86.590	738.63551	0.00000	0.00000
Density-Slope-Edge-Overlaps Males	66	4	6.23	0.2901	86.615	738.66091	0.00000	0.00000
EVI-Slope-Distance to Water-Overlaps Males-Overlaps All-Edge	66	6	5.11	0.3420	86.711	738.75635	0.00000	0.00000
EVI-Slope-Edge-Overlaps Males	66	4	6.19	0.2888	86.738	738.78369	0.00000	0.00000
Density-Slope-Distance to Water-Overlaps Males-Overlaps All-Edge	66	6	5.06	0.3397	86.936	738.98131	0.00000	0.00000
Distance to Water-Edge-Overlaps All	66	3	6.781447	0.2471	88.075	740.12105	0.00000	0.00000
Density-EVI-Removals-Slope-Distance to Water-Overlaps Males-Overlaps All-Edge	66	8	4.33	0.3780	88.464	740.50993	0.00000	0.00000
Density-EVI-Slope-Overlaps Males-Overlaps All-Edge	66	6	4.71	0.3239	88.493	740.53851	0.00000	0.00000
Density-EVI-Slope-Edge-Overlaps Males	66	5	4.95	0.2919	88.953	740.99915	0.00000	0.00000
Overlaps All-Edge	66	2	8.32	0.2090	88.990	741.03571	0.00000	0.00000
Density-EVI-Slope-Distance to Water-Edge-Overlaps Males	66	6	4.58	0.3179	89.077	741.12305	0.00000	0.00000
Removals-Edge-Overlaps All	66	3	6.30	0.2337	89.234	741.27945	0.00000	0.00000
Density-EVI-Slope-Distance to Water-Overlaps Males-Overlaps All-Edge	66	7	4.31	0.3420	89.390	741.43553	0.00000	0.00000
Removals-Distance to Water-Edge-Overlaps All	66	4	5.34	0.2592	89.424	741.46997	0.00000	0.00000
Density-Edge-Overlaps All	66	3	6.22	0.2313	89.446	741.49168	0.00000	0.00000
Density-Overlaps All-Edge	66	3	6.22	0.2313	89.446	741.49168	0.00000	0.00000
Density-Edge	66	2	7.87	0.1998	89.748	741.79363	0.00000	0.00000
Density-Removals-Edge-Overlaps All	66	4	5.18	0.2536	89.923	741.96896	0.00000	0.00000
Density-Distance to Water-Edge-Overlaps All	66	4	5.12	0.2513	90.130	742.17556	0.00000	0.00000
Slope-Distance to Water-Edge-Overlaps All	66	4	5.092717	0.2503	90.211	742.25649	0.00000	0.00000
EVI-Distance to Water-Edge-Overlaps All	66	4	5.07	0.2495	90.282	742.32755	0.00000	0.00000
Slope-Distance to Water-Overlaps All-Overlaps Females	66	4	5.009682	0.2473	90.481	742.52644	0.00000	0.00000
EVI-Edge-Overlaps All	66	3	5.70	0.2161	90.735	742.78072	0.00000	0.00000
Slope-Edge-Overlaps All	66	3	5.562572	0.2121	91.073	743.11895	0.00000	0.00000
EVI-Removals-Edge-Overlaps All	66	4	4.78	0.2386	91.241	743.28690	0.00000	0.00000
Removals-Slope-Edge-Overlaps All	66	4	4.72	0.2362	91.442	743.48790	0.00000	0.00000
Density-Removals-Distance to Water-Edge-Overlaps All	66	5	4.32	0.2647	91.442	743.48826	0.00000	0.00000
Density-EVI-Edge	66	3	5.39	0.2069	91.505	743.55104	0.00000	0.00000
Density-EVI-Edge-Overlaps All	66	4	4.65	0.2338	91.652	743.69771	0.00000	0.00000
Density-Slope-Edge-Overlaps All	66	4	4.63	0.2331	91.713	743.75852	0.00000	0.00000
Density-Edge-Overlaps Females	66	3	5.18	0.2003	92.054	744.09941	0.00000	0.00000
Density-Overlaps Females-Edge	66	3	5.18	0.2003	92.054	744.09941	0.00000	0.00000
Slope-Distance to Water-Overlaps Females-Overlaps Males	66	4	4.521597	0.2287	92.090	744.13594	0.00000	0.00000
Density-Removals-Slope-Edge-Overlaps All	66	5	4.11	0.2550	92.304	744.34988	0.00000	0.00000
EVI-Slope-Distance to Water-Overlaps All-Overlaps Females	66	5	4.11	0.2550	92.308	744.35361	0.00000	0.00000
Density-Slope-Distance to Water-Edge-Overlaps All	66	5	4.08	0.2538	92.410	744.45538	0.00000	0.00000
Density-EVI-Distance to Water-Edge-Overlaps All	66	5	4.06	0.2528	92.503	744.54915	0.00000	0.00000
EVI-Slope-Distance to Water-Edge-Overlaps All	66	5	4.03	0.2515	92.613	744.65874	0.00000	0.00000
Slope-Overlaps All-Overlaps Females	66	3	4.909244	0.1919	92.738	744.78372	0.00000	0.00000
Slope-Distance to Water-Overlaps Females-Overlaps Males-Overlaps All	66	5	3.989327	0.2495	92.793	744.83828	0.00000	0.00000
Density-Slope-Distance to Water-Overlaps All-Overlaps Females	66	5	3.94	0.2474	92.980	745.02530	0.00000	0.00000
EVI-Slope-Edge-Overlaps All	66	4	4.23	0.2172	93.066	745.11207	0.00000	0.00000
Distance to Water-Overlaps All-Overlaps Females	66	3	4.705856	0.1855	93.265	745.31068	0.00000	0.00000
Density-Slope-Edge-Overlaps Females	66	4	4.16	0.2143	93.309	745.35500	0.00000	0.00000
EVI-Distance to Water-Overlaps All-Overlaps Females	66	4	4.14	0.2137	93.364	745.40938	0.00000	0.00000

Model	**n**	**K**	**Fstat**	**r2**	**AiCc**	**ΔAICc (Δi)**	**Model likelihood**	**Wi**
Density-EVI-Distance to Water-Edge	66	4	4.14	0.2136	93.370	745.41562	0.00000	0.00000
Density-EVI-Slope-Edge	66	4	4.14	0.2134	93.387	745.43264	0.00000	0.00000
Density-EVI-Removals-Edge	66	4	4.07	0.2108	93.607	745.65264	0.00000	0.00000
EVI-Slope-Overlaps All-Overlaps Females	66	4	4.06	0.2101	93.661	745.70651	0.00000	0.00000
EVI-Slope-Removals-Edge-Overlaps All	66	5	3.78	0.2395	93.662	745.70772	0.00000	0.00000
Density-EVI-Edge-Overlaps Females	66	4	4.02	0.2085	93.799	745.84498	0.00000	0.00000
EVI-Slope-Distance to Water-Overlaps Females-Overlaps Males	66	5	3.74	0.2376	93.830	745.87597	0.00000	0.00000
Slope-Overlaps Females-Overlaps Males	66	3	4.480505	0.1782	93.854	745.89949	0.00000	0.00000
Density-Removals-Slope-Distance to Water-Edge-Overlaps All	66	6	3.58	0.2667	93.856	745.90146	0.00000	0.00000
Density-Distance to Water-Edge-Overlaps Females	66	4	3.98	0.2068	93.940	745.98577	0.00000	0.00000
Slope-Distance to Water-Edge	66	3	4.396943	0.1754	94.073	746.11916	0.00000	0.00000
Density-EVI-Slope-Edge-Overlaps All	66	5	3.68	0.2347	94.081	746.12680	0.00000	0.00000
Density-Removals-Edge-Overlaps Females	66	4	3.90	0.2037	94.198	746.24401	0.00000	0.00000
Density-Slope-Overlaps All-Overlaps Females	66	4	3.86	0.2021	94.325	746.37123	0.00000	0.00000
EVI-Overlaps All-Overlaps Females	66	3	4.26	0.1710	94.423	746.46915	0.00000	0.00000
Density-Slope-Distance to Water-Overlaps Females-Overlaps Males	66	6	3.56	0.2287	94.596	746.64211	0.00000	0.00000
EVI-Slope-Overlaps Females-Overlaps Males	66	4	3.75	0.1974	94.712	746.75788	0.00000	0.00000
EVI-Distance to Water-Overlaps Females-Overlaps Males	66	4	3.75	0.1972	94.729	746.77431	0.00000	0.00000
EVI-Slope-Distance to Water-Overlaps Females-Overlaps Males-Overlaps All	66	6	3.40	0.2568	94.740	746.78594	0.00000	0.00000
Slope-Distance to Water-Overlaps Males-Overlaps All	66	4	3.741921	0.1970	94.746	746.79130	0.00000	0.00000
Distance to Water-Overlaps Females-Overlaps Males	66	3	4.14167	0.1669	94.749	746.79482	0.00000	0.00000
Density-EVI-Slope-Distance to Water-Overlaps All-Overlaps Females	66	6	3.37	0.2555	94.858	746.90363	0.00000	0.00000
Density-EVI-Slope-Distance to Water-Overlaps Females-Overlaps All	66	6	3.37	0.2555	94.858	746.90363	0.00000	0.00000
Removals-Slope-Overlaps All-Overlaps Females	66	4	3.70	0.1950	94.909	746.95447	0.00000	0.00000
Density-EVI-Slope-Distance to Water-Edge-Overlaps All	66	6	3.36	0.2545	94.946	746.99183	0.00000	0.00000
Slope-Edge	66	2	4.804859	0.1323	95.091	747.13634	0.00000	0.00000
Density-EVI-Slope-Water-Edge	66	5	3.44	0.2228	95.102	747.14776	0.00000	0.00000
Slope-Overlaps Females-Overlaps Males-Overlaps All	66	4	3.632034	0.1924	95.129	747.17429	0.00000	0.00000
Density-Slope-Distance to Water-Edge-Overlaps Females	66	5	3.43	0.2223	95.146	747.19212	0.00000	0.00000
EVI-Overlaps Females-Overlaps Males	66	3	3.91	0.1592	95.362	747.40750	0.00000	0.00000
Density-Slope-Distance to Water-Overlaps Females-Overlaps Males-Overlaps All	66	6	3.27	0.2495	95.387	747.43277	0.00000	0.00000
Density-EVI-Removals-Slope-Edge	66	5	3.36	0.2187	95.447	747.49238	0.00000	0.00000
Density-Slope-Overlaps Females-Overlaps Males	66	4	3.53	0.1881	95.474	747.51969	0.00000	0.00000
Density-Removals-Slope-Edge-Overlaps Females	66	5	3.35	0.2180	95.505	747.55052	0.00000	0.00000
Density-EVI-Slope-Edge-Overlaps Females	66	5	3.34	0.2180	95.508	747.55399	0.00000	0.00000
Distance to Water-Overlaps Females-Overlaps Males-Overlaps All	66	4	3.519328	0.1875	95.524	747.56942	0.00000	0.00000
Density-Removals-Slope-Distance to Water-Overlaps All-Overlaps Females	66	6	3.23	0.2474	95.568	747.61407	0.00000	0.00000
Distance to Water-Edge	66	2	4.532731	0.1258	95.587	747.63291	0.00000	0.00000
Distance to Water-Edge-Overlaps Females	66	3	3.814589	0.1558	95.625	747.67077	0.00000	0.00000
Removals-Distance to Water-Overlaps Females	66	3	3.48838	0.1862	95.633	747.67833	0.00000	0.00000
Removals-Distance to Water-Overlaps All-Overlaps Females	66	4	3.48838	0.1862	95.633	747.67833	0.00000	0.00000
Density-Distance to Water-Overlaps All-Overlaps Females	66	4	3.47	0.1856	95.681	747.72716	0.00000	0.00000
Overlaps All-Overlaps Females	66	2	4.47	0.1242	95.708	747.75364	0.00000	0.00000
Density-EVI-Slope-Overlaps All-Overlaps Females	66	5	3.30	0.2154	95.722	747.76774	0.00000	0.00000
EVI-Distance to Water-Overlaps Males-Overlaps All-Overlaps Females	66	5	3.29	0.2151	95.751	747.79683	0.00000	0.00000
Density-EVI-Removals-Distance to Water-Edge	66	5	3.28	0.2148	95.772	747.81735	0.00000	0.00000
Density-EVI-Distance to Water-Edge-Overlaps All- Overlaps Females	66	5	3.27	0.2140	95.845	747.89036	0.00000	0.00000

Model	**n**	**K**	**Fstat**	**r2**	**AiCc**	**ΔAICc (Δi)**	**Model likelihood**	**Wi**
Density-EVI-Distance to Water-Edge-Overlaps Females	66	5	3.27	0.2139	95.849	747.89507	0.00000	0.00000
EVI-Slope-Removals-Overlaps All-Overlaps Females	66	5	3.24	0.2128	95.947	747.99231	0.00000	0.00000
Removals-Slope-Overlaps Males-Overlaps Females	66	4	3.39	0.1817	95.997	748.04252	0.00000	0.00000
Slope-Distance to Water-Edge-Overlaps Females	66	4	3.370933	0.1810	96.048	748.09330	0.00000	0.00000
Slope-Distance to water	66	2	4.28	0.1197	96.048	748.09399	0.00000	0.00000
EVI-Slope-Overlaps Females-Overlaps Males-Overlaps All	66	5	3.20	0.2104	96.144	748.19017	0.00000	0.00000
Slope-Overlaps Males-Overlaps All	66	3	3.596837	0.1482	96.215	748.26045	0.00000	0.00000
Density-Removals-Distance to Water-Edge-Overlaps Females	66	5	3.15	0.2080	96.343	748.38901	0.00000	0.00000
Density-EVI-Slope-Distance to Water-Overlaps Males-Overlaps Females	66	6	3.07	0.2379	96.397	748.44275	0.00000	0.00000
Density-EVI-Overlaps Females-Overlaps All	66	4	3.27	0.1767	96.399	748.44508	0.00000	0.00000
Overlaps Females-Edge	66	2	4.02	0.1132	96.529	748.57468	0.00000	0.00000
EVI-Slope-Distance to Water-Overlaps Males-Overlaps All	66	5	3.10	0.2052	96.578	748.62389	0.00000	0.00000
Edge	66	1	5.65	0.0812	96.604	748.64946	0.00000	0.00000
Density-Removals-Slope-Overlaps All-Overlaps Females	66	5	3.08	0.2044	96.640	748.68584	0.00000	0.00000
Distance to Water-Overlaps Males-Overlaps All	66	3	3.431886	0.1424	96.665	748.71067	0.00000	0.00000
EVI-Distance to Water-Edge-Overlaps Females	66	4	3.19	0.1730	96.693	748.73886	0.00000	0.00000
Density-Slope-Overlaps Females-Overlaps Males-Overlaps All	66	5	3.07	0.2036	96.707	748.75280	0.00000	0.00000
Overlaps Males-Overlaps Females	66	2	3.93	0.1108	96.708	748.75414	0.00000	0.00000
EVI-Edge-Overlaps Females	66	3	3.40	0.1414	96.745	748.79073	0.00000	0.00000
EVI-Removals-Overlaps All-Overlaps Females	66	4	3.16	0.1717	96.797	748.84315	0.00000	0.00000
Density-EVI-Slope-Overlaps Females-Overlaps Males	66	5	3.04	0.2024	96.814	748.85927	0.00000	0.00000
EVI-Overlaps Females-Overlaps Males-Overlaps All	66	4	3.15	0.1712	96.835	748.88032	0.00000	0.00000
Density-Overlaps All-Overlaps Females	66	3	3.35	0.1396	96.881	748.92650	0.00000	0.00000
Slope-Edge-Overlaps Females	66	3	3.32706	0.1387	96.953	748.99839	0.00000	0.00000
EVI-Distance to Water-Overlaps Males-Overlaps All	66	4	3.12	0.1697	96.954	748.99997	0.00000	0.00000
EVI-Slope-Removals-Overlaps Females-Overlaps Males	66	5	3.01	0.2005	96.971	749.01666	0.00000	0.00000
Slope-Distance to Water-Overlaps Males	66	3	3.302481	0.1378	97.020	749.06603	0.00000	0.00000
Removals-Distance to Water-Overlaps Females-Overlaps Males	66	4	3.067798	0.1675	97.131	749.17658	0.00000	0.00000
Density-Distance to Water-Overlaps Females-Overlaps Males	66	4	3.06	0.1672	97.154	749.19950	0.00000	0.00000
Density-Removals-Slope-Distance to Water-Overlaps Females-Overlaps Males	66	6	2.92	0.2289	97.179	749.22471	0.00000	0.00000
EVI-Slope-Overlaps Males-Overlaps All	66	4	3.05	0.1665	97.212	749.25783	0.00000	0.00000
Density-Slope-Distance to Water-Overlaps Males-Overlaps All	66	5	2.95	0.1975	97.216	749.26186	0.00000	0.00000
Density-EVI-Distance to Water-Overlaps Females-Overlaps Males	66	5	2.95	0.1974	97.220	749.26559	0.00000	0.00000
Distance to Water-Overlaps Males	66	2	3.60055	0.1026	97.317	749.36284	0.00000	0.00000
Density-EVI-Overlaps Females-Overlaps Males	66	4	3.00	0.1643	97.383	749.42829	0.00000	0.00000
Removals-Slope-Overlaps Males-Overlaps All-Overlaps Females	66	5	2.91	0.1952	97.401	749.44676	0.00000	0.00000
Density-EVI-Slope-Distance to Water-Overlaps Males-Overlaps Females-Overlaps All	66	7	2.87	0.2571	97.405	749.45058	0.00000	0.00000
EVI-Overlaps Males-Overlaps All	66	3	3.16	0.1327	97.410	749.45555	0.00000	0.00000
Removals-Slope-Edge	66	3	3.16	0.1325	97.422	749.46782	0.00000	0.00000
Removals-Distance to Water-Edge	66	3	3.15	0.1323	97.440	749.48544	0.00000	0.00000
Density-EVI-Slope-Distance to Water-Edge-Overlaps Females	66	6	2.85	0.2250	97.512	749.55761	0.00000	0.00000
Density-EVI-Removals-Slope-Distance to Water-Edge	66	6	2.85	0.2246	97.544	749.58979	0.00000	0.00000
Density-Removals-Slope-Distance to Water-Edge-Overlaps Females	66	6	2.83	0.2235	97.634	749.67986	0.00000	0.00000
EVI-Removals-Overlaps Females-Overlaps Males	66	4	2.90	0.1600	97.720	749.76580	0.00000	0.00000
Density-Removals-Slope-Overlaps Females-Overlaps Males	66	5	2.83	0.1906	97.780	749.82559	0.00000	0.00000
EVI-Slope-Distance to Water	66	3	2.99	0.1265	97.878	749.92370	0.00000	0.00000
Slope-Distance to Water-Overlaps Females	66	3	2.992082	0.1265	97.881	749.92631	0.00000	0.00000

Model	**n**	**K**	**Fstat**	**r2**	**AiCc**	**ΔAICc (Δi)**	**Model likelihood**	**Wi**
Removals-Distance to Water-Overlaps Females-Overlaps Males-Overlaps All	66	5	2.789489	0.1886	97.941	749.98660	0.00000	0.00000
EVI-Slope-Distance to Water-Edge-Overlaps Females	66	5	2.79	0.1886	97.942	749.98738	0.00000	0.00000
EVI-Distance to Water	66	2	3.25	0.0936	97.977	750.02282	0.00000	0.00000
Distance to Water	66	1	4.21	0.0617	97.987	750.03293	0.00000	0.00000
Density-Distance to Water-Overlaps Females-Overlaps Males-Overlaps All	66	5	2.77	0.1878	98.010	750.05549	0.00000	0.00000
Removals-Overlaps All-Overlaps Females	66	3	2.94	0.1247	98.017	750.06277	0.00000	0.00000
Slope	66	1	4.17	0.0611	98.028	750.07424	0.00000	0.00000
Overlaps Males-Overlaps All-Overlaps Females	66	3	2.94	0.1245	98.031	750.07727	0.00000	0.00000
Removals-Distance to Water-Edge-Overlaps Females	66	4	2.82	0.1560	98.036	750.08130	0.00000	0.00000
Density-Removals-Slope-Distance to Water-Overlaps Females-Overlaps Males-Overlaps All	66	7	2.75	0.2495	98.075	750.12042	0.00000	0.00000
Density-Slope-Overlaps Males-Overlaps All	66	4	2.80	0.1551	98.104	750.14936	0.00000	0.00000
Density-Removals-Distance to Water-Overlaps All-Overlaps Females	66	5	2.75	0.1862	98.134	750.17962	0.00000	0.00000
EVI-Slope-Edge-Overlaps Females	66	4	2.79	0.1545	98.149	750.19493	0.00000	0.00000
Density-Slope-Distance to Water	66	3	2.87	0.1219	98.226	750.27168	0.00000	0.00000
Slope-Distance to Water-Overlaps All	66	3	2.866023	0.1218	98.233	750.27891	0.00000	0.00000
Density-EVI-Slope-Overlaps Females-Overlaps Males-Overlaps All	66	6	2.72	0.2164	98.235	750.28064	0.00000	0.00000
Density-EVI-Distance to Water-Overlaps Females-Overlaps Males-Overlaps All	66	6	2.70	0.2152	98.334	750.37995	0.00000	0.00000
Removals-Slope-Overlaps Males-Overlaps All	66	4	2.73	0.1517	98.372	750.41745	0.00000	0.00000
Overlaps Males-Overlaps All	66	2	3.03	0.0878	98.393	750.43898	0.00000	0.00000
EVI-Slope-Removals-Overlaps Females-Overlaps Males-Overlaps All	66	6	2.66	0.2129	98.532	750.57796	0.00000	0.00000
Removals-Edge-Overlaps Females	66	3	2.67	0.1145	98.778	750.82358	0.00000	0.00000
Removals-Edge	66	2	2.83	0.0824	98.783	750.82872	0.00000	0.00000
Density-EVI-Overlaps Females-Overlaps Males-Overlaps All	66	5	2.59	0.1774	98.847	750.89248	0.00000	0.00000
EVI	66	1	3.27	0.0486	98.904	750.95016	0.00000	0.00000
Removals-Overlaps Females-Overlaps Males	66	3	2.59	0.1115	99.005	751.05111	0.00000	0.00000
Removals-Distance to Water-Overlaps Males-Overlaps All	66	4	2.542566	0.1429	99.051	751.09667	0.00000	0.00000
Density-EVI-Slope-Distance to Water-Overlaps Males-Overlaps All	66	6	2.56	0.2064	99.071	751.11697	0.00000	0.00000
Distance to Water-Overlaps All	66	2	2.671526	0.0782	99.087	751.13322	0.00000	0.00000
Density-Distance to Water-Overlaps Males-Overlaps All	66	4	2.53	0.1424	99.088	751.13414	0.00000	0.00000
EVI-Removals-Edge-Overlaps Females	66	4	2.53	0.1423	99.100	751.14536	0.00000	0.00000
Slope-Overlaps Males	66	2	2.643218	0.0774	99.142	751.18792	0.00000	0.00000
Density-Removals-Slope-Overlaps Females-Overlaps Males	66	6	2.54	0.2055	99.147	751.19248	0.00000	0.00000
EVI-Slope	66	2	2.63	0.0772	99.161	751.20635	0.00000	0.00000
Density-Overlaps All-Overlaps Females-Overlaps Males	66	4	2.51	0.1412	99.184	751.22962	0.00000	0.00000
Density-Distance to Water	66	2	2.60	0.0762	99.231	751.27697	0.00000	0.00000
Removals-Slope-Edge-Overlaps Females	66	4	2.49	0.1404	99.246	751.29218	0.00000	0.00000
Density-Removals-Overlaps All-Overlaps Females	66	4	2.48	0.1398	99.290	751.33530	0.00000	0.00000
EVI-Removals-Overlaps Females-Overlaps Males-Overlaps All	66	5	2.49	0.1718	99.297	751.34314	0.00000	0.00000
Density-Slope	66	2	2.54	0.0747	99.338	751.38374	0.00000	0.00000
Removals-Distance to water	66	2	2.50	0.0736	99.411	751.45719	0.00000	0.00000
EVI-Slope-Removals-Overlaps Males-Overlaps All	66	5	2.45	0.1695	99.481	751.52681	0.00000	0.00000
Density-EVI-Slope-Overlaps Males-Overlaps All	66	5	2.45	0.1693	99.491	751.53667	0.00000	0.00000
Removals-Distance to Water-Overlaps Males	66	3	2.396124	0.1039	99.564	751.61013	0.00000	0.00000
Overlaps Males	66	1	2.59	0.0390	99.569	751.61465	0.00000	0.00000
Density-EVI-Overlaps Males-Overlaps All	66	4	2.40	0.1358	99.593	751.63887	0.00000	0.00000
Density-EVI-Distance to Water-Overlaps All- Overlaps Males	66	5	2.40	0.1358	99.593	751.63887	0.00000	0.00000
Density-Removals-Distance to Water-Overlaps Females-Overlaps Males	66	5	2.42	0.1677	99.620	751.66545	0.00000	0.00000

Model	n	K	Fstat	r2	AiCc	ΔAICc (Δi)	Model likelihood	Wi
Slope-Overlaps Females	66	2	2.39688	0.0707	99.620	751.66583	0.00000	0.00000
EVI-Removals-Overlaps Males-Overlaps All	66	4	2.35	0.1336	99.765	751.81032	0.00000	0.00000
Density-EVI-Slope-Overlaps Females	66	4	2.35	0.1334	99.781	751.82665	0.00000	0.00000
Density-Removals-Slope-Distance to Water-Overlaps Males-Overlaps All	66	6	2.42	0.1976	99.800	751.84599	0.00000	0.00000
Density	66	1	2.31	0.0349	99.846	751.89219	0.00000	0.00000
Density-Overlaps Males-Overlaps All	66	3	2.28	0.0992	99.912	751.95762	0.00000	0.00000
Density-EVI-Distance to Water	66	3	2.22	0.0970	100.068	752.11390	0.00000	0.00000
Density-Overlaps Females	66	2	2.11	0.0628	100.178	752.22422	0.00000	0.00000
Density-EVI-Removals-Slope-Distance to Water-Overlaps Females-Overlaps Males-Overlaps All	66	8	2.47	0.2571	100.189	752.23520	0.00000	0.00000
Density-EVI- Overlaps Females	66	3	2.18	0.0953	100.197	752.24311	0.00000	0.00000
Slope-Overlaps All	66	2	2.086746	0.0621	100.227	752.27246	0.00000	0.00000
Distance to Water-Overlaps Females	66	2	2.077492	0.0619	100.245	752.29065	0.00000	0.00000
Density-EVI-Slope-Distance to Water	66	4	2.22	0.1272	100.252	752.29735	0.00000	0.00000
Removals-Slope	66	2	2.05	0.0612	100.295	752.34031	0.00000	0.00000
Density-Removals-Overlaps Females-Overlaps Males	66	4	2.20	0.1261	100.331	752.37691	0.00000	0.00000
Density-EVI	66	2	2.02	0.0603	100.357	752.40235	0.00000	0.00000
Density-Removals-Slope-Overlaps Males-Overlaps All	66	5	2.25	0.1577	100.408	752.45363	0.00000	0.00000
Density-Removals-Slope-Distance to Water	66	4	2.16	0.1241	100.486	752.53165	0.00000	0.00000
Distance to Water-Removals-Slope-Overlaps All	66	4	2.155231	0.1238	100.504	752.54933	0.00000	0.00000
Density-Removals-Distance to Water-Overlaps Females-Overlaps Males-Overlaps All	66	6	2.29	0.1889	100.516	752.56156	0.00000	0.00000
Density-EVI-Distance to Water-Overlaps Males	66	4	2.15	0.1235	100.530	752.57563	0.00000	0.00000
EVI-Slope-Removals-Edge-Overlaps Females	66	5	2.21	0.1558	100.559	752.60493	0.00000	0.00000
Density-Removals-Slope-Overlaps Females	66	4	2.14	0.1230	100.565	752.61064	0.00000	0.00000
Removals-Overlaps Males-Overlaps All	66	3	2.01	0.0885	100.688	752.73390	0.00000	0.00000
Density-EVI-Slope-Distance to Water-Overlaps Females	66	5	2.17	0.1532	100.757	752.80321	0.00000	0.00000
Density-EVI-Removals-Slope-Overlaps Females-Overlaps Males-Overlaps All	66	7	2.31	0.2182	100.770	752.81530	0.00000	0.00000
Density-EVI-Removals-Distance to Water-Overlaps Females-Overlaps Males-Overlaps All	66	7	2.28	0.2157	100.980	753.02564	0.00000	0.00000
Density-EVI-Slope	66	3	1.89	0.0838	101.031	753.07658	0.00000	0.00000
Density-Removals-Slope-Distance to Water-Overlaps Females	66	5	2.11	0.1494	101.059	753.10516	0.00000	0.00000
Removals-Distance to Water-Overlaps All	66	3	1.874165	0.0831	101.075	753.12101	0.00000	0.00000
EVI-Removals	66	2	1.65	0.0497	101.096	753.14197	0.00000	0.00000
Density-EVI-Slope-Distance to Water-Overlaps Males	66	5	2.09	0.1485	101.126	753.17135	0.00000	0.00000
Density-Removals-Distance to Water	66	3	1.85	0.0823	101.134	753.17968	0.00000	0.00000
Overlaps All	66	1	0.88	0.0136	101.286	753.33211	0.00000	0.00000
Density-EVI-Distance to Water-Overlaps Females	66	4	1.95	0.1133	101.289	753.33467	0.00000	0.00000
Removals-Slope-Overlaps Males	66	3	1.77	0.0788	101.384	753.43014	0.00000	0.00000
Density-EVI-Removals-Overlaps Females-Overlaps Males-Overlaps All	66	6	2.12	0.1777	101.420	753.46623	0.00000	0.00000
Density-Removals-Slope-Distance to Water-Overlaps Males	66	5	2.01	0.1437	101.498	753.54354	0.00000	0.00000
EVI-Slope-Removals	66	3	1.73	0.0772	101.505	753.55029	0.00000	0.00000
Density-Overlaps Males	66	2	1.42	0.0431	101.554	753.59983	0.00000	0.00000
Density-Removals-Distance to Water-Overlaps Males-Overlaps All	66	5	2.00	0.1429	101.558	753.60362	0.00000	0.00000
Density-Removals-Slope	66	3	1.67	0.0748	101.672	753.71772	0.00000	0.00000
Removals-Slope-Overlaps Females	66	3	1.59	0.0715	101.909	753.95479	0.00000	0.00000
Removals	66	1	0.23	0.0035	101.957	754.00277	0.00000	0.00000
Density-Overlaps All	66	2	1.16	0.0356	102.065	754.11097	0.00000	0.00000
Density-Removals	66	2	1.15	0.0353	102.085	754.13112	0.00000	0.00000
Density-EVI-Removals-Distance to Water	66	4	1.73	0.1018	102.139	754.18493	0.00000	0.00000

Model	**n**	**K**	**Fstat**	**r2**	**AiCc**	**ΔAICc (Δi)**	**Model likelihood**	**Wi**
Density-EVI-Overlaps Males	66	3	1.50	0.0677	102.176	754.22194	0.00000	0.00000
Overlaps Females	66	1	0.00	0.0000	102.192	754.23732	0.00000	0.00000
Density-EVI-Removals-Slope-Overlaps Females	66	5	1.86	0.1340	102.241	754.28667	0.00000	0.00000
Density-Removals-Overlaps Males-Overlaps All	66	4	1.68	0.0995	102.313	754.35889	0.00000	0.00000
Density-Removals-Overlaps Females	66	3	1.45	0.0656	102.324	754.36969	0.00000	0.00000
Density-EVI-Removals-Overlaps Females	66	4	1.65	0.0977	102.442	754.48758	0.00000	0.00000
Removals-Slope-Overlaps All	66	3	1.37	0.0621	102.570	754.61607	0.00000	0.00000
Density-EVI-Overlaps All	66	3	1.36	0.0619	102.584	754.62952	0.00000	0.00000
Density-EVI-Removals	66	3	1.33	0.0605	102.687	754.73229	0.00000	0.00000
Density-EVI-Slope-Distance to Water-Overlaps All	66	5	1.75	0.1273	102.748	754.79391	0.00000	0.00000
Density-EVI-Removals-Distance to Water-Overlaps Males	66	5	1.70	0.1243	102.973	755.01872	0.00000	0.00000
Density-Removals-Slope-Distance to Water-Overlaps All	66	5	1.70	0.1241	102.987	755.03300	0.00000	0.00000
Density-EVI-Removals-Slope-Distance to Water-Overlaps Females	66	6	1.83	0.1566	103.089	755.13506	0.00000	0.00000
Density-EVI-Slope-Overlaps All	66	4	1.48	0.0886	103.107	755.15276	0.00000	0.00000
Density-EVI-Slope-Overlaps Males	66	4	1.48	0.0883	103.129	755.17436	0.00000	0.00000
Density-EVI-Removals-Distance to Water-Overlaps Females	66	5	1.64	0.1201	103.291	755.33709	0.00000	0.00000
Density-EVI-Removals-Slope	66	4	1.40	0.0839	103.447	755.49263	0.00000	0.00000
Removals-Overlaps All	66	2	0.45	0.0141	103.524	755.56942	0.00000	0.00000
Density-EVI-Removals-Slope-Distance to Water-Overlaps Males	66	6	1.72	0.1486	103.712	755.75767	0.00000	0.00000
Density-Removals-Slope-Overlaps Males	66	4	1.33	0.0801	103.720	755.76591	0.00000	0.00000
Density-Removals-Slope-Overlaps All	66	4	1.31	0.0793	103.777	755.82284	0.00000	0.00000
Density-Removals-Overlaps Males	66	3	0.93	0.0432	103.893	755.93866	0.00000	0.00000
Removals-Overlaps Females	66	2	0.12	0.0038	104.206	756.25198	0.00000	0.00000
Density-Removals-Overlaps All	66	3	0.78	0.0365	104.351	756.39640	0.00000	0.00000
Density-EVI-Removals-Overlaps Males	66	4	1.11	0.0679	104.585	756.63111	0.00000	0.00000
Density-EVI-Removals-Distance to Water-Overlaps All	66	5	1.37	0.1025	104.597	756.64302	0.00000	0.00000
Density-EVI-Removals-Overlaps All	66	4	1.02	0.0626	104.959	757.00460	0.00000	0.00000
Density-EVI-Removals-Slope-Distance to Water-Overlaps All	66	6	1.46	0.1293	105.193	757.23916	0.00000	0.00000
Density-EVI-Removals-Slope-Overlaps Males	66	5	1.18	0.0893	105.559	757.60432	0.00000	0.00000
Density-EVI-Removals-Slope-Overlaps All	66	5	1.17	0.0886	105.611	757.65635	0.00000	0.00000