The interspecific relationships of black rhinoceros (*Diceros bicornis*) in Hluhluwe-iMfolozi Park

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B.Sc. (ConsBiolEcol) (Hons1); GradDipEd (Sec)

A thesis submitted to
Victoria University of Wellington
in fulfilment of the requirement for the degree of
Doctor of Philosophy in Ecology and Biodiversity

2014

"To Ryker, may the wild places of this world long remain protected to captivate and inspire you"

Black rhino near the Black iMfolozi River in Hluhluwe-iMfolozi Park, Zululand, South Africa (Photograph by Dale Morris).

"We learn more by looking for the answer to a question and not finding it than we do from learning the answer itself." Lloyd Alexander

ABSTRACT

As habitat loss, predators (human and non-human) and disease epidemics threaten species worldwide, protected sanctuaries have become vital to species conservation. Hluhluwe-iMfolozi Park (HiP) in South Africa is at the centre of one of the world's greatest conservation success stories. The formal proclamation of HiP in 1895 prevented the extinction of the south-central black rhino (*Diceros bicornis minor*) population. In recent times HiP has been a strategic source population for the *D. b. minor* range expansion program, facilitating an 18-fold population increase across southern Africa. However, HiP's own black rhino population appears to be in decline. Evidence for decline is most often attributed to overpopulation and poor habitat quality that is driving apparently significant increases in the average home range sizes, poor growth rates (i.e., low calf recruitment) and poor body condition of black rhino. Other factors such as non-human calf predation and parasitism have also been raised as potential causes of decline but remain untested. HiP does have some of the highest densities of lion (*Panthera leo*) and spotted hyena (*Crocuta crocuta*). HiP's black rhino population also suffers from remarkably severe chronic haemorrhaging lesions caused by a filarial parasite (*Stephanofilaria dinniki*).

Empirical evidence if or indeed why the HiP black rhino population might be in decline is lacking. Investigating this population's true status and any potential causes of an apparent decline is urgently needed.

This thesis therefore aimed to test three hypotheses for poor performance that included: (1) investigations of the average black rhino home range size, (2) confirmation of black rhino calf predation and (3) the relationship between filarial lesions and black rhino body condition. I inserted horn-implant VHF radio transmitters into 14 adult (i.e., >5 years) female black rhino in HiP and regularly monitored them on-foot over a three-year period. I found that average home range estimates (9.77 km^2) were not significantly dissimilar to estimates using a similar technique obtained forty years prior (i.e., 7.5 km^2). I also established the first confirmed link between predation attempts and tail amputation during a lion attack on a black rhino calf. Black rhino body condition, while significantly inversely and temporally correlated to lesion severity, did not appear to be driven by lesion severity

itself and highlights the need for further research.

An additional research focus for my thesis developed while in the field. I regularly witnessed red-billed oxpeckers (*Buphagus erythrorynchus*) feeding at black rhino filarial lesions while also alarm calling to alert them to my presence. Studies have found it difficult to empirically show how oxpecker-host interactions have net positive benefits that make it a mutualism. Thus, two chapters were designed to determine if red-billed oxpeckers were predominately mutualistic or parasitic when visiting black rhino. Determining this depended on whether I could identify net positive benefits or net costs to black rhino. Oxpeckers provide rhino with two possible benefits i.e., *benefit 1* is cleaning ectoparasites and *benefit 2* is increasing vigilance, and one *cost* i.e., lesion parasitism. More than 50 hours of behavioural observations established that oxpeckers favoured haemorrhaging filarial lesions over sites of tick attachment on black rhino. Moreover, black rhino appeared to be completely tolerant of oxpeckers that fed at lesions. To test whether oxpeckers increased rhino's anti-predator vigilance, I conducted 84 human approach trials towards black rhino both with and without oxpeckers present.

Results showed that rhino were immediately responsive to oxpecker alarm calls and benefitted from more than a two-fold increase in human detection rate and detection distance. Rhino predominately orientated to face towards their sensory blind spot (i.e., downwind) after an oxpecker alarm call. The traditional name (*Askari wa kifaru*) of the red-billed oxpecker, which translates as the rhino's guard, appears to be validated. However, future research will need to confirm whether black rhino's tolerance of parasitic oxpeckers is directly related to vigilance benefits.

In summary, black rhino managers in HiP can be confident that the average home range sizes have not increased significantly. Further, predation of calves might be a greater problem than previously realised and requires further investigation. Monitoring changes in the filarial lesion severity of black rhino might be a useful tool for detecting impending changes in a rhino's condition. Finally, black rhino are clearly eavesdropping and benefitting from oxpecker alarm calls – a co-evolution that has implications for conserving oxpecker populations as well.

ACKNOWLEDGEMENTS

I am most grateful to my supervisor Dr. Wayne Linklater for being so helpful and encouraging throughout. I could not have asked for someone that was more supportive of all that I was trying to achieve and for that I am forever thankful. Dr. Pete Ritchie, Victoria University of Wellington, was also a wonderfully supportive secondary supervisor to turn to – thank-you! Completing my and I presume all PhDs requires people that are at various times willing to provide assistance that is above and beyond a level I could ever have hoped for starting out. For this I especially thank Bom Ndwandwe for his invaluable efforts in the field. We spent countless days trekking out on foot together while dodging very large mammals, climbing trees and rushing to get back to our vehicle before darkness set in. My time with him afforded me opportunities to learn to read different animal behaviours, spoor and other bush survival techniques that kept me safe. The experience of being fully immersed into a vast untouched wilderness that is Zululand's Hluhluwe-iMfolozi Park is a rare opportunity that will stay with me forever! Special thanks go to Craig Reid, Sue van Rensburg and Dave Druce from Hluhluwe-iMfolozi Park Management and Research for their support. I am also very thankful for the support and information provided from ongoing personal communications with Dave Cooper, Head Veterinarian Ezemvelo KwaZulu-Natal Wildlife (EKZNW) Game Capture, Jacque Flammand, Black Rhino Range Expansion Project and Dennis Kelly, Section Ranger Mkhuzi Game Reserve, EKZNW. Professor Graham Kerley, Nelson Mandela Metropolitan University, Dr. Doug Armstrong, Massey University, and Benjamin Pocock, Wellington Zoo, are also thanked for their assistance.

Remote living in a single room hut in Masinda with no electricity and opportunity to move after dark made it essential to find opportunities to socialise outside the Park and for that opportunity I owe a huge gratitude to Chris Kelly and Simon Morgan at Mkhuze Game Reserve. They were not just good blokes to hang out with but highly experienced in the field with all things black rhino. I am thankful for the logistical support of Masinda and Mbhuzane Section Rangers San- Marie Ras and Emile Smidt.

I am very thankful to EKZNW, who approved my research (permit number: ZC/101/01). Regularly finding the rare beast that is the black rhino required horn-implant radio-transmitters to be inserted. I am grateful for the logistical expertise (i.e., helicopters, 4-WDs, people and rhino sedatives) of the amazing EKZNW Game Capture Team that made this possible. I especially thank Dave Cooper, Jeff Cooke, Paul Jennings and Quinton Rochat for both their professional expertise but also ongoing patience.The research was made possible through granted funds from the Australian Geographic Society, Rufford Small Grants (ref: 15.10.07), U.S. Fish and Wildlife Service administered Rhino and Tiger Conservation Act of 1994 (grant agreement numbers 98210-6-G102, 98218-8-G690) and Victoria University of Wellington Summer Scholarship Scheme grant. I also thank Kees Rookmaaker and the world's largest rhino information website for access to references (Rhino Resource Center: http://www.rhinoresourcecenter.com).

Although sporadic, my time as a student in the beautiful weather battered city of Wellington, New Zealand, was a pleasure. I thank everyone at the School of Biological Sciences at Victoria University of Wellington who played a part in making it such a colourful experience: Monica Awasthy, Beaux Berkeley, Ilse Corkery, Alex Dixson, Megan English, Elizabeth Heeg, Mary Murray, Gesine Pufal, Patricia Stein, Sandra Taylor and Gaius Wilson. I especially thank fellow VUW students Barnaby Dixson, Andrew Stringer and Leighton Thomas for being good friends in Wellington. Fellow black rhino PhD students Andrew Stringer and Rosalynn Anderson-Lederer are thanked for their field assistance, but also for being an ear for ongoing black rhino discussions. I thank Paul Marsden for running the SBS indoor Soccer team, providing me with a much needed physical outlet.

Finally, I thank my family and in particular my parents Linda and Tony Stumbles and my wife Liana Cahill for everything but also for putting up with my long absences and providing the emotional and often financial support that a PhD conducted over three continents requires – I can never repay your kindness.

Thanks also to Professor Des Cahill and Maria Cahill for their support, it is gratefully appreciated. Kelly and Mary-Jane Gate are thanked for looking after Liana at the Bethesda Hospital in Ubombo, where she volunteered for 6-months at a time while I pursued rhino.

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PROLOGUE

Bom and I avoiding trouble in the branches of a Marula tree

(Photograph by Dale Morris)

My PhD thesis encompasses two central themes. The first theme was initiated in response to management concerns regarding the apparently poor population performance of an endemic black rhino population that is, inflated home range sizes, calf loss via predation and parasitism. The second theme evolved after I initiated this research and became intrigued by the black rhino's role as a potential keystone in several multi-trophic parasitic interactions, in particular with the filarial nematode *Stephanofilaria dinniki* and red-billed oxpeckers. Although these themes might initially appear unrelated, I attempted to link these concepts through the chapters.

My PhD study was conducted in the 900 km^2 fenced Hluhluwe-iMfolozi Park (HiP) in KwaZulu-Natal, South Africa which holds the largest endemic south-central black rhino subspecies population. My research began as a local management response to better understand the dynamics of its endemic black rhino population. The HiP population appears to be performing poorly and is perhaps even in decline. Several hypotheses had been suggested as the potential cause of this apparent poor population performance; these include (1) poor habitat quality as evidenced by apparent increases in home range size, (2) undetected juvenile predation due to high densities of predators, as calves are difficult to sight after birth and (3) the potential role that endemic parasites and lesions might have on rhino body condition and growth rates. It was while I was developing a framework to investigate black rhino home ranges and under-acknowledged calf predation that I became intrigued about the potential influence of the remarkably severe filarial lesions that infect all adult HiP black rhino. Observing red-billed oxpeckers regularly foraging at these filarial lesions ultimately framed the design of **Chapters 5** and **6**. I focussed on untangling the complexity within these interspecific relationships. In this way my thesis ranges from a pragmatic and applied investigation framed to treat a conservation problem to a behavioural ecology study that nonetheless also has unexpected implications for rhino conservation.

The background to my PhD journey, including the conservation history of HiP's black rhino population, has been well documented in several popular articles (see **Appendix 1, 2, 3** and **6**). Together all **six Appendices** provides a useful background to each chapter, my experiences in the field and why I began this PhD study in the first place. The main aims of this thesis were divided into two parts which are intricately linked by the black rhino’s role in multi-trophic inter-specific relationships involving humans, non-human predators, oxpeckers and endo- and ecto-parasites. Each aim is discussed in greater detail in the Introduction (**Chapter 1)** which is as mentioned divided it into two parts.

1.

INTRODUCTION

Inserting a horn-implant radio-transmitter into a sedated black rhino in Hluhluwe-iMfolozi Park

(Photograph by Rosalynn Anderson-Lederer)

Part 1: Investigating the apparent decline of a strategic donor population

1.1. Black rhino: a history of rapid population decline to the beginnings of a turnaround

Humans (*Homo sapiens*) have driven many large mammal species to the brink of extinction (e.g., black rhino, *Diceros bicornis*, Western and Vigne 1985; American bison, *Bison*, Isenberg 2000; Orang-utans, *Pongo* sp., Goossens et al. 2006). Endangered species are increasingly managed within fenced sanctuaries. Critically endangered species such as the black rhino (IUCN 2012) are today almost entirely managed within fenced reserves (Emslie and Brooks 1999; Linklater et al. 2011). Guarding black rhino from the negative human influences of illegal poaching and habitat destruction has slowed previously rapid population decline. The basis of a recent population turnaround, however, has come from an over 50 year intensively managed translocation and range expansion programme (e.g., *c.* 5, 081 today, Fig. 1, cf. *c.* 1,200 in 1992; Emslie 2001; Emslie and Knight 2014). The protection and relocation management of the south-central black rhino subspecies (*D. b. minor*), in particular, is one of the world's most successful conservation stories (Morris 2009, **App. 2**).

Historically, *D. b. minor* avoided inevitable extinction when the last 100 individuals in two remaining Zululand (South Africa) populations received formal protection in 1895 (e.g., Hluhluwe-iMfolozi Complex and nearby Mkhuze Game Reserve, MGR; Skinner and Smithers 1990). After gradual stabilisation the attention of conservation managers shifted towards species recovery. In the 1960s a harvesting and relocation programme began and was first named *Operation Rhino* and is known today as the *Black Rhino Range Expansion Project* (BRREP). Out of necessity, Hluhluwe-iMfolozi Park (HiP) with the largest and most stable population became the major source of *D. b. minor* for ongoing harvesting and relocation (Emslie 2001). Today the Rhino Management Group (RMG), a collection of select state conservation agencies tasked with the implementation of this strategy, monitors and evaluates the performance of the entire black rhino meta- population (i.e., separated populations of the same species linked by translocations). Achieving rapid meta-population growth rates of at least 5% annually has become the RMG's underlying rationale for black rhino population recovery management across Africa (Emslie 2001). In HiP, ongoing harvesting at 5% of the total population is believed to be sustainable because density dependent large mammals such as rhino are expected to grow faster when maintained at just below the maximum population size for a reserve (i.e., below carrying capacity; Emslie 2001). Significant population growth, however, is expected to come from newly established (i.e., relocated) *D. b. minor* populations, where rapid growth is supported by lower densities and abundant resources (Emslie 2001).

For the most part the BRREP has gone as planned. As expected, HiP has been the source for a significant sub-species range expansion from one park in Zululand to a *D. b. minor* meta-population that covers most of southern Africa (Fig. 1). Some new populations such as in the Great Fish River Reserve in the Eastern Cape, South Africa, achieved well above the desired 5% annual growth levels (e.g., 17% annual growth; Emslie 2001; Lent and Fike 2003; Fig. 2). As expected this has led to an increase in the overall D*. b. minor* population (i.e., 100 to 1,800 individuals; Skinner and Smithers 1990; Emslie and Knight 2014). Unexpectedly, however, there has been the lack of stimulation in the growth rates of the HiP black rhino population, currently at 3% annually (i.e., below the RMG desired 5 %; Fig. 2). In fact, many report that several key performance indicators point to a black rhino population in decline (Emslie 2001; Fanayo et al. 2006; Adcock 2009). Unfortunately, only a handful of other black rhino populations, such as in Kruger National Park (South Africa), have developed into what the RMG define as a key source population suitable for ongoing harvesting (i.e., > 100 individuals and positive growth; Emslie and Brooks 1999; Emslie 2001). Founding populations start small and despite rapid growth, new black rhino reserves take time to establish themselves. The RMG's short-term 10-year goal is to achieve a *D. b. minor* meta-population of 3 060 individuals (i.e., up from 1 800; Fig. 1) by maintaining populations at a growth rate of at least 5% per annum. However, the key HiP black rhino source population is growing at a relatively low 3% (Fig. 2) and even thought to be declining by some (Emslie 2001; Reid et al. 2007). Regardless, the RMG remains heavily reliant on sourcing the majority of individuals from the HiP black rhino population.

The RMG's attention has necessarily been focussed on expanding the range and population recovery of the species. Attention has begun to shift towards understanding the performance of the key black rhino source population within HiP. Achieving this will require the suspected causes of apparently poor performance to be identified and tested. The next section of this introduction focuses on some of these causes and what ultimately forms the basis of my investigations in **Chapters 2, 3** and **4** of this thesis.

1.2. Hypotheses for the poor performance of a key black rhino source population

All available performance indicators for black rhino in HiP appear to show that the main indicators of growth rates, calf recruitment, inter-calving intervals and body condition are below average to poor (Emslie 2001; Fanayo et al. 2006; Adcock 2009). Regular harvesting was expected to maximise population growth rates to at least 5% per annum, which would correlate with above average performance indicators. Various hypotheses have been proposed as to why this *D. b. minor* population has failed to respond as expected to the intensive harvesting strategy. Hypotheses include social disruption of the population as a result of ongoing removals (Balfour 2001; Clinning et al. 2009), historical overestimation of population numbers such that apparent population declines have not actually occurred (Clinning et al. 2009), high levels of calf predation (Brain et al. 1999; Fanayo et al. 2006), increasing competition from other browsers (Emslie 1999; Fanayo et al. 2006; Landman et al. 2013), decreasing quality and quantity of black rhino browse leading to significant increases in average home range sizes (Emslie 1999; Reid et al. 2007).

There is no empirical evidence to indicate if or indeed why this population is performing poorly (Fanayo et al. 2006; Clinning et al. 2009). Central to this uncertainty is the variable quality of the data that is available for the HiP *D. b. minor* population (e.g., Clinning et al. 2009; Plotz and Linklater 2009; Linklater et al. 2010, **App. 4**). Studies that focus on improving data quality and testing the various hypotheses are needed. Clinning et al. (2009), as one of a few studies attempting to do so, addressed the hypothesis that historical black rhino population estimates for

HiP have been historically inflated. Reworking the population records, they identified where individual rhino had been recorded multiple times as several different rhino – thereby inflating overall population estimates. The reasons were most likely due to the historical use of ambiguous identification techniques (e.g., body parts such as pink lip, wrinkles). Since 1992 a much more reliable identification technique has been in use (ear notching sequence; Hitchins 1990). Clinning et al. (2009) demonstrate both the value and need for conducting empirical investigations into all suspected hypotheses for poor performance for this population. If HiP managers and the RMG are going to meet their meta- population goals they will need a much better understanding of the status of this key source population. HiP managers might then be able to identify negative factors on performance and take action to improve performance in the long term.

In this context, HiP management have proposed that a number of additional studies be initiated to test these various hypotheses (Fanayo et al. 2006; Clinning et al. 2009). In response to this request I chose three hypotheses to investigate. The first two were raised by management; the third I proposed. They are:

Hypothesis 1: Significant increases in average black rhino home range size inferred to be due to a decline in habitat quality

Authors have reported an apparent 306% increase in HiP's average black rhino home range size (i.e., from 7.50 km^2 to 23.02 km^2) over the last forty years as evidence of a reduction of black rhino habitat quality (i.e., population exceeded carrying capacity; Reid et al. 2007; Slotow et al. 2010; **App. 5**).

Several authors contend that home range size estimates are inversely correlated to habitat quality for black rhino (e.g., Emslie 1999; 2001; Reid et al. 2007; Slotow et al. 2010). Although there are some animal species with supporting empirical evidence for this (e.g., elk, *Cervus elaphus*; Anderson et al. 2005), for others there is not (e.g., brown bears, *Ursus arctus*; bobcat, *Lynx rufus*; Conner et al. 2001; klipspringer, *Oreotragus oreotragus*; Druce et al. 2009). For some animals, ranges are guided more by social relationships or their predation risk (Druce et al. 2009). Like many aspects of our understanding of black rhino ecology, there is a lack of qualitative data. Even if home range size was inversely proportional to habitat quality for black rhino, HiP's historical home range studies, like elsewhere (see Lent and Fike 2003), are fraught with a range of methodological issues that prevent meaningful inter-study comparison (e.g., inconsistent use and reporting of location number, time period and analysis - described in detail in Linklater et al. 2010).

Comparisons between studies continue to be made regardless and debate by management regarding appropriate harvesting levels are influenced by unsubstantiated inferences of declining habitat quality (Morris 2009; Linklater et al. 2010). Some argue that harvesting levels need to be increased to stimulate increased growth rates (Emslie 2001). Others are concerned that this population is being over harvested (Balfour 2001; Clinning et al. 2009). Populations are more heavily harvested if range sizes appear to have increased. As a first step, management requires ecologically accurate and comparable home range estimates for the HiP population. This formed the basis of **Chapter 2**'s aims.

Hypothesis 2: Higher than expected calf predation

HiP management has speculated that long inter-calving intervals might be a reflection, in part, of higher than anticipated calf depredation (Fanayo et al. 2006). Better performing populations with high growth rates generally have relatively short inter-calving intervals. However, if predators are targeting calves at higher than anticipated levels this could be inflating inter-calving intervals of HiP's black rhino population. HiP does have the full suite of Africa's large predators, in particular lions (*Panthera leo*) at increasing densities (Grange et al. 2012) and some of the highest densities of spotted hyenas (*Crocuta crocuta*) (Graf et al. 2009) - both implicated in black rhino predation (Kruuk 1972; Elliot 1987; Brain et al. 1999; Plotz and Linklater 2009). Some black rhino populations with a full array of large predators, like HiP, have relatively poor growth rates, while other reserves have good growth rates and no predators (e.g., Great Fish River Reserve, South Africa; Lent and Fike 2003; Fig. 2). It might not be realistic to expect HiP and other reserves with higher densities of large predators to be able to grow as fast as rhino populations where predators are absent (Plotz and Linklater 2009), even with ongoing harvesting.

A major limitation in determining the effect of predation on juvenile black rhino is the lack of evidence that it occurs. Berger (1994) states that up to 94% of the missing ears and tails regularly seen in individual black rhino can be attributed to attempted predation on calves. It is possible that black rhino calf predation is significantly under reported. Indeed the HiP black rhino population have about 7% of the population with missing ears and tails suspected of being caused by lion or spotted hyena depredation attempts (Hitchins 1986; Plotz and Linklater 2009).
Even if rhino are radio-tagged, young calves are not readily noticed until they are several months old. Thus, a significant number of calves could be born and lost to predators before identification and artificially inflate inter-calving intervals (Plotz and Linklater 2009). Apparently poor calving rates and intervals reported might reflect other factors such as non-human predation (i.e., lion and spotted hyenas) (Fanayo et al. 2006).

Despite Hitchins (1990) and Berger (1994) warning about a link between failed depredation attempts and ear and tail loss in black rhino, there has been ambiguous evidence to support this assertion. Actual observations of juvenile black rhino depredation is rarely reported (Brain et al. 1999) and so managers rarely factor in predation when making decisions about rhino population performance.
Thus, if observations of non-human depredation attempts on calves were made and the link between predation attempts and ear and tail loss in black rhino calves confirmed, then managers might have the impetus they need to consider this in their management plans. My attempts to find the link between calf depredation and ear and / or tail loss in HiP black rhino formed the basis of **Chapter 3**.

Hypothesis 3: Filarial parasitism and rhino body condition

Parasitism has not to my knowledge been considered as a cause of poor performance in black rhino populations. However, HiP's black rhinos are infected by a filarial parasite that produces distinctive chronic haemorrhaging lesions (Hitchins and Keep 1970). After observing the size and severity of black rhino's filarial lesions (e.g., 26cm wide; Hitchins and Keep 1970), I wondered if the HiP population would be able to perform optimally.

Other than identifying the cause (*Stephanofilaria dinniki*; Round 1964), little other research on filarial lesions has occurred since the late 1960s (Hitchins and Keep 1970). First-hand accounts from wildlife practitioners report that filarial lesions become progressively more severe (i.e., flaring) whenever black rhino are exposed to a stressful event. For example, black rhino harvested for relocation are first held in enclosures for up to a week or two. In these rhino, the severity of filarial lesions increased dramatically (D. Cooper, *Pers. comm.*). 'Flaring' of lesions was also associated with marked declines in rhino body condition over time. If lesion severity and body condition are indeed correlated, it poses a potential dilemma for management. HiP's black rhino have the most severe filarial lesions recorded for any of the populations where lesions are known to occur (Schulz and Kluge 1960; Parsons and Sheldrick 1964; Tremlett 1964; Hitchins and Keep 1970). The increased severity of lesions might, in part, explain why HiP's black rhino also have below average body condition scores (Fanayo et al. 2006). It might also explain why some non-infected populations appear to have much higher growth rates (Emslie 2001; Lent and Fike 2003). An ability to monitor and detect the flaring of lesions might be a useful to managers to detect periods of stress in affected black rhino populations.

Research on domestic cattle (*Bos Taurus*) demonstrated that low body condition scores were temporally correlated with increased treatment for haemorrhaging lesions of the sole (i.e., lameness) two to four months later (Green et al. 2014). I speculated whether such a temporal relationship might also exist for HiP's black rhino. If such a relationship existed I would expect to see an inverse temporal correlation between body condition scores and the amount that filarial lesions haemorrhage (i.e., severity). Testing this would require reliable field measures of body condition and filarial lesion severity for HiP's black rhino.

Fortunately there is a five point visual scoring system already in use for black rhino (Reuter and Adcock 1997). This body condition (BC) scoring system is reliable, as Perissodactyls (e.g., rhino, horses and elephants) store their body fat directly under their skin (Carroll and Huntington 1988; Henneke al. 1983; Keiper 1991; Reuter and Adcock 1998). Unfortunately a reliable field technique for scoring filarial lesions is not available. Thus, it is not currently possible to compare lesion severity and body condition scores to look for a temporal signal.

Filarial parasitism's role in the welfare of black rhino is largely unknown. Should a temporal signal exist between lesion severity and body condition it could, in part, add weight to the argument that HiP's black rhino population is performing poorly due to an unknown stressor (Emlsie 2001). Some suggest, for instance, that HiP has poor quality habitat for black rhino due to overpopulation (i.e., exceeded carrying capacity; Emslie 1999; Reid et al. 2007). If poor nutrition was an underlying stressor it could be causing HiP's black rhino population to present with the most severe lesions yet recorded, as well as below average body condition (Fanayo et al. 2006). Nonetheless, the reasons remain unknown, including why there is such a disparity in lesion severity across the populations of black rhino that have lesions (Tremlett 1964; Hitchins and Keep 1970; Mutinda et al. 2012). To improve the understanding of how filarial lesions effect black rhino populations there is a need for greater inter-study comparisons. To facilitate comparisons between reserves I surveyed and plotted all current black rhino reserves presenting with filarial lesions. Together with investigations into a temporal signal this formed the basis of **Chapter 4** of this thesis.

1.3. Study site: Hluhluwe-iMfolozi Park

Hluhluwe-iMfolozi Park (HiP) is a 960 km^2 fenced reserve located in Zululand, KwaZulu-Natal (KZN), South Africa (Fig. 3). Mean annual rainfall and altitude decrease from Hluhluwe in the North (990 mm and 450 m asl), to iMfolozi in the south (635 mm and 60 m asl), with April to September being the dry season (Balfour and Howison 2001). Average monthly temperatures range between 13°C (winter) to 33°C (summer) (Whateley and Porter 1983). Rainfall remains highly variable and seasonal, with average warm wet summers (October to March) of 378 mm and cool dry winters of 201.9 mm (Masinda weather station; G. Clinning, unpubl. data). HiP also experiences periodic oscillations in rainfall lasting approximately nine years (Walters et al. 2004). HiP currently holds approximately 218 south-central black rhino (*D. b. minor*) (Clinning et al. 2009) and is the largest surviving endemic population of only two in Africa (Brookes and MacDonald 1983). HiP undergoes annual black rhino harvesting (c. 5 to 8 % of the population) because it is a strategic donor source population for species rescue and range expansion (Emslie 2001).

Hluhluwe-iMfolozi Park's non-human predator history

Following local extinction in 1958 the first lone male lion re-entered the iMfolozi Game Reserve (Southern half of HiP), followed by two females in 1965 (Anderson 1981; Grange et al. 2012). By the 1980s approximately 60 lions had been recorded (Maddock et al. 1996). Lions were eliminated from the Hluhluwe section (Northern part of the Park) between 1988 and 1992, to be replaced by 13 female and 3 male lions brought from Namibia between 1999 and 2001 (Trinkel et al. 2008). Between 2003 and 2004, the total lion population declined from 80 to 61 (Trinkel et al. 2008), but had rebounded to 114 by 2008 and reached an estimated 200 individuals in 2010 (Grange et al. 2012).

HiP's spotted hyena population (excluding cubs) has been estimated at 321 individuals (Graf et al. 2009). The average spotted hyena density in HiP is relatively high for southern Africa, but intermediate if compared to East African areas (Graf et al. 2009).

1.4. Focal study species: south-central black rhino (*D. b. minor*)

Black rhino are able to occupy areas wherever substantial herb and woody browse occurs. Their range represents a wide range of habitats from deserts, semi-deserts, wooded savannahs, woodlands, forests and even sub-alpine heathlands (Amin et al. 2006). However, sustainable population densities in these habitats range from 1 rhino per 100 km^2 in the south-western desert plains of Namibia, to more than 1 rhino per 1 km^2 in the thicket vegetation (Amin et al. 2006) of the mesic eastern parts of the continent (Swart and Ferguson 1997). Over the last two centuries a significant area of rhino habitat has been fragmented due to land clearing for human agricultural and settlement needs (Amin et al. 2006). More recently, however, human demand for rhino horn threatens rhino survival (Ashley et al. 1990; Swart and Ferguson 1997; Rookmaaker 2005; Amin et al. 2006; Beech and Perry 2011). Rhino horn is used to carve ornate handles for ceremonial daggers in Yemen (known as jambiyas) and in traditional Chinese medicine (Ashley et al. 1990; Emslie and Brooks 1999; Amin et al. 2006).

Obtaining accurate data on black rhino calf births, survival rates and inter-calving intervals is challenging. Firstly, black rhino require intensive long-term monitoring due to the asynchronous 15 month gestation periods with an additional three months before gestation is again possible (Skinner and Smithers 1990). Secondly, black rhino regularly inhabit dense vegetation, especially in the first six months of a calf's life (Skinner and Smithers 1990).

Black rhino are categorized as Critically Endangered by the IUCN Red List (IUCN 2012) and are divided into three (previously four) sub-species distributed throughout sub-Saharan Africa (Emslie and Brooks 1999; Amin et al. 2006: Fig. 1). The south-central black rhino sub-species, *D. b. minor*, are most numerous with the largest endemic sub-species population in HiP, KwaZulu-Natal Province, South Africa. HiP's population was estimated at 218 individuals in 2009 (Clinning et al. 2009) and is one of only two reserves that have greater than 100 black rhino (other Kruger National Park). The practice of translocating black rhino, largely from HiP, has been an important tool in stabilising and increasing their overall number.

Black rhino in HiP are one of a few known populations to suffer from large haemorrhaging ulcerative filarial lesions (Hitchins and Keep 1970). The severity of lesions also varies between infected populations. Lesions are almost unnoticeable in some populations (Meru National Park, Kenya; Mutinda et al. 2012) but remarkably severe in others (Tremlett 1964; Hitchins and Keep 1970; Skinner and Smithers 1990). Lesions are caused by the filarial nematode *Stephanofilaria dinniki* (Schulz and Kluge 1960; Round 1964) that is vectored by blood sucking flies (*Rhinomusca dutioti* and *R. brucei*; Zumpt 1964; Parsons and Sheldrick 1964; Mihok et al. 1996).

As with other filarial nematode species it is speculated that *S. dinniki's* distribution is physically limited by rainfall-humidity and temperature because moisture limits the range of its fly vector (e.g., bloodsucking fly: *R. dutoiti/ brucei;* Zumpt 1964). Dipteran larva requires moisture in order to progress through the several larval stages before adulthood (Lehane 2005). Nonetheless, it is unclear why there should be variation in lesion severity between populations where the vector does occur. Determining the causes of this variation is hindered, in part, by limited knowledge about this filarial nematodes biogeographic range within Africa.

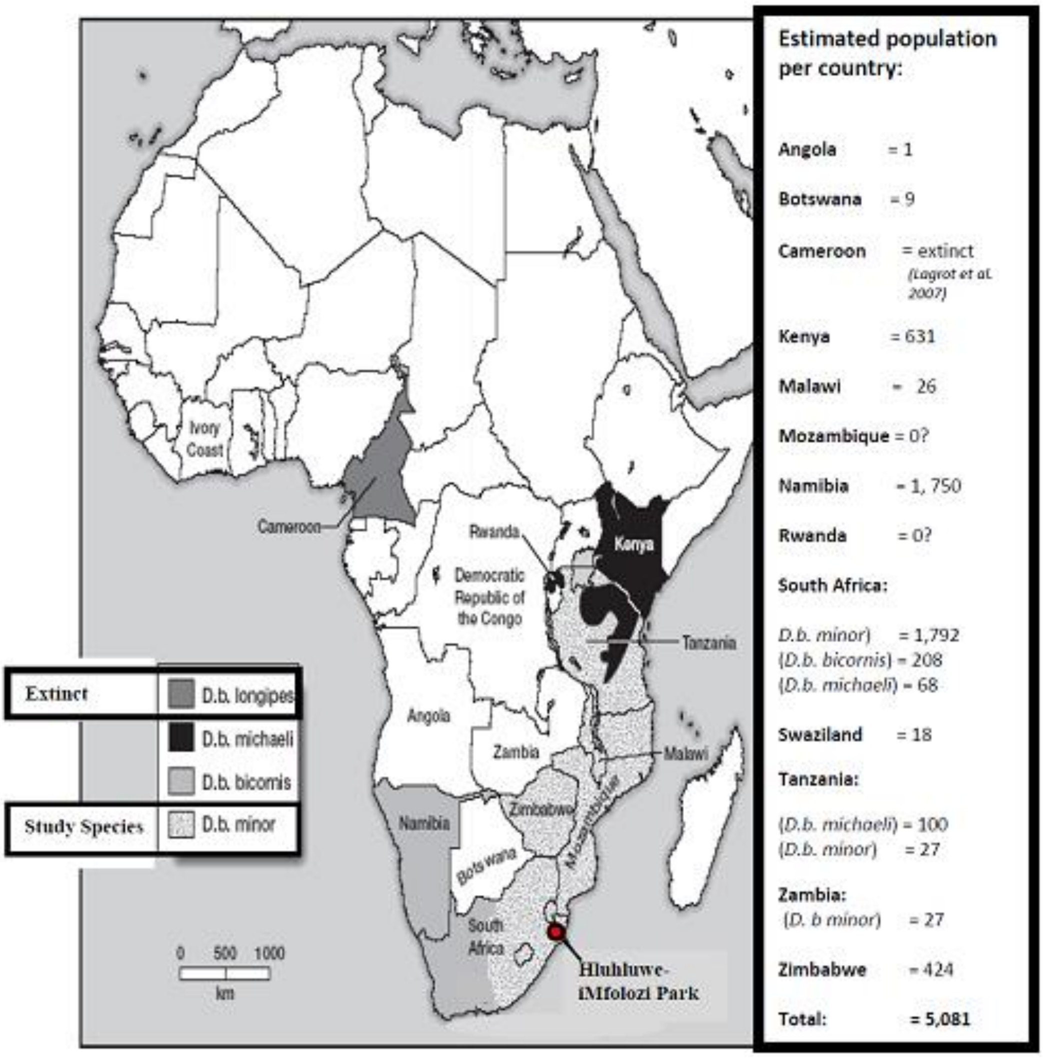
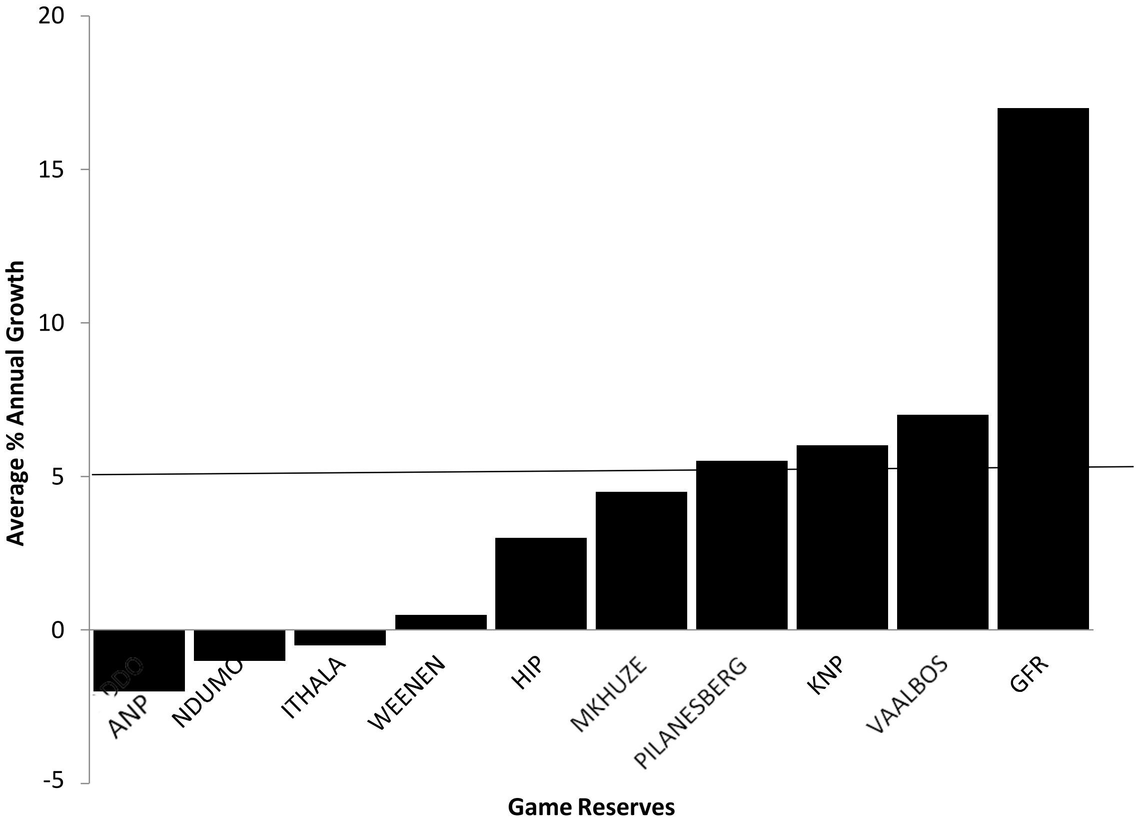


Figure 1: Distributional range of the four black rhino sub-species including the estimated populations for each country within its distributional range. All current *D.b.minor* populations were sourced from Hluhluwe-iMfolozi Park and nearby Mkhuze Game Reserve (red circle: for security reasons precise locations of populations are not shown). Population estimates listed above as of 31 December 2012 (Emslie and Knight 2014). Map Source: Emslie and Brooks 1999. Note that Mozambique population is extinct and Angola, Botswana and Zambia had black rhino relocated post the design of the map in 1999, hence uncoloured.



Adapted from Knight (2001)

Figure 2. Average annual percentage growth of selected South African black rhino populations from 1989-1998 (Rhino Management Group Data). Achieving rapid meta-population growth of $\geq$5% annually (black horizontal line) is the underlying rationale for black rhino population management across Africa. Expanded abbreviations: ANP = Addo National Park; *GFR= Great Fish River; KNP= Kruger National Park; HiP= Hluhluwe-iMfolozi Park.*

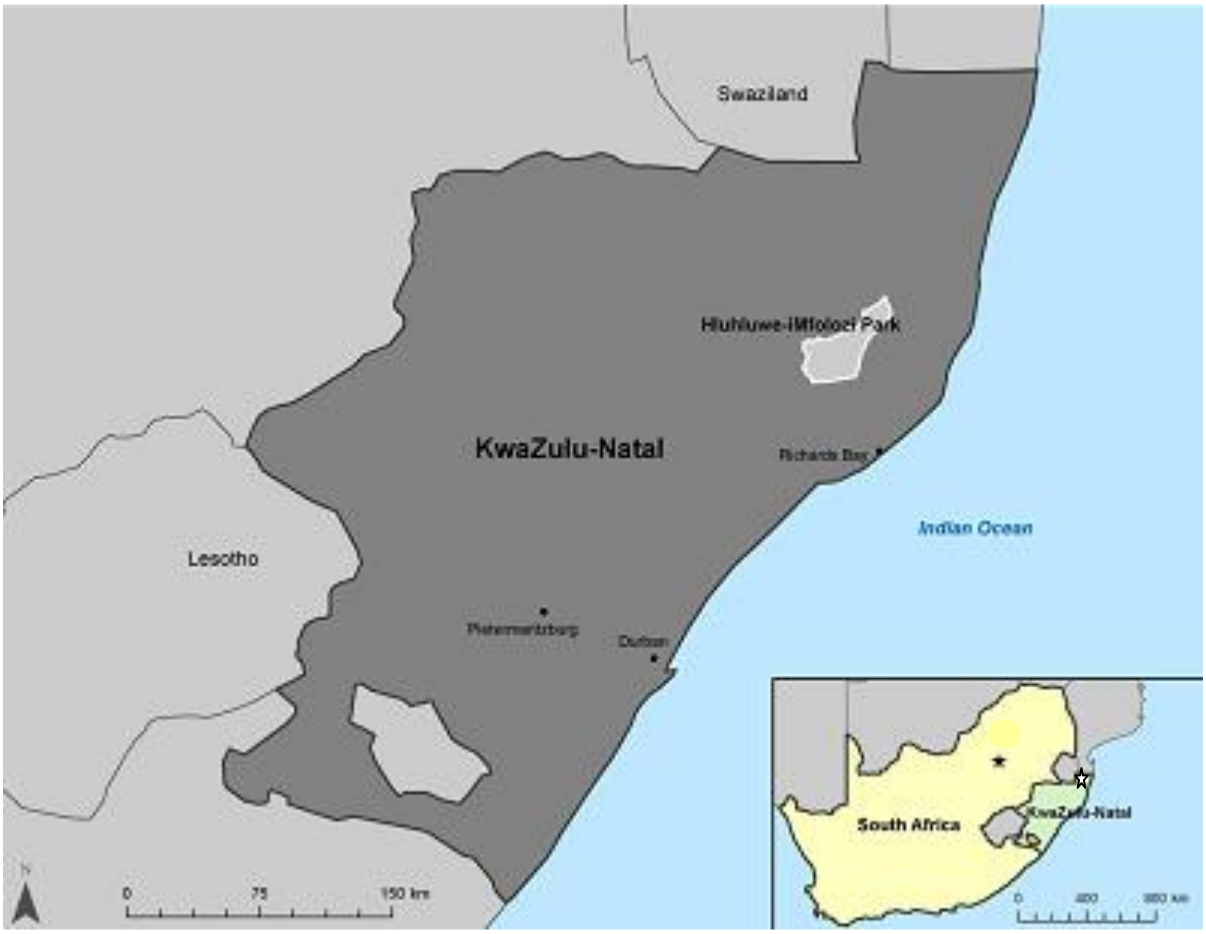


Figure 3. Study site showing location of Hluhluwe-iMfolozi Park in KwaZulu-Natal Province with inset showing location of province within South Africa (Map source: Darnell 2012).

Part 2: Understanding the conditionality of mutualisms

1.5. The cost versus benefit tug-of-war in cleaning symbioses

Mutualisms, commensalism and parasitism have historically been regarded as discrete categories of interspecific relationships. Increasingly these relationships, particularly mutualisms, are being recognised for their variability under changing environmental conditions (Bronstein 1994a, b; Del-Claro 2004; Cheney and Cote 2005; Plantan 2009). Mutualisms are defined as interspecific interactions where the benefits from the association outweigh the costs (Bronstein 1994a, b). However, changes to the biotic and abiotic settings within which mutualistic interactions occur can alter the outcome (Holland et al. 2002; Plantan 2009). Relationships might therefore shift from mutually beneficial (mutualism) to costly (parasitic) under changing environmental conditions. Cleaning symbioses, where a cleaner species removes ectoparasites from a larger host, are thought especially prone to variable outcomes because benefits between the two interacting species are mediated by the presence of another (Bronstein 1994a, b). Mutualistic interactions that vary according to such ecological factors are termed "conditional mutualisms" (Bronstein 1994a; Herre et al. 1999; Del-Claro 2004; Plantan 2009).

Understanding that cleaning symbioses are prone to conditional outcomes is a relatively recent consideration (Cheney and Cote 2005; Plantan 2009). Since the early 20th century a cleaning symbiosis that has engendered considerable debate and research interest about its true nature is the oxpecker (*Buphagus* sp.) -ungulate relationship (Moreau 1933; Weeks 2000; Nunn et al. 2011). Some have argued that oxpeckers benefit ungulates by removing ticks (Craig 2009; Nunn et al. 2011). Others believe that ungulates are harmed by oxpeckers predilection for wound feeding (van Someren 1951; Attwell 1966; Keet et al. 1997; McElligot et al. 2004; Weeks 1999, 2000).

Initial investigations attempted to resolve the debate by examining the stomach contents of oxpeckers. Ticks (Ixodiid) were found in the birds' stomachs (Bezuidenhout and Sutterheim 1980; Stutterheim et al. 1988), however, blood digested too quickly to allow meaningful comparisons to be made. Studies began to focus on oxpecker feeding behaviour from a cost (blood) versus benefit (tick removal) point of view. Evidence that oxpeckers meaningfully reduced tick loads remained elusive (Hart et al. 1990; Weeks 1999, 2000). Indeed, some authors discovered that oxpeckers preferred blood from wounds over ticks (Moreau 1933; Attwell 1966; Keet et al. 1997; Stutterheim et al. 1988; Weeks 1999, 2000; McElligot et al. 2004; Plantan et al. 2009). Arguments that the oxpecker-ungulate relationship was costly for a host and perhaps more akin to a parasitism began to gain traction (Weeks 2000; McElligot et al. 2004).

When the interests of mutualists are not perfectly aligned, maintaining mutually beneficial outcomes and stabilizing mutualisms can come from control mechanisms that modulate interactions (Skelton et al. 2014). Some authors believe that ungulates use of oxpecker rejection behaviours (e.g., roll, run and shake) are specifically aimed at deterring blood feeding oxpeckers and align interests back towards mutual benefits (Keet et al. 1997; Koenig 1997; Plantan 2009; Bishop and Bishop 2014). However, a lack of qualitative data on rejection behaviours and cost- benefit analysis in oxpecker-ungulate interactions prevents the level of conclusion that can be drawn from this.

One study in particular has looked beyond just placing individual oxpecker-ungulate interactions into discrete categories (i.e., mutualism or parasitism). Plantan (2009) designed and implemented foraging experiments involving interactions between red-billed oxpeckers (*B. erythrorynchus*; Fig. 4A) and a donkey (*Equus africanus asinus*) in captivity. The oxpeckers were provided with a variety of Ixodid tick species to select from and the ratio of the most preferred tick species were placed at various densities on the donkey host. At the same time a full container of cow's blood was also strapped to the donkey – giving oxpeckers a clear choice between ticks and blood. Plantan (2009) discovered that if preferred tick species remained abundant, foraging oxpeckers did very little blood feeding and significantly reduced overall tick loads on the host (i.e., a cleaning mutualism).
Conversely, preferred tick species kept at low densities caused oxpeckers to switch foraging behaviour and feed mainly on blood from the container. Plantan (2009) also monitored the behavioural interactions of several free-ranging ungulates (e.g., giraffe, *Giraffa camelopardalis*; zebra, *Equus quagga*; impala, *Aepyceros melampus*) and oxpeckers. Ungulates were found to be significantly more intolerant towards

oxpeckers that wound than tick fed (Plantan 2009). The idea that ungulates use rejection behaviours to deter blood feeding oxpeckers appears to have support.

An investigation of the marine cleaning symbiosis adds weight to Plantan's (2009) investigations. Cheney and Cote (2005) conducted field experiments observing Caribbean cleaning gobies (*Elacatinus evelynae*) feeding behaviour on longfin damselfish (*Stegastes diencaeus*) over a wide geographic range. They found that natural variations in ectoparasite abundance similarly influenced the parasitic (scales and tissue) versus mutualistic (ectoparasites) foraging behaviour of the cleaning goby. Rejection behaviours towards cleaners that adopt parasitic feeding behaviour also appeared to be the control mechanism to prevent overexploitation (Farrell et al. 2014).

For a symbiosis to be a mutualism benefits received must exceed costs incurred for both partners. The cost versus benefit outcome of any oxpecker- ungulate interaction appears therefore to be heavily dependent on ectoparasite abundance and to an unknown extent by host rejection behaviours. However, there is one additional benefit oxpeckers might be providing ungulates that has yet to receive meaningful research attention (but see Weeks 1998). Oxpeckers have distinctive alarm calls that are suspected of alerting hosts to the presence of predators (i.e., increased vigilance; Schenkel and Schenkel-Hulliger 1969; Weeks 1998). Historically hunters attest to oxpeckers alerting their quarry (Craig 2009). However, it is unknown whether hosts actually benefit from increased vigilance.
Weeks (1998) attempted to test this but results remained inconclusive.

The lack of quantitative information of this conditional feeding association in the wild limits the level of conclusion that can be drawn, although the significance of ectoparasite abundance for oxpeckers foraging habits appears to be clear (Plantan 2009). Research of oxpecker-ungulate interactions with a broader scope is needed. The multiple hosts and variable environments that oxpeckers and ungulates inhabit present a plethora of conditional outcomes for any one interaction. Understanding interactions within its conditional context will require consideration for all of the known costs and benefits, host rejection behaviours and ectoparasite abundance at the time. The challenge therefore is to find an ideal ungulate species that is not only sympatric with oxpeckers but allows all of the costs, benefits and rejection behaviours in oxpecker-ungulate interactions to be monitored and where tick densities are quantifiable.

1.6. Black rhino – an ideal host to test all of the known costs versus benefits in oxpecker interactions

I propose that black rhino in HiP are the ideal wild host species to investigate the conditional nature of this terrestrial cleaning mutualism because observations of the tick versus blood utilisation patterns on black rhino are made possible as:

(1) Black rhino have three specific and easily observable (hairless) sites of tick attachment (i.e., nostrils, anogenital region and ears; Penzhorn et al. 1994).

(2) HiP black rhino have two chronic and prominent haemorrhaging filarial lesions on their anterior flanks (see section 1.2. of the Introduction and Hitchins and Keep 1970).

Moreover, (3) tick abundance is seasonally quantifiable in HiP as Ixodid tick species in the southern latitudes of Africa undergo a well-documented reproductive diapause and are absent during the cooler winter months in KwaZulu-Natal i.e., (April to September; Walker et al. 2000; Horak et al. 2003, 2009; Randolph 2008).

Finally, (4) testing for the benefit of increased vigilance is made possible as black rhino are the oxpecker host most associated with oxpeckers sentinel behaviour (Schenkel and Schenkel-Hulliger 1969). Indeed, the Swahili name (*Askari wa kifaru*) for the red-billed oxpecker translates as the rhino’s guard.

Therefore, black rhino in HiP will hopefully allow me to broaden the traditional scope of oxpecker-ungulate investigations (i.e., tick or wound feeding) into a study that examines both known benefits (i.e., 1. tick removal, 2. increased vigilance) and the one known cost (i.e., blood feeding), while also monitoring black rhino rejection behaviours towards oxpeckers. The ability to quantify seasonal tick densities in HiP will also enable me to factor in the mechanism (i.e., ectoparasites) that appears to be drive the conditionality of both marine and terrestrial cleaning symbioses (Cheney and Cote 2005; Plantan 2009). I predicted that in a scenario of low tick abundance (i.e., during cool dry winters) that oxpeckers in HiP ought to target filarial lesions as a food resource but that the costs of this behaviour might be ameliorated by the benefit of increased vigilance from sentinel behaviour. Determining this will depend upon whether I can provide evidence that black rhino respond and receive increased vigilance benefits from red-billed oxpeckers.

1.7. Focal study species: Red-billed oxpeckers and their known relationship with black rhinoceros

The red-billed oxpeckers are an endemic African passerine species belonging to the family Sturnidae (Van Someren 1951; Attwell 1966; Hustler 1987; Craig 2009). Oxpeckers distribution is fragmented across several countries as they are dependent on wild and/or domesticated ungulates for food (Craig 2009). Red-billed oxpeckers are principally an east African species, ranging from the Central African Republic east to Ethiopia and south to South Africa (Fig. 4B). Only red-billed oxpeckers are sympatric with HiP black rhino as the yellow billed (*B. africanus*) is locally extinct (Stutterheim and Brooke 1981).

Oxpeckers are well adapted to clinging and crawling across ungulate bodies in search of food. They have sharp, curved claws and their tail feathers are long and stiff to provide balance and support (Plantan 2009). Plucking, pecking, scissoring and controlling ticks are aided by a flattened beak with a sharp edge (Attwell 1966; Breitwisch 1992; Koenig 1997). Oxpeckers, like other birds, have excellent eyesight for searching and plucking ticks on hosts (Craig 2009). Acute vision also contributes to their capability as sentinels; many a hunter has attested to oxpeckers distinct alarm calls alerting grazing animals to their approach (Craig 2009). The benefits and role of sentinel behaviour for oxpeckers and their hosts within interspecific relationships has thus far received little attention in the literature (but see Weeks 1998).

Analysis of the stomach contents of oxpeckers shows that ticks appear to form a considerable part of their diet (i.e., 52.3% by mass of stomach contents of 53 birds; Moreau 1933; van Someren 1951; Mengesha 1978; Bezuidenhout and Stutterheim 1980). However, other research points towards oxpeckers preferring blood over ticks and might actually be parasites of their hosts (Keet et al. 1997;

Weeks 1999, 2000). Indeed, herders regarded oxpeckers as the killers of domestic stock for opening and feeding from the wounds of cattle, hence the origin of their genus Buphaga – Latin for ox-eater (van Someren 1951; Craig 2009). Whether oxpeckers are mutualists or parasites of ungulates is an ongoing debate (Weeks 2000; Nunn et al. 2011).

Background to the oxpecker- black rhino relationship

Oxpeckers feeding on black rhino filarial lesions: Regular observations of red-billed oxpeckers feeding on wounds and lesions led to suspicions that they were the cause of black rhino's filarial lesions in HiP and MGR (Spinage 1960). Although the cause was subsequently identified to be a filarial nematode, the role that wounds and lesions play in oxpecker foraging habits on black rhino (Hitchins and Keep 1970; Skinner and Smithers 1990; McElligot et al. 2004; Craig 2009) and other large mammals still garners attention (Keet et al. 1997; Weeks 1999, 2000).

Oxpeckers feeding on black rhino ticks: Both ear (*Rhipicephalus appendiculatus*; Baker and Keep 1970) and blue ticks (*Boophilus decloratus*; Stutterheim et al. 1988; Plantan 2009) have been identified as the two most favoured tick species by red-billed oxpeckers. However, there is currently no data available on oxpeckers tick feeding preferences when visiting black rhino. Although black rhino have been identified as the most favoured symbiont of red-billed oxpeckers in HiP (Stutterheim 1980), they are known to only host one of oxpeckers two preferred tick species (i.e., ear tick; Baker and Keep 1970).

Black rhino intolerance towards oxpeckers: McElligot et al. (2004) showed that captive black rhino, without filarial lesions or ticks, were highly intolerant of red-billed oxpeckers that attempted to feed on their wounds. There is no empirical data I am aware of from observations between free-ranging black rhino and oxpeckers. It remains to be tested whether oxpeckers are parasitic (i.e., lesions preferred over ticks) and whether black rhino, like other large mammals, are intolerant towards blood-feeding oxpeckers (Plantan 2009).

Increased vigilance from oxpecker sentinel behaviour: The black rhino is most associated with oxpeckers' anti-predator alarm calling behaviour, especially towards people (Alexander 1836; Leslie 1876; Schenkel and Schenkel-Hulliger

1969; Goddard 1970, 1973; Skinner and Smithers 1990). Although untested, experienced observers describe being able to walk undetected to within a few paces of black rhino when no oxpeckers were in attendance (Leslie 1876; Schenkel and Schenkel-Hulliger 1969; Goddard 1970, 1973). Despite their large size (i.e., *c.* 1000kg; Owen-Smith 1988), black rhino are solitary and visually impaired animals easily approached undetected (e.g., Leslie 1876; Goddard 1970). Indeed, adult black rhino are largely immune to non-human predation (Owen-Smith 1987), although young calves remain vulnerable (e.g.; lion, *Panthera leo*, and spotted hyena, *Crocuta*; Plotz and Linklater 2009). However, a role for non-human predators in anti-vigilance behaviour between oxpeckers and black rhino cannot be ruled out. In the context of poor eyesight, human and non-human predation pressure, black rhino might benefit from oxpecker sentinel behaviour and increased vigilance. For HiP's non-human predator history see section 1.3 of the Introduction.

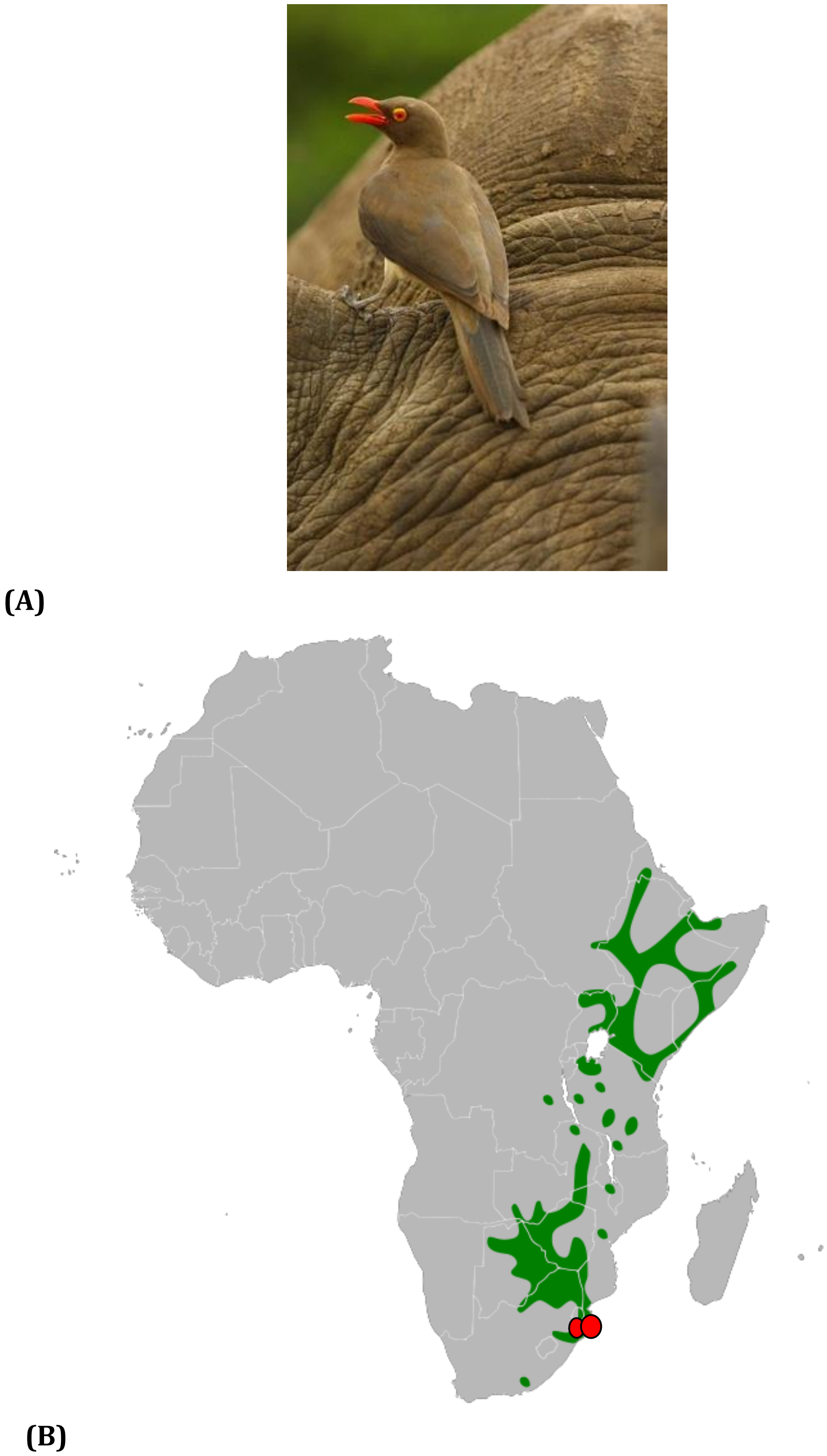


Figure 4 (A). A red-billed oxpecker (*Buphagus erythrorynchus*) (Photograph by Jed Bird) and **(B)** known distribution (Craig 2009; BirdLife International and Durham University 2012). Note red circle on map is the location of Hluhluwe- iMfolozi Park in South Africa.

1.8. Thesis structure

The overall aims of this thesis are to (1) test hypotheses for the apparently poor growth and declining population rate of HiP's black rhino population and (2) to advance the current knowledge of the cost versus benefit of the black rhino-red- billed oxpecker relationship. To achieve this I adopted a methodological approach that investigated multiple inter-specific interactions spanning the disciplines of spatial and behavioural ecology.

To begin, in **Chapter 2** I examine the hypothesis that average black rhino home range sizes in HiP have increased by more than 300% in forty years. This shift has been used by some to support the theory of a HiP black rhino population in decline, as range size has been shown to increase with declining carrying capacity in some mammal species. Unfortunately, black rhino home range studies are plagued by data deficiencies, inconsistent definition and interpretation of analyses. This has hindered meaningful inter-study comparisons and maintained a generally poor understanding of black rhino spatial ecology. Home range studies that adequately report on methodology and other potential sources of error are urgently needed to improve overall accuracy and interpretation. Therefore this chapter's two main aims were (1) to investigate if dissimilar methodology best explains the apparently significant shift in the average home range sizes of HiP black rhino and (2) to test a well-defined methodology and report on the effect of potential sources of error on home range estimations. To achieve this 24 HiP black rhino were fitted with horn-implant transmitters and monitored over wet and / or dry seasons and calendar years. Specifically, the number of locations needed to accurately measure home range size was calculated and the two most common techniques were used to construct rhino home ranges to aid inter-study comparison. Finally, I measured the effect of both observer and triangulation error on home range size calculations. It is my hope that this study will act as a baseline for further inter-study comparisons and encourage future black rhino home range studies to standardize their methods and reporting of error.

In **Chapter 3** I report on a rarely documented lion depredation attempt on a black rhino calf that resulted in the amputation of its tail and severe tissue damage around the anogenital region, ultimately causing its death. This study provides the first direct link between predation as the most likely cause of tail and ear loss incidences sighted in several black rhino populations, including HiP. The conservation management implications of this observation are explored within the context that calf predation might be causing HiP's apparently long inter-calving intervals and low calving rates.

During field research I also noticed that adult HiP black rhino suffered from large haemorrhaging lesions on both anterior flanks. Although known to be caused by a parasitic filarial nematode there has been little to no attention given to the role, if any, that chronic lesions might have on the condition of black rhino.

Research on domestic cattle has shown there to be a clear inverse temporal correlation between the severity of chronic lesions (non-filarial) and body condition. In **Chapter 4** I posited that if such a temporal signal also existed between lesion severity and body condition for black rhino in HiP, managers could monitor this accordingly. Managers might be able to better predict when the black rhino population was under stress by monitoring BC and LS. HiP black rhino are known to have the most severe filarial lesions recorded for any population. The severity of their lesions might, in part explain why HiP's rhino have below average body condition scores compared to other better performing populations. Although reliable five point body condition score exists there is no reliable measure for filarial lesion severity in the field. Therefore, the three main aims of this study were to (1) test the application of a novel field measuring technique for the filarial lesions of HiP's black rhino population and use it to (2) test whether a temporal correlation exists between filarial lesion severity and black rhino body condition.

At the same time I wanted to facilitate more inter-study comparisons in future by

(3) updating the current biogeographic range of filarial lesions in black rhino populations. It is my hope that this might encourage further research into the role that filarial parasitism has on critically endangered black rhino populations.

The next two chapters also have their origins from field observations. I regularly witnessed red-billed oxpeckers feeding at black rhino filarial lesions while also alarm calling to alert them to my presence. I began to wonder how costly parasitic foraging behaviour balanced with the seemingly beneficial sentinel behaviour of oxpeckers. Studies have found it difficult to empirically show how oxpecker-host interactions have net positive benefits that make it a mutualism.

Thus, the next two chapters were designed to determine if red-billed oxpeckers were predominately mutualistic or parasitic when visiting black rhino.

Determining this will depend on whether I can identify net positive benefits or net costs to black rhino. There are two possible benefits i.e., *benefit 1* is cleaning ectoparasites and *benefit 2* is increased vigilance, while *cost 1* is lesion feeding.

Therefore, in **Chapter 5** my aim was to determine whether red-billed oxpeckers favoured filarial lesions (*cost 1*) or sites of tick attachment (*benefit 1*) when visiting black rhino. I conducted over 50 hours of observations of rhino- oxpecker interactions where the rhino's body was divided into several regions and oxpecker visits tallied according to the body locations they visited. Finally, the tolerance behaviour of black rhino during oxpecker visits was also monitored as other studies have found that hosts are highly intolerant towards oxpeckers that attempted to feed at wounds.

In **Chapter 6** I focussed on whether oxpeckers increased the vigilance of black rhino (*benefit 2*). This benefit has not yet been looked at before. To achieve this I conducted multiple field approach experiments where I, as an observer, monitored the approaches of a human 'threat' such that I could determine whether oxpecker presence made a significant impact on the approach distances achievable by a human threat. This novel experiment completed the cost versus benefits investigation between oxpeckers and black rhino.

I conclude the thesis in **Chapter 7** by presenting a synthesis of my main findings and discuss how the three hypotheses contributed to the debate around whether the HiP black rhino population is performing poorly. My thesis highlights the need for black rhino research to evaluate data quality before making management recommendations for a critically endangered species. Finally, the investigations of the oxpecker-black rhino interaction used a novel field experiment to gain a much improved understanding of how mutualisms vary depending on species and context.

This thesis is presented in the style of four separate research chapters that are formatted for submission to peer-review journals, followed by six appendices. This style inevitably results in some repetition, particularly in the methods, some of the introductory sections and the reference lists. However, the advantage of this style is that specific research questions can be addressed within a broader context.

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2.

Shifts in the Home Range Estimates of an Endemic Black Rhinoceros Population are shaped by Procedural Error: a Baseline Study to Standardize Methods

Bom (front) and I (back) searching for black rhino amongst the rolling hills of the Masinda area of Hluhluwe-iMfolozi Park (Photograph by Dale Morris).

ABSTRACT

Home range studies of black rhino (*Diceros bicornis*) have been plagued by data deficiencies and methodological inconsistencies, and concerns about researcher error and influence. Recent comparisons from Hluhluwe-iMfolozi Park (HiP), South Africa have disregarded these problems and reported a significant range increase. From 2004-2009 we gathered 1939 location estimates amongst 25 black rhino in the same park. We tested the hypotheses that rhino ranges had increased over time. We demonstrated that average annual 95% MCP home ranges were 9.77 km^2 ± 0.94, whereas 95% kernel home ranges were 20.36 ± 1.17 km^2. Procedure alone accounted for a 53.36 ±1.90 % difference between estimates. Nonetheless, comparisons between our MCP home range sizes and earlier studies in the same Park indicate ranges have not increased significantly over the last forty years.

Moreover, other sources of error investigated included number of locations needed, human observer influence on rhino movement and triangulation error. Researcher visits to black rhino did not significantly increase the daily travel distances of rhino. However, triangulation error increased substantially when researchers where >1 km from the animal (angle error) and when triangulation sets took longer than 1 hour to complete (animal movement). A minimum of 20 locations per 6-month season and 40 per annum were required for accurate home range estimation by minimum convex polygon (MCP). We recommend that more care is taken to collect adequate numbers of rhino locations within standardized time periods (i.e., seasons or years) and comparison of home ranges constructed using dissimilar procedures be avoided.

KEYWORDS: home ranges, observer influence, radio-telemetry, triangulation error, incremental accumulation curves, *Diceros bicornis minor*, Hluhluwe-iMfolozi Park, MCP, kernel, conservation management

INTRODUCTION

Recently, managers of the critically endangered (IUCN 2013) black rhino (*Diceros bicornis*) population expressed concern that monitoring by researchers and others (e.g., ecotourism) might negatively impact on rhino spatial behaviour by displacing them from preferred habitat (Beytell 2010; Odendaal 2011; Linklater et al. 2010). This concern threatens to limit the contribution of research to species conservation and requires investigation. Previous studies of black rhino have not addressed the impact of observers on home range and their estimation. Black rhino home range studies have not measured the influence of triangulation error and have been plagued by data deficiencies and inconsistent definition and interpretation of home range analyses (Lent and Fike 2003; Linklater et al. 2010). The historical sequence of published home range estimates for black rhino in Hluhluwe-iMfolozi Park (HiP), South Africa, illustrates these problems and the potential for home range studies to be misleading (Linklater et al. 2010). Authors have used an apparent 54% increase in HiP's black rhino home range estimates (1991 – 2001; Emslie 1999 cf. Reid et al. 2007) as evidence for over-population and deteriorating habitat quality (Reid et al. 2007) but the home ranges were calculated differently. How do we test hypotheses regarding shifts in the home range sizes of black rhino if our estimates of home ranges are dogged by inaccuracies and inconsistencies?

Accurate home range estimates are important because they provide insight about the needs of an organism (Harless et al. 2010) and, when accurate, are relied upon for conservation planning and monitoring efforts towards species recovery. However, the accuracy of home range estimates and their reliability as a conservation tool has been eroded by the tendency for studies to ignore sources of error and use dissimilar techniques that prevent meaningful inter-study comparisons (Harris et al. 1990; Linklater et al. 2010; Gula and Theuerkauf 2013). Studies that address sources of error in home range methodology and interpretation are needed (Gula and Theuerkauf 2013).

Measurement error and observer influence on animal movement may substantially affect the outcome of animal home range studies (Lee et al. 1985;

Harris et al. 1990; Schmutz and White 1990; White and Garrott 1990; Saltz 1994; Woodroffe 2011). Reliable home range estimates also require a minimum number of animal locations. Lastly, comparisons of home range estimates between studies depend on understanding how different procedures for defining home ranges influence outcomes. Quantifying the influence of observers and procedural choices provides confidence in home range estimates, but these are rarely achieved or reported.

Tourists and hunters are implicated in the altered behaviour and distribution of several animal species (e.g., Adele, *Pygoscelis adeliae*, and Magellanic penguins, *Spheniscus magellanicus*, impala, *Aepyceros melampus*, kudu, *Tragelaphus strepsiceros*, lions, *Panthera leo*, sable, *Hippotragus niger*, and spotted hyena, *Crocuta crocuta*; Culik and Wilson 2002; Beale and Monaghan 2004; Matson et al. 2005; Walker et al. 2005; Hayward and Hayward 2009; Kolowski and Holekamp 2009; Crosmary et al. 2012). Understanding anthropogenically induced changes in animal behaviour is important because they may affect animal population dynamics (Geist 1970; Woodroffe 2011). Conservationists are increasingly concerned about the effects of human disturbance on wildlife (Carney and Sydeman 1999), however animal disturbance by researchers, and their influence on home range, has rarely been considered (but see Theuerkauf and Jedrzejewski 2002).

Radio-telemetry has been fundamental to animal home range studies (i.e., >75% studies used radio-telemetry; Laver and Kelly 2008) as it facilitates the reliable identification and monitoring of free-ranging animals via direct sightings and signal triangulation. This reliability has persuaded many to treat radio- telemetry data as exact (Lee et al. 1985; Saltz 1994). The technique, however, is susceptible to a number of errors. Bearings are inherently imprecise, especially as a consequence of radio signal reflection and bearing bias (White and Garrott 1990), increasing observer distance from the signal, and animal movement during triangulations (Schmutz and White 1990; Saltz 1994; Lee et al. 1985). Home range estimates, therefore, vary according to the sum of observer influenced animal displacement and triangulation inaccuracy. Understanding triangulation error is therefore vital to ensuring reliable measures of home range. The magnitude of observer influence and triangulation error on location and home range estimates is likely to differ according to species, time, and place. Assessing and reporting such errors in radio-telemetry studies should be standard scientific protocol, yet for many studies it is not reported or reported inadequately (Saltz 1994). The number of locations, observation period, and methodology used to construct home ranges will also bias estimates in varying ways (e.g., Downs and Horner 2008; Laver and Kelly 2008; Boyle et al. 2009; Gula and Theuerkauf 2013) but are also often not reported (Laver and Kelly 2008).

In this study, I present home range data for the largest cohort (n=25) of black rhino yet fitted with VHF radio-transmitters and monitored intensively over an extended period (2004-2009). I make the first report on the effect that observer influence and triangulation error has on location data in HiP. I also estimated the minimum number of sequential locations required for accurate black rhino home range estimates over annual and seasonal time periods. Finally, I apply the lessons learnt to test prevailing hypotheses about changing black rhino home range sizes in HiP, South Africa. This study aims to motivate improvements in the accuracy of black rhino home range studies and to facilitate more meaningful comparisons between studies

STUDY AREA

Hluhluwe-iMfolozi Park (HiP) (S28° 0′ to 28° 25′, E31° 42′ to 32° 0′) is a 960 km^2 fenced reserve located in Zululand, KwaZulu-Natal (KZN), South Africa. Mean annual rainfall and altitude decrease from Hluhluwe in the North (990 mm and 450 m asl), to iMfolozi in the South (635 mm and 60 m asl), with April to September being the dry season (Balfour and Howison 2001). The temperature ranges from an average minimum of 13°C (winter) and maximum of 33°C (summer) (Balfour and Howison 2001). During this six-year study (2004 – 2009) average summer (October to March) rainfall was 378.0 mm and winter rainfall 201.9 mm (Masinda weather station; G. Clinning, unpubl. data). HiP has had a quasi-periodic wet-dry rainfall oscillation lasting approximately nine years (Walters et al. 2004). During this study, the Park was in a period of below average rainfall initiated in c. 2001 (see Berkeley and Linklater 2010).

HiP holds approximately 218 south-central black rhino (*D. b. minor*) (Clinning et al. 2009) – the larger endemic population of only two in Africa (Brookes and MacDonald 1983). HiP undergoes annual black rhino harvesting (*c*. 5 to 8 % of the population) as it serves as a strategic donor (source) population for species rescue by reintroduction and restocking (Emslie 2001, Linklater et al.
2012).

MATERIALS AND METHODS

Transmitter Installation Procedures

From January 2004 to October 2008 black rhino were intermittently captured after immobilization, as part of a larger investigation into the dynamics of HiP's black rhino population (see Plotz and Linklater 2009; Linklater and Hutcheson 2010). Horn implant radio-transmitters were inserted into 25 black rhino (18 females, 7 males) as per Anderson and Hitchins (1971) and Shrader and Beauchamp (2001). The radio-transmitters were either Telonics (U.S.A.) or Sirtrack Pty Ltd. (NZ) models, and VHF radio-telemetry signals were recorded via a TR-4 receiver (Telonics, Inc., Mesa, AZ, U.S.A.). All capture and study procedures were approved by Ezemvelo KwaZulu-Natal Wildlife (EKZNW) research department (Hill Top; permit no: ZC/101/01), Victoria University of Wellington Animal Ethics Committee (2007R2) and Zoological Society of San Diego (IACUC number 169).

Data Collection and Analysis

Home range construction and size: Four experienced rhino researchers and trained field rangers collected location data from 2004 to 2008, while I collected data from 2007 to 2009. Rhino were located randomly at least once a fortnight between dawn and dusk. For seasonal home range estimates, locations for each rhino were ordered from the start to end of the wet (start of October to end of March) and dry seasons (start of April to end of September) respectively. We were able to gather regular locations for 14 rhino during the wet season and 32 rhino during dry seasons over the 6-year field study. Annual home range locations were also ordered sequentially (i.e., chronological order), but over any consecutive 12-month period. Locations over 12-months were obtainable for 17 different rhino.

Direct sightings began by initially obtaining a signal from high elevation; this was then verified by tracking the rhino downwind on foot until the rhino was sighted. Triangulation estimates involved taking bearings from two or more elevated positions. A hand-held compass was used to estimate the direction of the radio-signal to an accuracy of 1°. Positions of direct sighting and bearing points of triangulation were determined via hand-held GPS units (Garmin e-trex model). All triangulation location estimates were converted into GPS locations using Locate III software (Nams 2006). Triangulation bearings less than 60 and greater than 180 degrees apart were excluded from estimates of rhino locations because they result in lines that intersect gradually and are known to provide unrealistic ranges (White and Garrott 1990). All estimated and actual locations were transferred to a Geographic Information System (GIS), ArcView 10.0, to determine rhino home range size (ESRI, Redlands, CA, USA and its Home Range extension) (Hooge and Eichenlab 1997).

Calculations of range size of individual animals should be based on subjects for which there are sufficient locations for a plot of range size against number of locations needed to reach an asymptote (e.g., Buckle 1997). These asymptotes are based on minimum convex polygon (MCP) estimates, which produce smoother asymptotes than the other methods and they are comparatively simple and more robust where location number is small (Mohr 1947; Harris et al., 1990; Harless et al. 2010). Incremental MCPs were estimated at fixed locations to determine how many were needed to estimate black rhino seasonal and annual home ranges to within 10% of the total estimated size (Harris et al. 1990; Buckle et al. 1997; Hayward et al. 2009). Defining exactly where asymptotes begin and the number of locations required is subjective and so a 90% (i.e., within 10%) of the total home range was used as a defining threshold. Incremental MCP descriptions of home range to estimate the number of locations necessary because They are also the most common metric used in home range studies – facilitating comparisons with most other black rhino and other animal home range studies (Harris et al. 1990; Lent and Fike 2003). MCPs are also most comparable to Hitchins (1971) visual approximation analysis also from black rhino in HiP. Only those individuals with sufficient locations were included for further analysis (e.g., Lent and Fike 2003).

I compared MCP's constructed using 95% of locations (Mohr 1947; Kenward 1987), by removing 5% of extreme locations, with the 50% and 95% utilisation distribution (UD) contours from a bivariate kernel calculated using a smoothing parameter (h) of 500 m and a cell size of 100 m (Fig. 1) to allow comparison with recently evaluated home ranges of black rhino in HiP (Reid 2007; Slotow et al. 2010). Borger et al. (2006) state that 95% kernel UDs should be avoided because of their significant error and recommend the use of 50 to 90 % UDs instead. Thus, along with 50% and 95% kernel UDs, 90% kernels were also calculated in this study. All MCP and kernel density estimation was carried out in R version 2.14.2 using the packages 'adehabitatHR' (Calenge 2006) and 'maptools' (Lewin-Koh et al. 2012), in an African Albers-Equal Area projection calculated using ArcGIS 10 (ESRI, U.S.A.).

Lastly, the ratio of 50% (core) to 95% kernel home ranges was calculated to evaluate the intensity of home range use. Home ranges used more evenly should have higher ratio scores, while lower ratio scores are associated with the importance of smaller patches within the home range (Linklater et al. 2000; Lent and Fike 2003).

Other Sources of Error

Observer influence: From January 2004 to December 2009, the locations of black rhino (n=106) were estimated by remote triangulation 24 hours after they had been visited by a researchers to obtain a visual location. During visits the observers were typically <50 m from the rhino. The locations of the same population of black rhino were also estimated by remote triangulation 24 hours before they were visited by researchers (n=116). Observer influence on rhino movement was measured by comparing the distance (km) travelled by each rhino before and after an observer visit (i.e., the dependent variable). Bearings for triangulation data were typically taken from several hundred and sometimes thousands of meters away and are, therefore, unlikely to have disturbed rhino. All triangulation estimates were converted into Global Positioning System (GPS) locations via Locate III software (Nams 2006).

To quantify observer disturbance on the average daily displacement of rhino, I scored each rhino's awareness and response to the observer during visits for the 106 samples which were then followed up with a location triangulation 24 hours later. Each rhino's disturbance by observers was scored on an ordinal scale from 0 to 3: 0 = rhino not visibly alert and did not respond to the observer, 1 = rhino alert but only head and ears raised toward observer, 2 = rhino alert and walked away from the observer, and 3 = rhino ran from the observer. I compared the subsequent 24-hour displacement (km) of rhino with their recorded disturbance scores.

Rhino have a bimodal activity pattern with early morning and late afternoon activity peaks (Kiwia 1986) that may modify their response to observers. Also, repeated experience of being observed may have a habituation affect, where rhino displace less over time for the same level of disturbance. Moreover, due to individual differences some rhino may be more responsive to observer disturbance than others. In analyses, therefore, active (08h00-10h00, 15h00-18h00) and inactive (10h01-14h59) time periods, the numerical sequence of each sample, and rhino identity, were included as covariates. Repeated measures ANOVA was used to test whether observer visit, sample order, and time period (fixed effects), and rhino identity (random-effect), impacted on the daily distance travelled by a rhino. All statistical procedures were conducted in SPSS (SPSS Inc., version 19, 2010). For all statistical tests I regarded the critical value (α) of ≤ 0.05 as statistically significant.

Triangulation accuracy: Triangulation accuracy was measured by comparing a black rhino's estimated location by triangulation with a known location obtained from a direct sighting conducted immediately after said triangulation. Test data resulted from 62 locations of rhino first estimated by triangulation and then visually located. All observer positions used to take bearings during triangulations and the actual locations of rhino were converted into Global Positioning System (GPS) locations. Also, bearing locations and associated angles were entered into Locate III software to calculate triangulation estimated locations (Nams 2006).

Direct sightings are absolute values while triangulations are estimates with associated error. Thus, factors known to induce the greatest inaccuracy in triangulation estimates include; the animal's distance from the observer because greater distances correspond to increased signal refraction, and compound errors in observer interpretation of signal direction (Lee et al. 1985; Schmutz and White 1990; Saltz 1994). Also, increased time between completed triangulations and direct sightings will contribute to differences because animals move (Lee et al. 1985; Schmutz and White 1990). The large size and undulating terrain of HiP mean that the bearing positions, which are the locations where an observer stands to measure the angle to the strongest signal received from the rhino's radio-transmitter, and the subsequent time required to sight that rhino varied substantially. Therefore, I tested the effect that bearing distance and the time taken to take bearings had on triangulation accuracy (i.e., distance between triangulation estimated and actual locations of rhino). To accomplish this I transferred triangulation estimates and actual sighting locations to a Geographic Information System (GIS), ArcView (10.0) and measured the discrepancy in distance (km) between triangulation and actual location estimates.

For analysing the effect that distance of the bearing point had on the accuracy of triangulation estimates relative to the actual location, I used the bearing point location taken farthest from the rhino for each triangulation of an individual rhino. I also calculated the median point in time between the first and last triangulation bearing (for consistency) and the visual sighting of the rhino to test for the effect that time had on triangulation accuracy. A univariate ANOVA was used to test whether observer distance from rhino and time from triangulation to direct sighting significantly impacted on triangulation error (i.e., the dependent variable). Finally, the fact that HiP is large and has variable terrain meant that the mean maximum distance from rhino from which triangulation bearings were taken was 2.0 ± 0.14 km (range = 0.32- 5.71 km).

To highlight the effect that observer distances had on triangulation error (distance between triangulation estimate and direct sighting) in HiP, I compared the mean triangulation error according to the following designated categories of observer distances: long (> 2km plus), medium (1.01 to 2.0 km) and short (<1km). Categories of distance were chosen purely on the basis that they divided the range of points roughly into thirds while providing the typical range of spatial distances that I as an observer needed to traverse when triangulating rhino in a large Park like HiP. Distances greater than 3 km resulted in too much interference for reliable signal strengths to be received. Similarly, the average time taken to achieve a direct sighting was 78 ± 8.7 minutes (range = 7 - 269 minutes) and so I also compared the mean triangulation error relative to the following categories of time from triangulation to direct sighting of rhino: long (> 121 minutes plus), medium (61 to 120 minutes) and short (<60 minutes). Categories of time were chosen purely on the basis that they divided the range of points roughly into thirds while providing the typical range of time periods that I as an observer needed to consider when triangulating and walking to sight rhino in a large Park like HiP.

RESULTS

Home Range Construction and Size

A total of 1939 usable locations or location estimates were obtained. 47% (n = 906) were direct sightings and 53% (n = 1033) were triangulations making this study the most intensive radio-telemetry study reported for this species to date (cf. Gottert et al. 2010). Five triangulated locations were excluded because they estimated the individual to be outside of the reserve's fence.

Mean consecutive 12-month (annual) 95% MCP home range size for females was 10.37 ± 1.36 km^2 (n=11) and 8.67 ± 0.89 km^2 for males (n=6). Mean annual 95% bivariate kernel home ranges for females were 21.01 ± 1.67 km^2 and 19.01 ± 1.27 for males and 50% core areas 4.95 ± 0.48 and 4.67 ± 0.53, respectively. Our 95% MCP estimates of home range size were consistently around 53.36% ± 1.90 smaller than 95% bivariate kernels (Fig. 1). Borger et al. 2006 report that 50 - 90% kernels are significantly more accurate than 95% kernels. Thus, to improve accuracy for future inter-study comparisons I calculated mean annual 90% kernel estimates as well: Females were 16.83 ± 1.38 km^2 and 15.07 ± 1.12 km^2 for males.

Mean 95% MCP home range size over the dry season for females was 9.07 ± 0.99 km^2 (n=26) and 4.20 ± 0.63 km^2 for males (n=6), and wet season for females was 6.24 ± 1.79 km^2 (n=7) and 8.16 ± 2.37 km^2 for males (n=7).

The ratio of 50 to 95% bivariate kernels was 0.24 ± 0.01, indicating that black rhino spent half their time in just 24% of their annual home range. The ratio of use was identical between the sexes (male 0.24 ± 0.02, female 0.25 ± 0.01).

Achieving an accuracy of > 90 % of actual home range size for black rhino required a minimum of 20 locations seasonally and at least 40 locations annually with some variation between the sexes. Detecting asymptotes from the incremental total home range area plots of locations showed that at least 40 locations for females and 55 for males were required to achieve greater than 90% of total MCP home range estimate over a consecutive 12-month period. This was exceeded for six males with 55 to 71 locations, and 11 females with 40 to 79 locations (Fig. 3A). Three males with 30 to 35 locations and 19 females with 30 to 46 locations exceeded the approximately 30 locations that were needed to estimate home range size during the 6-month dry seasons (Fig. 3B). Finally, six males with 30 to 38 locations and six females with 25 to 30 locations exceeded the minimum 20 and 25 locations needed, respectively by the sexes, to accurately estimate wet season range size (Fig. 3C).

Observer Disturbance

Mean distances travelled by black rhino during the 24 hours before they were visited by an observer was 1.54 ± 0.10 km (± 1SE, range = 0.13 - 4.64 km; Fig. 4). In comparison, rhino visited 24 hours previously travelled an average of 1.82 ± 0.13 km (range = 0.14 - 8.20 km). Visited rhino were displaced an average 300 m further than unvisited rhino but the difference was not statistically significant (GLM repeated measures: $F_{1, 222} = 1.6$, $P = 0.2$). There was no significant effect of observer visits (GLM: $F_{1, 222} = 1.6$, $P = 0.6$), sampling order (i.e., acclimation: $F_{1, 222} = 1.1$, $P = 0.3$), time of day ($F_{1, 222} = 0.6$, P=0.4) and rhino identity ($F_{1, 222} = 1.1$, $P = 0.4$) on daily displacement.

Although rhino that were seen to run from the observer during observations (i.e., disturbance score 3) were displaced further on average (2.2 ± 0.29 km: range = 0.23 - 8.2 km) compared to unaware rhino (disturbance score 0; 1.7 ± 0.19 km: range = 0.25 - 4.6 km), this difference was not statistically significant (ANOVA: $F_{1, 106} = 0.6$, $P = 0.6$; Fig. 4).

Triangulation Accuracy

Increasing distance of an observer from a rhino when triangulating its location (bearing positions) significantly affected triangulation accuracy (ANOVA: $F_{1,62}$= 49.1, P = 0.0, R^2 = 0.6; Fig. 5A). Although the larger differences between locations were also associated with times to complete the triangulation and visual location > 60 minutes, the time taken to complete the triangulation and obtain a direct sighting of rhino did not significantly affect triangulation accuracy (ANOVA: $F_{1,62}$ = 0.8, P = 0.1, R^2 = 0.3; Fig. 5B).

The mean distance between locations estimated by triangulation and actual locations was 0.90 ± 0.10 km (range = 0.03 - 3.8 km). Average triangulation error was reduced to a mean of 0.33 ± 0.05 km when taken from less than 1 kilometre from the rhino (short distance: Fig. 5A). Even though the time between triangulation and visual sighting (i.e., the potential for rhino movement) was not a significant factor on triangulation accuracy, spatial error was also reduced by more than half on average, if triangulations were completed in less than 60 minutes (short time: 0.45 ± 0.06 km; Fig. 5B). Results demonstrate that the accuracy of triangulated locations could be improved almost three-fold (e.g., 326 ± 5 m cf. to 900 m overall) if bearings were taken from no more than 1.0 km from the rhino (Fig. 5A). The observers distance from an animal's unknown location might be adequately gauged from the strength (gain) of the radio signal. In our experience estimates of radio-receiver gain < 3.0 were associated with distances too large for bearings to result in reliable location estimates (i.e., an average gain of 4.2 ± 0.01, range 3.2 to 5.1, equated to average observer distance from rhino of 492 ± 6 m, n = 27, R.D. Plotz, Victoria University of Wellington, unpublished data; see also Linklater and Swaisgood 2008, P1061 for a similar estimate).

DISCUSSION

Home Range Construction and Size

MCPs and bivariate kernels produced very different estimates of home range size in this study. Average annual 95% kernel home range estimates were more than twice as large as 95% MCP home range sizes, primarily due to the interpretation of density around peripheral locations (Fig. 1). Gula and Theuerkauf (2013) compared MCP and Kernels on wolf home range analysis and demonstrated similar discrepancies between procedures. It is now clear that black rhino home ranges that are estimated using different techniques cannot be compared in the way they have in previous studies (see Table 1, Fig. 2 and Reid et al. 2007; Linklater et al. 2010; Slotow et al. 2010).

Our estimates of annual home range size are comparable with the few estimates in other populations where the adequacy of location numbers is quantified and similar home range estimate procedures are used. For example, our home range estimates are similar, if slightly smaller, than those reported for a reintroduced and expanding black rhino population in the less arid Great Fish River Reserve (i.e., 95% MCPs 11.7 km^2; 50% kernel 6.8 km^2, Lent and Fike 2003). The ratios of use (24% of the home range used 50% of the time) are also similar to that reported by Lent and Fike (2003: 21% of the home range). Compared to other animals for which ratios of use are available (horses 12%, and spotted turtles 8%: Linklater et al. 2000, Lewis and Faulhaber 1999) rhino appear to use core areas within their home ranges less intensively, perhaps a reflection of their larger body size and dependence on larger amounts of lower quality forage (Owen-Smith 1988).

Seasonal home ranges are seldom reported for black rhino and the number of locations across seasons is seldom adequate for reliable seasonal range estimates. Interestingly, the largest average home ranges of the sexes occurred in different seasons – male in the wet season and females in the dry season – which might reflect the interaction between resource availability (i.e., water and forage) and breeding activity in determining movement patterns for the sexes. Females probably move less during the wet season due to the greater availability of water and forage. Males, however, are likely to move more during the wet breeding season when most conceptions occur (Berkeley and Linklater 2010). The larger seasonal home ranges approached the size of annual home ranges, reflecting the importance of seasons as drivers of annual black rhino home ranges.

Estimating seasonal and female home ranges required fewer locations than annual and male home ranges, and wet season home ranges required the least number of locations. Males are probably more mobile with larger home ranges because black rhino are polygynous breeders (Garnier et al. 2001). Natal dispersal in males involves greater distances and dominant bulls' ranges overlap multiple female ranges (Lent and Fike 2003). Estimating dry season ranges probably required more locations because water access is limited to fewer sites and forage quality is poorer, thus motivating rhinos' greater movement between sequential locations. Generally, more than 20 locations per 6-month season were required but more than 30 per season unnecessary. These values are similar to others estimates (i.e., 40 per annum, Lent and Fike 2003). Home range studies of black rhino should report the number of locations used and not use fewer than 20 locations per season or 40 per annum for constructing black rhino home ranges. These sampling requirements are a comparatively low for such a large mammal (cf. 180 fixes for lions; Hayward et al. 2009) and reaffirms that the movements of black rhino are spatially conservative (e.g., Lent and Fike 2003; Linklater and Hutcheson 2010).

Observer Disturbance

Repeated radio-telemetry monitoring of black rhino that included visiting rhino for direct observation often resulted in animal disturbance and displacement but had no significant effect on their daily travel distance. Although rhino moved an average 300 m more during the 24-hours after a visit, they did not appear to be displaced sufficiently from their chosen home ranges to alter home range location and area. Indeed, even actively disturbed rhino (i.e., those that fled out of sight), did not travel significantly further over the course of 24 hours than rhino that were recorded as being oblivious of the observer (at least to the end of each visit, Fig. 4). Moreover, rhino that appeared unaware of the observer during a visit moved 1.66

km, similar to the average 1.54 km per day travelled by rhino that had not been visited (i.e., triangulations 24 hours before a direct sighting).

Beytell (2010), in the only other study to quantify black rhino (*D. b. bicornis*) displacement by observers, found them easily disturbed by humans, slow to resume pre-disturbance behaviours and recommended approach distances of no less than 100 m. Their recommendation mirrors those for other taxa. Theuerkauf and Jedrzejewski (2002), for example, recommended that observers tracking wolves (*Canis lupus*) ought to do so from between 200m and 400m to reduce their influence on wolf movements. In terms of displacement distances' effects on home range size, no such limitations appear necessary for HiP black rhino based on our findings. I found the disturbance created by visiting rhino to within 50 m for visual identity and location as frequently as once a fortnight to have an innocuous influence on black rhino movements in HiP. Nevertheless, I recommend precautionary measures of observers' influence should be a standard part of intensive monitoring efforts of any endangered species, including rhino.

Populations may vary in their sensitivity to anthropogenic disturbance.

I did not, however, determine if preferred patch use within chosen ranges was altered by regular observer disturbance. In Kenya, for example, wild dogs in human versus non-human dominated areas had similar home range sizes but area avoidance and intra-species overlaps increased in human dominated areas (Woodroffe 2011). Further investigations of black rhino disturbance behaviour and resource use are required.

Triangulation Accuracy

Triangulation error will inflate home range estimates. The average 900 m discrepancy between triangulation-estimated locations and visually confirmed locations highlights the amplifying effect that observer distance can have on spatial error when triangulating. Although there was also a positive relationship between triangulation error and time to complete the triangulation – probably due to animal movement while the estimate was taking place – it was a poorer explanation of location error.

Ours is the first black rhino study to measure triangulation error. It raises concerns about the accuracy of black rhino home range studies that use substantial numbers of radio-triangulation estimates without considering location error (e.g., 81% of all locations in Gottert et al. 2010 were triangulations). Spatial error should be measured and reported and, if necessary and possible, mitigated in home range studies by triangulation.

Theuerkauf and Jedrzejewski (2002) achieved a mean radio-triangulation error of 0.19 km by having 75% of their triangulations on wolves conducted at an observer distance of between 0.20 and 1.2 km. Our results show that observers aiming to improve the precision of triangulations ought to pay particular attention to triangulate black rhino from < 1.0 km (avoiding triangulations from distances > 2.0 km) and also consider achieving the triangulation within 60 minutes (Fig. 5A, B).

The magnitude of triangulation error is likely to differ between species, populations and sites. Reporting measures of spatial error, like those above, would permit the development of objective thresholds for data inclusion (Saltz 1994; Gula and Theuerkauf 2013) to improve radio-telemetry data and improve inter-study comparisons. At this time, triangulation error is rarely reported in studies of home range.

Home Range Ecology and Population Management

Home ranges may vary amongst sites and through time as a consequence of variation in population demography (e.g., density, sex ratio) and resources (e.g., water, food, shelter). Some have used the historical sequence of home range size estimates in HiP (see Table 1 and Fig. 2) to draw the conclusion that habitat for black rhino in the park is deteriorating or the reserve is over-stocked because more recent home range sizes are larger than historical estimates (Reid et al. 2007, Slotow et al. 2010). Previously, the short-comings of this approach have been identified (Linklater et al. 2010). In particular, constructing home ranges with too few, and fortuitous (spatially biased) animal locations collected over several years, and comparing adaptive kernels with more rudimentary, temporally defined, home range procedures might inflate home range size and differences. I am now able to furnish our concerns with evidence for how these impact home range size estimates for black rhino in HiP.

Our kernel home range estimates using larger numbers of animal locations (average 51 ± 3.3 locations) from a single year are 12% smaller (2.7 km^2) than the average of those presented by Reid et al. (2007: i.e., 20.36 km^2 cf. 23.02 km^2; see Fig. 2) that include as few as 10 locations collected fortuitously across from three to 11 of the same years (Table 1). This comparison indicates the degree to which home range size in Reid et al (2007) might be inflated by multi-year data collection and small sample size. Also, adaptive kernel methods used by Reid et al. (2007) are known to consistently overestimate the area of the distribution compared to the fixed bivariate kernel UD techniques adopted in this study (Seaman and Powell 1996).

Our range size estimates were smaller than those reported by Reid et al. (2007) and Slotow et al. (2010), but I expected their use of small amounts of location data spread across multiple years, amongst other short-comings in the data, to result in a much larger home range inflation (Linklater et al. 2010). While this is expected to be generally true, it is clearly not the case for black rhino. This finding might be because the actual degree of home range inflation in Reid et al. (2007) and Slotow et al. (2010) is larger than 12% because our estimates are also somewhat inflated due to the spatial error from triangulations which contributed to about 40 % of locations used (i.e., 45 out of 105 locations > 1 km or 60 minutes; see Fig. 5A, B). Our finding could also indicate, however, that for established populations of black rhino home ranges may be remarkably stable between years, and perhaps for large portions of a rhino's reproductive life (i.e., up to 11 years). This conservatism of range use by rhino is consistent with Linklater and Hutcheson's (2010) observation that black rhino are reluctant to shift their ranges even when harvesting reduces the density of same-sexed conspecifics in adjacent habitat. Although Lent and Fike (2003) describe inter-annual range shifts, these are probably a feature of their reintroduced and expanding population and not necessarily typical of endemic populations.

Our average annual MCP home range estimate for all rhino was 9.77 km^2, which is 19.5% (2.2 km^2) larger than Hitchins (1971) estimate (7.50 km^2) from a radio-telemetry study in the same Park over 40 years earlier (Table 1 and Fig. 2). Reasons for our marginally larger estimates overall is probably best explained by Hitchins (1971) not using MCPs in their strictest sense. Instead he drew a line around all peripheral location points in sequence i.e., approximating a type of maximum (cf. minimum) convex polygon, which produces ranges smaller than conventional MCP's from the same location points. Hitchins (1971) estimates were therefore likely to be conservative – accounting for their slightly smaller ranges compared to this study. Our estimates are also likely to be larger because just over half of our locations were triangulation estimates (i.e., our average spatial error = 900 m), whereas Hitchins (1971) locations used only direct sightings for his locations. Hitchins (1969) smaller ranges (c. 3.5 km^2) are not meaningfully comparable to Hitchins (1971), or this study, as the time period and number of locations are not reported.

Importantly, the comparison of our MCP home range sizes with Hitchins (1971) estimates confirms that the home ranges for black rhino in HiP have not increased significantly over the last 40 years. Previously, authors have claimed a substantial (54%) increase in black rhino home range size in HiP and attributed it to deteriorating habitat or the reserve being over-stocked (Reid et a. 2007; Slotow et al. 2010). Unfortunately, they compared the kernel estimates using as few locations as 10 collected across from three to 11 years with earlier values derived from a smaller portion of the same dataset and using different techniques (Table 1, Fig. 2). The comparison is flawed because, as I demonstrate, kernel techniques using the same data produce much larger home range estimates (e.g., 53% larger than MCPs; Fig. 1).

The debate about whether small numbers of fortuitous locations of black rhino across multiple years can be used to construct reliable estimates of home range size that are then used to evaluate the status of the black rhino population or its habitat (Reid et al. 2007, Linklater et al. 2010, Slotow et al. 2010) is resolved by our comparisons. It would be preferable that data not be used to construct home ranges in the way Reid et al (2007) and Slotow et al. (2010) did as it will inflate home range size. Kernel home ranges should not be compared with other more rudimentary techniques (e.g., MCPs; Borger et al. 2006).

Lastly, it is unlikely that black rhino home range sizes in HiP have changed substantially in over 40 years, rather that MCP home ranges have always been ~ 9 km^2 and kernel home ranges about 20 km^2 in size. There is no evidence from changes in home range size for habitat deterioration or over-stocking. Moreover, if home ranges are mutually exclusive as with white rhino (*Ceratotherium simum*) territories (Shrader and Owen-Smith 2002) then there would be larger home ranges with the suspected decline in HiP's population size and not increasing. Black rhino's spatial ecology is not well enough understood to be confident that a predicted inverse relationship between home range size and habitat deteoriation exists for black rhino (Emslie 1999; Reid et al. 2007; Slotow et al. 2010).
Management should consider a more credible explanation for larger home range sizes reported in Emslie (1999; 2001), Adcock (2009), Reid et al. (2007) and Slotow et al. (2010) is likely to be because home ranges were constructed using a growing multi-year dataset and different techniques are compared.

Management Implications

Researchers and managers monitoring black rhino, at least in HiP, will be reassured that direct observations often causing disturbance and animal displacement at bi-weekly intervals had little impact on rhino daily movements and the habitat-use at larger scales. However, triangulation error, insufficient numbers of locations and comparisons of estimates using different procedures can lead to substantial errors in home range location and size. Studies ought to report the influence of observers and triangulation error on location data, and location number on home range size. I recommend that bearings for triangulation of black rhino' locations occur from < 2 km, and preferably <1 km most of the time, and be completed within 60 minutes. Further, at least 20 locations per season, or 40 per annum, appear to be required to build home ranges for black rhino, but more than 30 per season is likely to be unnecessary. In southern Africa, average home range area estimates have been considered to determine reserve stocking (carrying capacity) and harvesting levels for black rhino populations (Emslie 2001). Inaccurate home ranges have the potential to mislead black rhino population management (Linklater et al. 2010). Apparent, but spurious, increases in home range size could lead to over-harvesting (Clinning et al. 2009; Morgan et al. 2009; Slotow et al. 2010). Comparisons of home range size should not be made unless they are estimated in similar ways with similar location data and sources of error are considered.

Table 1. Detailed comparisons of methodology across this and previous historical home range studies of black rhino *Diceros bicornis minor* in Hluhluwe-iMfolozi Park, South Africa.

	Hitchins 1969	**Hitchins 1971**	**Adcock 1996; Emslie 1999**	**Reid et al. (2007)**	**This study**
Methods					
Data Collection	Ground search, fortuitous observations	Radio-telemetry (twice daily)	Fortuitous observations	Fortuitous observations	Radio-telemetry, random stratified approach
Data Analysis	visual approximation using all points	visual approximation using all points	1km^2 grid occupancy data	95% adaptive kernel	95% MCP, 50%, 90% and 95% bivariate kernels
Obser. period	< 1 year (1962-63)	From 3 month - 1 year 1 month (Nov. 1969-Dec. 71)	c. 4 years* (c. 1991-94)	c. 11 years* (c. 1991-Feb. 2002)	annual and seasonal (wet & dry – see methods) (Jan. 2004-Dec. 09)
Locations per rhino	Not Reported	47-503**	~6-20	$\geq$10	40-79 for 12 consecutive months & 25-38 for 6-month seasons
Focal population	4f, 2m	4f, 10m	Not reported	125	18f, 7m
Park Sections	Nqumeni (Hluhluwe)	Nqumeni (Hluhluwe)	Manzibomvu (Hluhluwe)	All five management sections	Mbhuzane, Masinda (iMfolozi) & Nqumeni (Hluhluwe)

Table adapted from Linklater et al. (2010)

*Reid et al. (2007) used an 11-year data set (c. 1991-2002) that incorporated the same Adock (1996) four-year data set (1991-1994) i.e., lack of independence between data sets. Also, Reid et al. (2007) did not just present home ranges from lumped together data over the 11-year period, but also represent seasonal ranges from data that lump together locations from summer/ winter in one year with summer/ winter locations from several other years between 1991-2002 (See Linklater et al. 2010).

** Locations collected twice daily

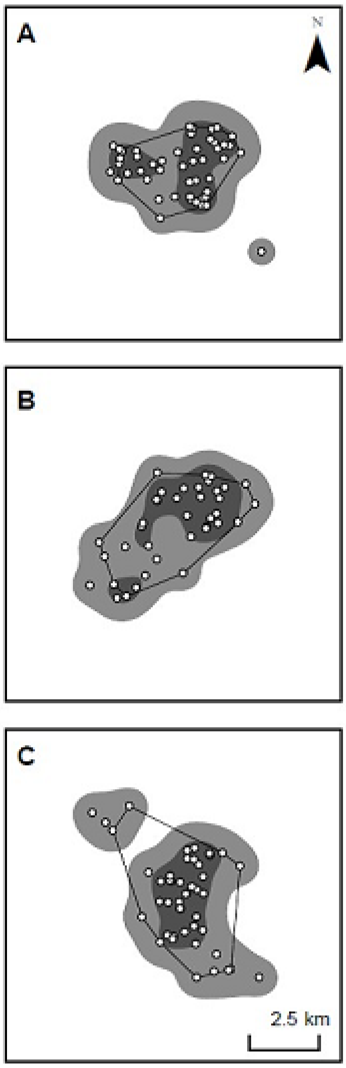

Figure 1. Illustrated comparison of the two analysis techniques used for producing annual black rhino home-range estimates in Hluhluwe-iMfolozi Park, South Africa. Contours of bivariate kernel utilisation distributions are illustrated by the 50% (dark grey) and 95% (mid-grey), using a smoothing parameter (h) of 500 m and cell size of 100 m in an African Albers Equal Area projection. 95% Minimum Convex Polygon (MCP) range estimates are illustrated by the dark black line polygon.
Actual positions from radio-telemetry relocation are illustrated by the white filled circles. Note that Rhino A and B were classified as adults (≥8 years), Rhino C was a sub-adult (< 8 years) and 95% kernels produced consistently larger estimates than 95% MCPs.

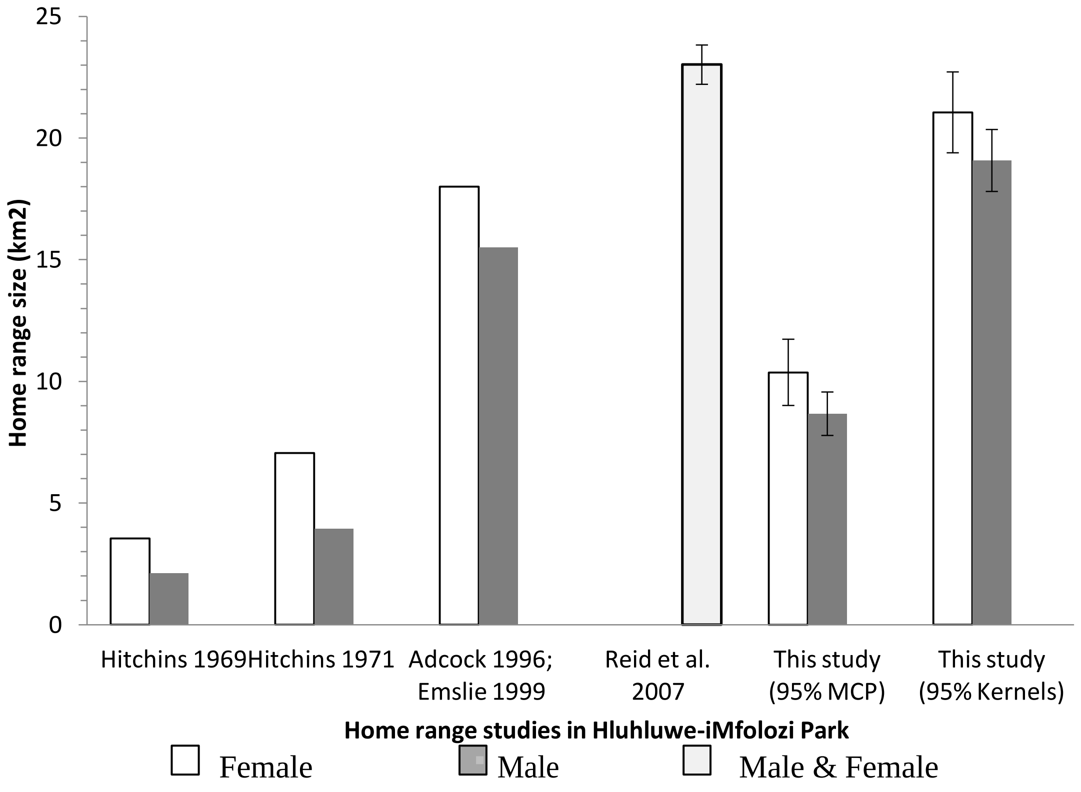

Figure 2. Historical sequence of home range estimates for black rhino *Diceros bicornis minor* in Hluhluwe-iMfolozi Park, South Africa. Included for comparison are the two home range estimates from this study where different analysis techniques were used (i.e., 95% MCP's and 95% kernels). Standard error is included for home range estimates where possible.

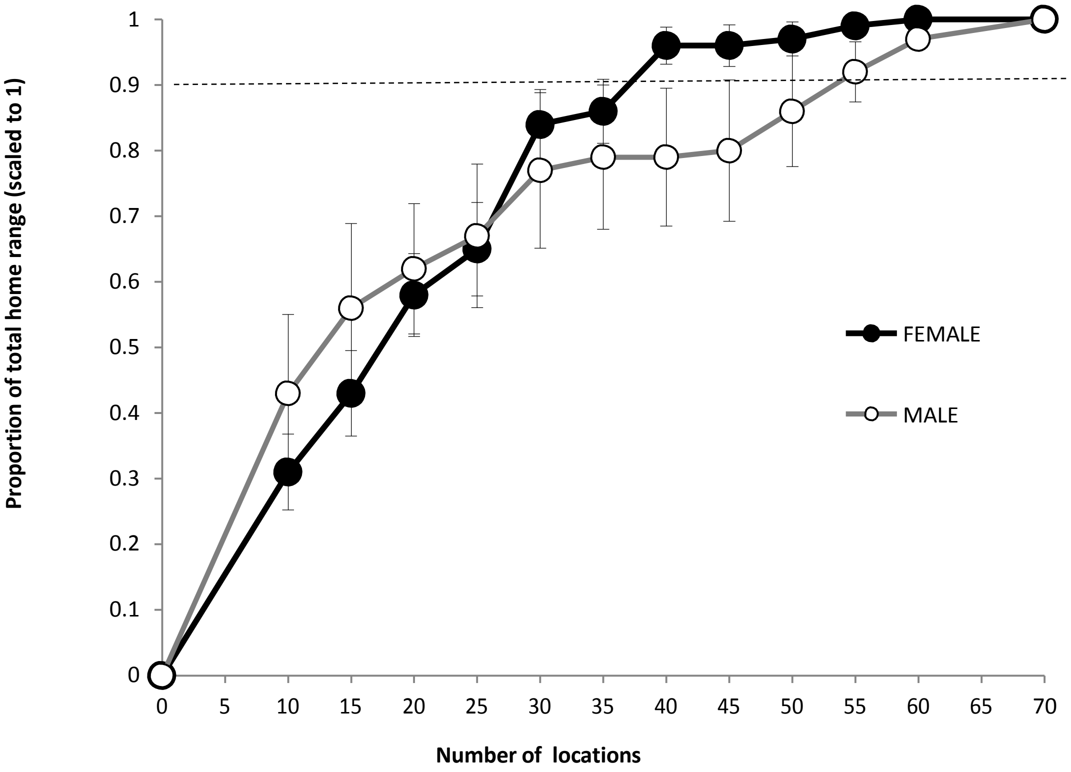

Figure 3(A). Incremental accumulation curve showing the number of locations required to more accurately estimate the annual (any consecutive 12- months) home ranges for black rhinoceros in Hluhluwe-iMfolozi Park, South Africa. Note that the horizontal dashed line represents the within 10% level of the total home range recommended for increased accuracy.

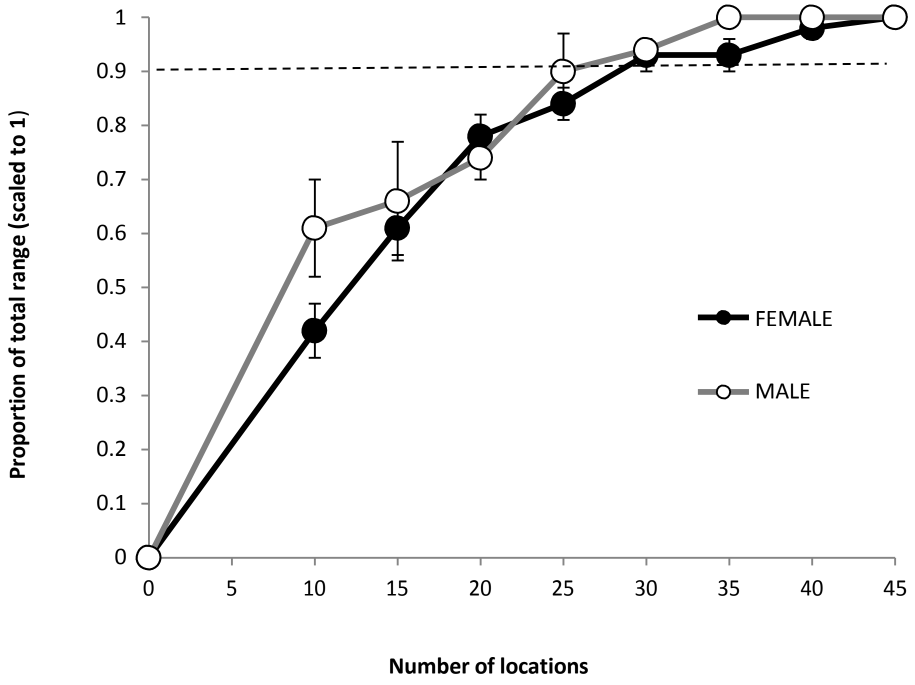

Fig. 3B

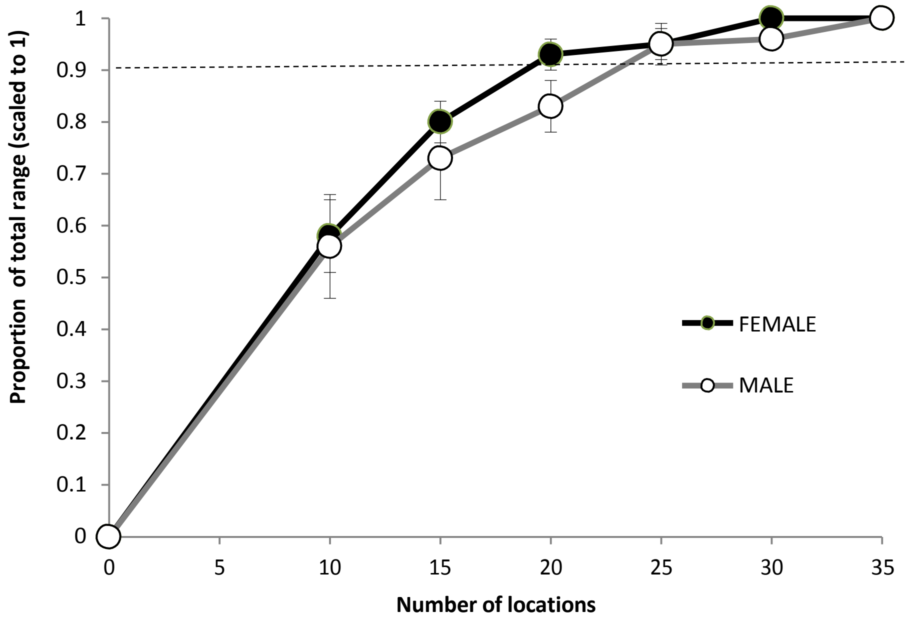

Fig. 3C

Figure 3 (B). Incremental accumulation curve showing the number of locations required to accurately estimate the wet (Oct-Mar) and **(C)** dry season (Apr- Sep) home ranges for black rhino in Hluhluwe-iMfolozi Park, South Africa. Note that the horizontal dashed line represents the within 10% level of the total home range recommended for increased accuracy.

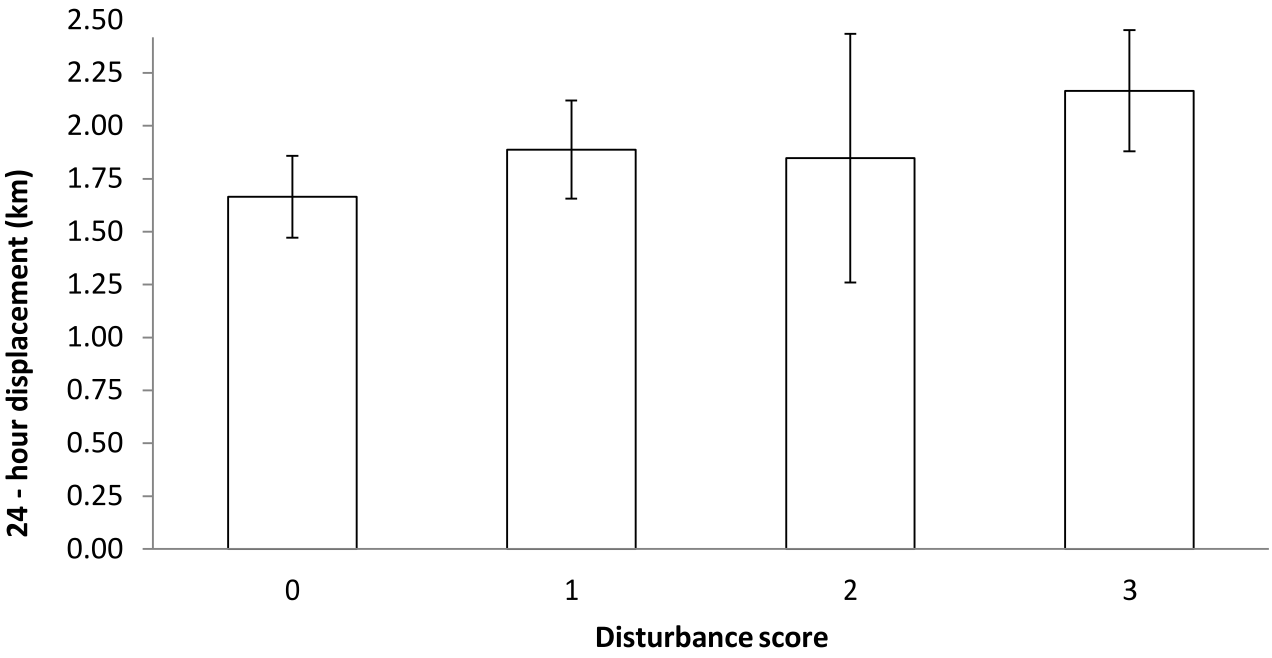

Figure 4. Mean estimated black rhino displacement distance from 106 triangulated locations 24 hours after an observer disturbance in Hluhluwe-iMfolozi Park, South Africa. For each observer disturbance event (i.e., direct sighting), each rhino disturbance by observers was scored on an ordinal scale from 0 to 3: 0 = rhino not visibly alert and did not respond to the observer, 1 = rhino alert but only head and ears raised toward observer, 2 = rhino alert and walked away from the observer, and 3 = rhino ran from the observer.

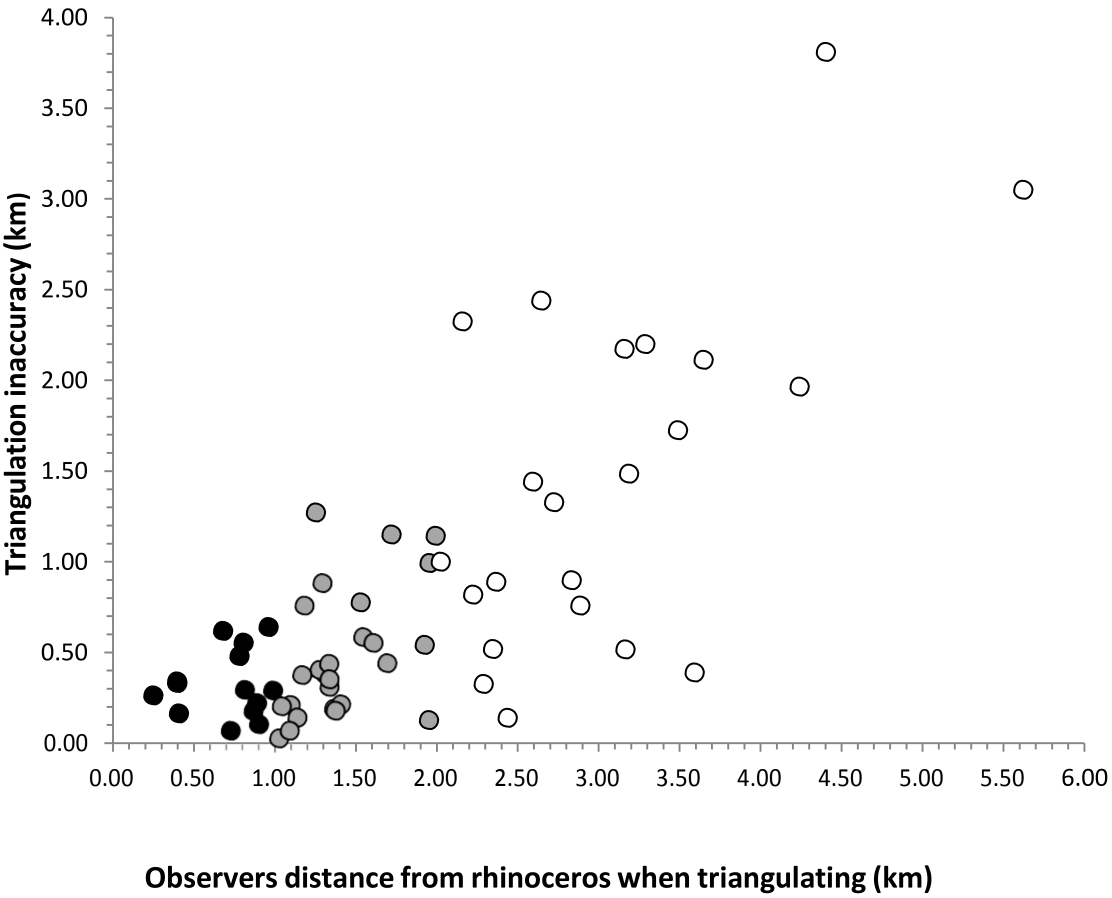

Figure 5 (A). Trend in discrepancy (km) observed between locations recorded with triangulation (estimate) and the direct sighting location of black rhino to the observers distance from rhino (used bearing taken farthest away) in Hluhluwe-iMfolozi Park, South Africa. To illustrate the effect of that an increasing range of observer distances had on triangulation error the following categories of observer distances are compared: long (white > 2km plus), medium (grey, 1.01 to 2.0 km) and short (black, <1km).

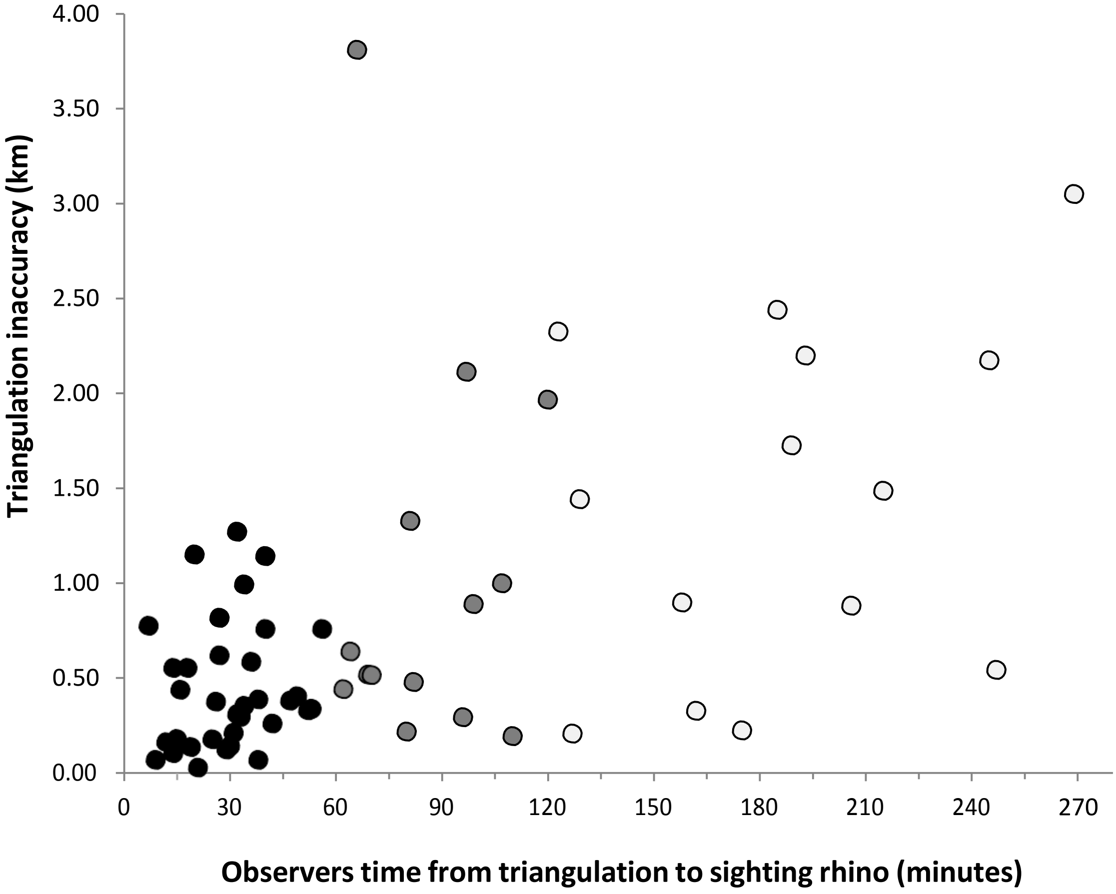

Figure 5 (B). Trend in discrepancy (km) between locations recorded with triangulation (estimate) and direct sightings of rhino recorded immediately afterwards and according to the observer's time taken from completing the triangulation set to directly sighting black rhino in Hluhluwe-iMfolozi Park, South Africa. The discrepancy and relationship for triangulations that took longer to complete are shown according to the following categories (black < 60 minutes, grey 60-120 minutes, and white >2 hours).

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3.

Black Rhinoceros (*Diceros bicornis*) Calf Succumbs after Lion Predation Attempt: Implications for Conservation Management

Two short-sighted rhino seemingly oblivious to a resting lioness in a Marula tree in the Masinda Section of Hluhluwe-iMfolozi Park (Photograph by Roan Plotz)

Authors note - this chapter is presented as the published manuscript in the format of the journal African Zoology where it appears as:

Plotz, R. D. and Linklater, W.L. (2009). Black rhinoceros (*Diceros bicornis*) calf succumbs after lion predation attempt: implications for conservation management. African Zoology 44(2): 283-287.

ABSTRACT

Actual observations of black rhino predation are rarely reported and are limited to two incidences involving sub-adults. Nevertheless, some authors attribute tail and ear deformities in up to 7.1% of some populations to predation attempts. In August 2008 I observed a mother with dependent *c*. 8-month-old female black rhino calf in Hluhluwe-iMfolozi Park (HiP), South Africa. The calf had a recently amputated tail, wounds to the anogenital region, right posterior flank and right side of the neck resembling a lion attack. Thirteen days later and on three subsequent occasions, the mother was sighted alone, suggesting that the calf had succumbed to its injuries. This incident provides evidence to suggest a link between attempted lion predation and tail amputation in black rhino. Significantly, it implies that amputated tails and ears throughout Africa may represent failed depredation attempts and that calf predation may be more prevalent than previously appreciated. Predation is seldom considered in the management of black rhino but should be when attributing cause to poor population performance of this critically endangered species.

KEYWORDS: *Diceros bicornis minor*, predation, tail amputation, conservation management.

Reports of black rhino (*Diceros bicornis*) predation are rare. Owing to the large size of adults, they are largely immune to non-human predation (Schenkel and Schenkel-Hulliger 1969; Owen-Smith 1988; Berger 1994), but young black rhino may be vulnerable to predation by spotted hyenas (*Crocuta crocuta*) and lions (*Panthera leo*) (Skinner and Smithers 1990). The only documented case of lions killing black rhino are three sub-adults depredated at a waterhole in Etosha National Park, Namibia (Brain *et al.* 1999). Elliot (1987) also presents circumstantial, but persuasive, evidence that a lion killed a two-year-old black rhino in HiP. Other evidence presented in support of calf predation is limited to observations of unsuccessful attempts, apparently healthy and nutritionally dependent calves not sighted again with their mother, and particularly ill-formed or missing parts of ears and tails (Goddard 1967; Kruuk 1972; Hitchins and Anderson 1983; Sillero-Zubiri and Gottelli 1991). Ill-formed or missing ears and tails can be common in black rhino populations (e.g.: HiP, 3.7 to 4.0% of individuals, Hitchins 1990; Emslie 1999; uMkhuze Game Reserve (uMGR), 7.1% of individuals, D. Kelly, pers. comm.) and might indicate, therefore, the potential for high calf mortality. Missing calves and apparent mutilations, however, might not be injuries from predators but caused by accident, disease or parasitic and genetic deformities, and failed attempts do not necessarily indicate other successful depredations. Thus, there is uncertainty about how important predation is in black rhino population dynamics.

Uncertainty about the frequency of juvenile black rhino predation means that it is rarely considered in the conservation management of this critically endangered species (IUCN 2008). When comparing black rhino population performance in different reserves, relatively poor fecundity and low population growth is usually attributed to over-stocking and habitat deterioration (Emslie *et al.* 2001; Reid *et al.* 2007), although the reserves compared differ in their densities of large predators. Some reserves do not have large predators, but in others predators occur at remarkably high densities and could contribute to poor population growth (Balfour 2001). Between 1990 to 2003, four out of seven calf deaths in the Ngorongoro Crater, Tanzania, were due to predation (Amiyo 2003), suggesting that for some populations predation can severely limit population growth.

In this context, the disappearance of a maternally dependent black rhino calf after a predation attempt that amputated its tail and left it with multiple wounds, resembling a lion attack, indicates that predation of juveniles may be more common than previously appreciated. I detail this observation and discuss the potential importance of predation in the management of black rhino.

OBSERVATIONS

Observations of adult female, ear notch sequence number 321 and identification code C441 were made from July to September 2008 as part of a project investigating the reproductive performance and ecology of black rhino in HiP (described in Plotz *et al.* 2008). Observations were made with the unaided eye or assisted using binoculars (Nikon 8 x 40) and field spotting scope (Bushnell 20 x 60).

C441 had been regularly sighted by field rangers in the Masinda and Nqumeni sections of HiP since 4 November 2003, when she was first ear notched and her age estimated as between 3.5 to seven years old. On 26 September 2007 she was captured for translocation but instead released at the capture site because she was assessed as pregnant. C441's sighting record indicates that the subsequent female calf, her first documented, was born between 9 and 30 December 2007. We first sighted C441 when her calf was aged *c.* seven months (21 July 2008). The calf was injury free on that occasion.

On 14 August 2008 field ranger Mr. Bom E. Ndwandwe and RDP were walking in the Nqumeni section monitoring a different female black rhino fitted with a horn-implant radio-transmitter, when they sighted female C441 accompanied by her female calf with injuries. The calf's injuries included tissue trauma to the anogenital region with an amputated tail, claw or canine puncture wounds to the neck region and skin lesions resembling claw marks to the rump and right posterior flank (Fig. 1 and 2). On four subsequent occasions, 27 August, 9, 14 and 22 September 2008, C441 was sighted without her calf. Observations post 22 September 2008 were not possible as she was translocated to another reserve.

DISCUSSION

Eight-month-old black rhino calves are still nutritionally dependent on their mothers and so the confirmed disappearance of C441's calf suggests that the calf succumbed to its injuries. I did not witness the lion attack or recover the calf's carcass and so spotted hyena cannot be ruled out as a potential cause of the calf's wounds or ultimate disappearance. However, three characteristics about the record of sightings and photographic evidence are consistent with an attack by at least two lions (1) Puncture and tear wounds at the calf's neck suggest one lion attempted to suffocate the calf in the fashion typical of lion attacks on ungulates (Skinner and Smithers 1990). Elliot (1987) and Brain *et al*. (1999) report similar puncture wounds to the neck in sub-adult black rhino killed by lion. (2) Tissue trauma, severed tail, and claw marks suggest that another lion attempted to feed from the anogenital region. Brain *et al*. (1999) witnessed a lioness beginning to feed between sub-adults back legs during an attack, while Elliot (1987) discovered a sub-adult carcass with anogenital wounds consistent with this feeding behaviour. (3) Hyena claws are unable to make the skin lesions at the rump and along the back and flank of the calf, all of which were characteristic in spread and size of lion claws and canines (Skinner and Smithers 1990). In addition, the tissue damage, including amputated tail, was still red and weeping with dipteran maggots embedded within the tissue. This implies that the wounds were inflicted relatively recently (i.e. 1 to 2 days prior) and concomitantly, thus making it highly unlikely that spotted hyena were able to inflict these wounds either prior to or post this particular lion predation attempt.

In this predation attempt the calf's tail was amputated to approximately a third of its original length. Berger (1994) states that 97% of ear and tail deformities in black rhino throughout Africa (Goddard 1969; Hitchins and Anderson 1983; Hitchins 1986, 1990) can be interpreted as the scars of historical predation attempts, although there are other possible explanations such as genetic or parasite-induced deformities during development. Until now, however, there has been no direct link between these deformities and amputation during a predation attempt. Our observations suggest that tail and ear mutilations might indeed represent failed predation attempts. In 2007-08 I observed five out of 93 different black rhino in HiP (5.4%) with mutilated tails or ears, similar to historical mutilation rates in the same reserve (i.e., 3.7 to 4.0%, Hitchins 1990; Emslie 1999). Importantly, nearby uMGR where spotted hyenas occur but not lions, five out of 70 identifiable black rhino have missing ears and tails (i.e., 7.1%, D. Kelly, pers. comm.), so spotted hyenas can also be implicated in black rhino predation. These values and Ngorongoro Crater's documented 56% calf predation rate (Amiyo 2003), indicate that predation of juvenile black rhino may be more common than previously appreciated.

Predation on black rhino juveniles might be under reported because both births and carcasses are rarely detected. Neonatal black rhino calves are cryptic and difficult to sight. Not only are they small but mothers tend to be sedentary in densely vegetated habitat during the calves' first months of life. Thus, unless individual adult females are intensely monitored (e.g., pregnancy detection and radio telemetry, Plotz *et al*. 2008; MacDonald *et al*. 2008), parturition and neonatal mortality will typically be undetected, especially in large populations and reserves like HiP. Moreover, on the few occasions that field rangers recover black rhino calf carcasses the cause of death is rarely determinable. A good illustration of this difficulty was the rescue of an ill and abandoned six-month-old black rhino calf that died in the Ezemvelo KwaZulu-Natal Wildlife (EKZNW) Game Capture holding pens. The carcass was placed outside the game capture compound and on the following morning the EKZNW veterinarian could find almost no evidence that the calf had been there. Searching revealed only small pieces of its horn and jaw (D. Cooper, pers. comm.). Juvenile predation could, therefore, be common even though the evidence is not.

Black rhino mothers have killed lion that threaten their calves (Goddard 1967; Owen-Smith 1988, P126-7). C441 was a young mother and maternal inexperience may have contributed to her calf's vulnerability. The offspring of inexperienced mothers tend to incur higher mortality rates (Tardif *et al*. 1984; Novak *et al*. 2000, Barber-Meyer and Mech 2008, P15). Nevertheless, our observation also indicates that maternal defence is not always sufficient to deter predators.

Conservation managers rarely factor in predation when managing a black rhino population for improved productivity, although predation's role in HiP's black rhino population performance has been debated before (Balfour 2001; Fanayo *et al*. 2006). Poor population performance has largely been attributed to density dependence but evidence suggests that predation of black rhino juveniles may also, at least in part, account for longer inter-calving intervals, low numbers of calves per adult female, and poor population growth. It might not be realistic to expect a black rhino population living with high densities of lion and spotted hyena to grow as fast as one in a reserve without large predators. When attributing cause to poor population performance the presence of large predators should be considered.

Figure 1. Black rhino calf (c. 8 months old) in Hluhluwe-iMfolozi Park with recent tissue trauma to the anogenital region, an amputated tail, and puncture and tear wounds on the neck consistent with a lion attack. Note also claw marks (dark grey lines) on rump and flank and what appears to be dipteran maggots (white) embedded in raw tissue on tail and anogenital area (Photograph by Roan Plotz).

Figure 2. The anterior right flank of calf showing one of two weeping puncture wounds on the neck consistent with the canine of a lion (other puncture wound obscured by reeds and shadow) (Photograph by Roan Plotz).

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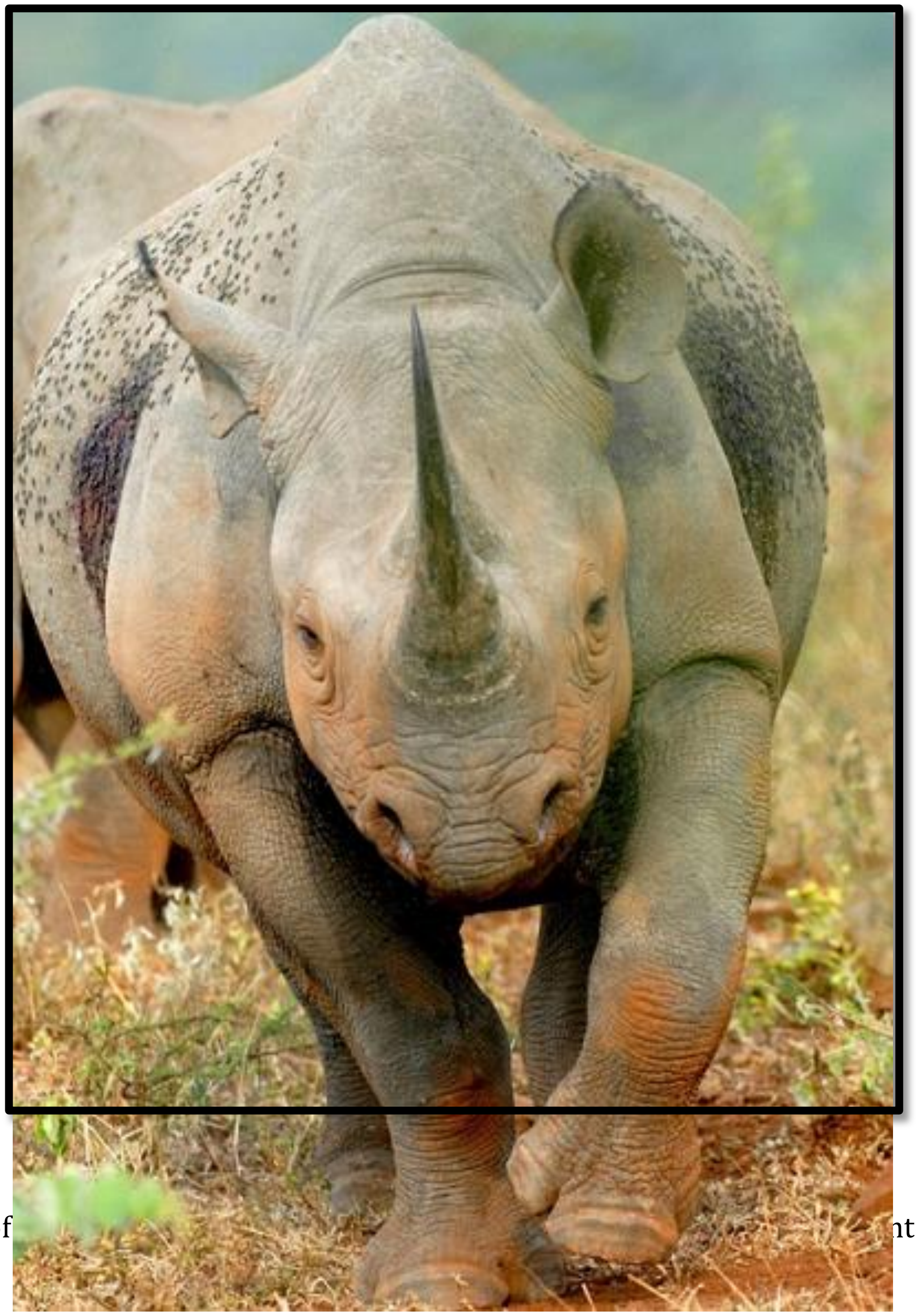
4.

Temporal association between Filarial (*Stephanofilaria dinniki*) Lesion Severity and Body Condition in Black Rhino



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ABSTRACT

The impact of parasites on animals is well known. Parasites have the potential to reduce individuals' reproductive success and survival in wild animal populations, often through effects on body condition. It is difficult to determine the degree to which these impacts regulate populations, particularly in the wild, because of the logistics of conducting the necessary experimental manipulations of either hosts or parasites. Several populations of the critically endangered black rhino (*Diceros bicornis*) exhibit anterior flank filarial lesions caused by a host specific nematode i.e., *Stephanofilaria dinniki*. In Hluhluwe-iMfolozi Park (HiP), South Africa, lesions can be remarkably large and occur in all adult (>6 years) black rhino. Anecdotal reports suggest that severity of filarial lesions is temporally associated with poor body condition in black rhino. This population provided an ideal opportunity to test the relationship between lesion severity and body condition in black rhino.

Thus, I used HiP's endemic black rhino population to obtain detailed measurements of rhino's lesion severity and body condition. I devised a novel field technique to measure lesion severity and compared direct measurements at close proximity with the remote field technique to show that variation was strongly correlated - justifying its viability for use in future. In HiP, black rhino's lesions averaged a remarkable 441 ± 36 cm^2 (from direct measures) and a significant temporal association existed between lesion severity and body condition. There was also no indication that seasonal differences (i.e., resources) played a role in lesion severity and body condition (i.e., both appeared non-seasonal). As a pilot study further investigation of the specific drivers of the significant negative temporal relationship between lesion severity and body condition in HiP's black rhino needs to be determined.

Limited information on the current distribution of lesions across Africa's rhino populations prevents comparisons between populations. This study determined that lesions were localised to two distinct regions in east Africa (i.e., Kenyan Highlands) and North-east South Africa and Swaziland. The biogeographic distribution map created in this study facilitates future intra- and inter-population comparisons between black rhino populations with and without lesions.

KEYWORDS: parasites, free-ranging, temporal association, *Diceros bicornis minor*, Hluhluwe-iMfolozi Park, *Stephanofilaria dinniki*, body condition, filarial lesions, nematode, *Rhinomusca dutioti / brucei,* prevalence

INTRODUCTION

Animals mount protective and energetically costly immune responses to parasite infection. Organisms have finite energy reserves and chronic responses to parasite infection might divert resources from other functions, including the maintenance and storage of energy reserves for maintaining body condition (reviewed in Thomas et al. 2005; Morand et al. 2006). Filarial nematodes are widespread, and have caused large ulcerative haemorrhaging lesions in domestic livestock and subclinical effects such as reduced body condition and growth rates (Irvine 2006; Sutherst et al. 2006). Wildlife with chronic filarial parasitism and healing ulcers might therefore also suffer from lower overall body condition.

Filarial infection might be more common and severe in high-density populations that are nutritionally stressed (e.g., density-dependence) and less able to divert resources (e.g., protein) towards immunological defence and healing (Anderson and May 1981).

Large haemorrhaging ulcerative filarial lesions have been reported in several populations of black rhino (*Diceros bicornis*: Rhinocerotidae) but not all (Schulz and Kluge 1960; Parsons and Sheldrick 1964; Tremlett 1964; Hitchins and Keep 1970; Mutinda et al. 2012). The severity of lesions also varies between infected populations. Lesions are almost unnoticeable in some populations (Mutinda et al. 2012) but remarkably severe in others (Tremlett 1964; Hitchins and Keep 1970; Skinner and Smithers 1990). Lesions are caused by the filarial nematode *Stephanofilaria dinniki* (Schulz and Kluge 1960; Round 1964) that are vectored by blood sucking flies (*Rhinomusca dutioti* and *R. brucei*; Parsons and Sheldrick 1964; Zumpt 1964; Mihok et al. 1996).

Uncertainty around *S. dinniki's* effect on black rhino welfare means that it is rarely, if ever, considered in the conservation management of this critically endangered species (IUCN 2013). When comparing black rhino population performance in different reserves, relatively poor fecundity and low population growth is usually attributed to over-stocking and habitat deterioration (e.g., Emslie et al. 2001; Reid et al. 2007), although the reserves compared differ in the prevalence and severity of filarial parasitisation. Some reserves do not have filarial parasites, while for others infection and lesions are severe and could result in reduced body condition with poor breeding rates and population growth.

The endemic population of rhino (*D. b. minor*) in Hluhluwe-iMfolozi Park (HiP), South Africa have the most severe lesions recorded (Schulz and Kluge 1960; Parsons and Sheldrick 1964; Tremlett 1964; Hitchins and Keep 1970; P. Hitchins and D. Cooper, pers. comm.). By adulthood (i.e., six years of age; Law and Linklater 2014) lesions are typically present to varying degrees of severity and size on both anterior flanks of all HiP's black rhino (Hitchins and Keep 1970). Anecdotal comparisons suggest that rhino in East Africa (*D. b. michaeli*) have less severe filarial lesions. Lesions up to 15cm wide are reported in Meru National Park, Kenya (Mutinda et al. 2012) but up to 37 cm wide in HiP (Hitchins and Keep 1970). The more severe lesions in HiP's black rhino might be significant to the debate about why this population appears less fecund than some others (Emslie 2001; Fanayo et al. 2006). The severity of their lesions might, in part, also explain why HiP's rhino have below average body condition scores compared to other better performing populations (Emslie 2001).

It has largely been assumed that filarial parasitism and lesions have no impact on rhino welfare or reproductive performance and recruitment (Skinner and Smithers 1990). However, first-hand accounts from wildlife practitioners in HiP report that filarial lesions become progressively more severe (i.e., increased haemorrhaging) when individual black rhino are exposed to the stress of captivity before relocation. For example, before relocation black rhino can be held in enclosures for several weeks (D. Cooper, *pers. comm.*). After several days in captivity the severity of black rhino's lesions increased dramatically (i.e., flared; D. Cooper, *Pers. comm.*). This delayed 'flaring' of LS in response to a stressor was also associated with marked declines in rhino body condition (BC). LS might therefore be temporally associated with poor BC in black rhino. Captive-raised rhino, for example, regularly suffer superficial necrotic dermatitis (i.e., non-filarial lesions) that may be associated with stress since captive rhino experience weight loss, pregnancy and oestrus bleeding and a two-fold increase in mortality (Dorsey 2008; Dorsey et al. 2010). In other animals such as domestic cattle (*Bos taurus*) low body condition scores are also correlated with inceased treatment for haemorrhaging lesions of the sole (i.e., lameness) up to two to four months later (Green et al. 2014).

If LS is temporally associated with BC in black rhino, managers might then be able to monitor both factors to better predict and manage the population under stress. Testing for a temporal association will require the ability to reliably conduct field estimates for both BC and LS of black rhino. Fortunately a reliable field based BC scoring system already exists for black rhino (e.g., Reuter and Adcock 1998; Fig. 1). Five-point visual BC scores presented by Reuter and Adock (1998) has proved to be a useful indicator of body fat in rhino's and other Perissodactyls (e.g., horses) because these animals store their body fat directly under the skin surface. BC scores tested against subcutaneous measures of body fat (a marker of condition) have been shown to be accurate predictors of levels of body fat in horses (Carroll and Huntington 1988; Henneke al. 1983; Keiper 1991). Reuter and Adcock (1998) have modified the black rhino BC scoring system to closely match the one used for horses. However, there is no field based scoring system to estimate LS in black rhino and testing the temporal association between LS and BC is not currently possible.

Understanding how filarial parasitism impacts upon black rhino populations would be improved by making intra- and inter population comparisons (see Diamond and Chase 1986) where traditional experiments are not possible. At this time however reporting of lesion prevalence within Africa's *c.* 134 (Emslie and Knight 2012) rhino populations is incomplete. Reports of lesion occurrence are limited to HiP (Round 1964; Hitchins and Keep 1970), Meru National Park (Mutinda et al. 2012) and Tsavo National Park, Kenya (Tremlett 1964) but anecdotal observations suggest several other rhino populations also present with lesions (P.M. Hitchins, pers. comm.). The first step towards testing if filarial lesion severity is temporally associated with BC, or impacts upon the welfare of black rhino populations in general is a synthesis of current knowledge about lesion distribution so that comparisons between populations can be achieved.

Therefore, the three main aims of this study were to (1) design and test the reliability of a novel filarial lesion field scoring system for HiP's black rhino population, (2) investigate whether there is a temporal association between BC and LS in black rhino and, (3) update the current biogeographic range of filarial lesions for all of Africa's black rhino populations. It is my hope that this will enable additional research to be conducted into the role that filarial parasitism has on the welfare of rhino populations.

MATERIAL AND METHODS

Study site and population

Hluhluwe-iMfolozi Park (HiP: S28.000-28.430, E31.716-32.015) is a 960 km^2 fenced reserve located in Zululand, KwaZulu-Natal (KZN), South Africa. The park's topography of lowland flood plains and rolling hills in the south to steep hill country in the North ranges from 20 to 580 m elevation above sea level. Rainfall remains highly variable and seasonal, with warm wet summers and cool dry winters (Berkeley and Linklater 2010). Also, HiP has a strong south-west (*c.* 635mm annually) to North-west (*c.* 1000mm annually) rainfall gradient (Whateley and Porter 1983). During the period of data collection rainfall averaged 579.9 mm annually, and 378 mm and 201.9 mm over the wet and dry seasons respectively (central Park weather station at Masinda; G. Clinning, unpubl. data). HiP, therefore, experienced a below average rainfall during the study – i.e., a drought that began *c.* 2001 (Berkeley and Linklater 2010). Average monthly temperatures range between 13°C (winter) to 33°C (summer) (Whateley and Porter 1983; Walters et al. 2004).

HiP currently holds approximately 218 south-central black rhino (*D. b. minor*) (Clinning et al. 2009) and is the largest of two surviving endemic populations of the subspecies (Brookes and MacDonald 1983). From January 2007 to October 2008, 14 black rhino were captured by remote chemical immobilization from a the southern and central sections by helicopter and fitted with horn implant radio-transmitters (combinations of Sirtrack Pty Ltd., NZ or Telonics, USA models; techniques used described in Shrader and Beauchamp 2001) . The Ezemvelo KZN

Wildlife (EKZNW) Game Capture Team, including wildlife veterinarian, administered capture and drug protocols that are described in detail elsewhere (Hitchins et al. 1972; Rogers 1993; Linklater et al. 2006; Morkel and Kennedy-Benson 2007).

Data collection

From March 2007 to October 2009, I monitored the 14 adult (≥ 6 years) female black rhino fitted with horn-implant radio-transmitters. Rhino were radio-tracked to obtain repeated visual samples in random sequence. Repeated observations of other male and female rhino marked with unique ear notch sequences were also made whenever encountered. For all these individuals I collected and compared:

(1) Body condition scores

Black rhino body condition (BC) was estimated using Reuter and Adcock's (1998) five-point visual scoring scheme, where scores are recorded in 0.5 increments, where1 indicates poor and 5 excellent body condition (Fig. 1). HiP management currently use this system to score black rhino condition (Emslie 2001). BC scores are not dependably obtainable from rhino that are sedated and lying down (Reuter and Adcock 1998). Comparisons between BC scores taken at close quarters against field scores were therefore not possible.

(2) Direct measurements of filarial lesion severity

I measured the width and height of each lesion to the nearest centimetre on both the left and right anterior flanks of 14 chemically immobilised adult (> 6 years) female black rhino using an L-shaped ruler. Lesions are typically asymmetrically taller than they are wide (i.e., they are ovate) and so the area (cm^2) of each lesion was estimated using the formula for the area of an oval: (*width* cm) x (*height* cm) *0.8. (Fig. 2). The proportion (%) of the lesion estimated to be haemorrhaging (PH) was also estimated. Rhino captured to meet park management objectives targeted adult female rhino during the winter (i.e. April – October) and so all direct measurements were from 14 captured females during winter.

(3) Remote estimates of filarial lesion severity

Rhino were radio-tracked to obtain repeated visual samples in random sequence. A novel method for remotely estimating the dimensions of lesions was implemented. For example, the *w* and the height *h* of lesions were compared to the width of the rhino's nearest upper-foreleg to that lesion. Upper foreleg width was always assigned a width of 1.0 and all *w* and *h* estimates were recorded at intervals of 0.1 relative to 1.0 (Fig. 3). To convert remotely obtained scaled lesion dimensions to metric measurements for subsequent analysis, I multiplied all estimates by the average recorded upper-foreleg width of an adult black rhino (i.e., 26 cm). Purchase (2007) showed adult foot length for black rhino to be 26 cm, where foot length has an approximate 1:1 ratio with the width of the upper-foreleg. The entire lesion area (ELA; cm^2) included both necrotic and haemorrhaging tissue. Unhealed haemorrhaging sections of lesions were deemed more likely to stimulate an ongoing immune response from rhino and require healing. Thus, I defined lesion severity (LS) as the proportion of the ELA haemorrhaging (PH).

The ELA (cm^2) was calculated using the same formula for the area of an oval that I used for calculating direct area measurements of lesions: (*w: scaled from 0.1 to 1.0 relative to upper foreleg width**26 cm) x (*h: scaled 0.1 to 1.0 relative to upper foreleg width* *26 cm) *0.8 ELA (cm^2). The method used to calculate the LS is detailed in Fig. 3.

Comparing direct and remote field lesion severity measurements

I attempted to justify the novel remote field technique for measuring LS by comparing LS estimates from field estimates with direct measurements of the 14 rhino within 14 days of each other i.e., reduce the effect that time has on variations in LS. Unfortunately, this was only possible for seven individuals. The time between the direct and the remote estimates for the other seven rhino was several months apart and therefore not included in analysis. Differences between estimates would most likely be due to effect of time and not the technique that was used. To compare the techniques I used photographs to measure direct LS taken from captured rhino with estimates taken remotely.

I compared direct (using photographs) and field measurements (novel technique) for estimates of the following: ELA (i.e., the whole lesion area that included both the haemorrhaging and healed tissue), the proportion (%) of the entire lesion that was haemorrhaging (PH) and finally LS estimates (i.e., amount in cm^2 bleeding). I included regression plots of the remote versus direct scores to illustrate variation between them.

Temporal association between lesion severity and body condition scores

I predicted that a temporal association ought to exist between LS and BC in black rhino and used a general linear model (GLM) with random effect for rhino identity to statistically test for the relationship. All statistical procedures were conducted in SPSS (SPSS Inc., version 19, 2010). For all statistical tests I regarded the critical value (α) of ≤ 0.05 as statistically significant.

I predicted that one factor (i.e., LS or BC) ought to have a temporal influence on the other. Anecdotal evidence also suggests that LS and BC is negatively correlated in black rhino. To this end, I set up my data set chronologically and tested the following two hypotheses statistically.

Testing for a temporal signal:

I investigated whether the association between LS and BC had a temporal signal. To test this I predicted that BC and LS in future (t+1) should be inversely correlated to BC and LS at time (t). To test this I formulated the following hypothesis:

(1) If BC and LS temporally associated ($\Longrightarrow$) with each other, then I predicted that either LS or BC in the future (time +1) should be significantly negatively correlated with previous estimates of the other (time, t) respectively: e.g., *If*

$BC \Longrightarrow LS$, then $LS_{time\ (t)\ +1}$ should predict BC_t better, or *If $LS \Longrightarrow BC$ then BC_{t+1} should predict LS_t better.* I also analysed this hypothesis from the

perspective of BC's impact on lesion healing (i.e., Lesion Healed (LH) = ELA – LS). I was attempting to determine if rhino's BC in the past impacted on LH in future.

Finally, I investigated whether changes in BC and LS caused the inverse temporal correlation. In other words, I was considering whether a specific shift in BC and LS over time was the significant driver of this temporal association. To test this I formulated the following hypothesis:

(2) If BC and LS was temporally influenced by the degree of change (Δ) over the other, then I predicted that Δ in BC or LS over time should have a significant inverse influence over Δ in LS and BC, respectively: e.g., *If BC* $\Longrightarrow$ *LS Δ BC* ($BC_{t+1} - BC_{t}$) *should predict Δ LS* ($LS_{t+1} - LS_{t}$), or *If LS* $\Longrightarrow$ *BC then Δ LS* ($LS_{t+1} - LS_{t}$) *should predict Δ BC* ($BC_{t+1} - BC_{t}$) *better.*

Survey of the current bio-geographical distribution of filarial parasitism in black rhino populations

Published reports of *S. dinniki* related lesions in black rhino populations are limited to a handful of African reserves: (e.g., HiP and Mkhuzi Game Reserve in South Africa and Meru and Tsavo National Parks, Kenya; Tremlett 1964; Schulz 1961; Hitchins and Keep 1970; Tremlett 1964; Mutinda et al. 2012; Ndeereh et al. 2012). In this context, I contacted personnel involved in rhino population management, veterinary work, and research in 27 parks / protected areas across Africa and asked if filarial lesions or parasites existed in their black rhino populations. I mapped the current distribution of *S. dinniki* and lesions using the volunteered and published information.

RESULTS

Body condition scores, direct and field measurements of filarial lesion severity

Average body condition scores, direct and field measurements of filarial lesion severity are summarised in Table 1. There was not a significant difference in the ELA between the left and right anterior flanks (e.g., mean LS of left was 428 ± 32 cm^2 Range: width 11-37 cm and length 18-40 cm and right 442 ± 41 cm^2; Range: width 16-30 cm and length 18-47 cm; Paired t-test, P=0.6) and so left and right anterior flank lesion estimates were combined for one mean value. Average ELA measurements for 14 adult females captured during winter were 441 cm^2, with average LS of 262 cm^2. I also obtained 208 remote estimates of lesions (i.e., ELA and PH) and BC scores from the 57 marked rhino. Mean ELA, PH and LS are summarized according to sex and season in Table 1.

Females presented with larger average lesion areas (i.e., LS, PH and ELA) than male rhino. Males did appear to have greater variability in lesion area and almost double the severity in summer than winter compared to females where lesions were similarly severe between seasons. Although there was a discrepancy between remote and direct measurements in Table 1, regression plots show that the techniques were closely correlated and differences could reflect the large discrepancy in sample sizes. The average female LS in winter was 262 cm^2, while remote estimates averaged 412 cm^2.

Comparing direct and remote field lesion severity measurements

Comparisons of ELA, PH and LS were all plotted as direct measurements versus the field technique to represent R^2 values (Fig. 4). I was able to compare direct and field estimates within 14 days for the left filarial lesions of six, and right filarial lesions of seven, adult female black rhino. Unfortunately, comparisons between direct and remote lesion measures for the other seven rhino were too far apart (i.e., several months) and were therefore not reliable for comparing techniques. Nonetheless, comparisons between direct and field estimates were closely correlated (See Fig. 4 for regressions and R^2 values).

Temporal signals between lesion severity and body condition

(1) BC was temporally associated with significantly reduced LS ($R^2 = 0.10$: $F_{1, 275} = 138$; $P=0.04$) and increased LS was also temporally associated with significantly reduced BC ($R^2 = 0.13$: $F_{1, 275} = 150$; $P=0.01$; Fig. 5). Prior BC did not significantly reduce the amount of the lesion that healed (LH) ($R^2 = 0.02$: $F_{1, 275} = 152$; $P=0.9$) and previous LH did not significantly reduce future BC ($R^2 = 0.01$: $F = 152$; $P=0.9$).

(2) Change in BC and LS was not associated with a significant negative relationship with change in either respectively ($R^2=0.01$: $F_{1, 275} = 152$; $P=0.8$; Fig. 6).

Distribution of filarial parasitism and lesions across Africa

Filarial lesions appear to be localised to two regions in Eastern Africa with mesic climates and absent from the drier western areas of southern Africa (Fig. 7). Both regions with filarial lesions included several rhino reserves in close proximity in Swaziland i.e., Mkhaya Game Reserve and North-east South Africa i.e., North-East KZN: HiP, Itala, Mkhuze, Ndumo, Pongola, Tembe and Thanda Game Reserves, Phinda-Munyawana Conservancy, Zululand Rhino Reserve, southern Kruger National Park in Mpumalanga Province and East Africa i.e., Kenyan Highlands: Aberdares, Lake Laikapia District, Lake Nakuru District, Meru, Mount Kenya, Nairobi and Solio National Park, Lewa Wildlife Conservancy.

DISCUSSION

To my knowledge this is the first study that has attempted to investigate the relationship between LS and BC in black rhino. Comparisons with direct measures of LS indicated that the remote technique appeared to be a reliable method for measuring the severity of black rhino's filarial lesions in the field. However, with a sample of seven rhino that were able to have their lesions compared within 14 days, comparisons are needed in future for greater confidence. Based on direct measurements, however, HiP's black rhino population presented with the largest filarial lesions yet recorded. Lesions covering an average 441 ± 36 cm^2 were recorded on 14 females and more severe lesions occurred on black rhino in poor condition (Fig. 5).

Temporal association between filarial lesion severity and body condition

As predicted there was a temporal signal to the correlation between LS and BC for black rhino, where current BC or LS was negatively associated with future LS or BC respectively. Despite this inverse temporal correlation, I could not detect that changes in LS or BC were driving the association. This could either be because LC and BC are not temporally causative on each other or the field methods used for estimating BC and LS are not fine scaled enough to detect causation. Therefore the most that this study can say is that LS and BC appeared to have an inverse temporal association, but neither appeared causative of the association (i.e., LS and BC do not appear to be driving the inverse relationship and something else is).

Temporally associated but not temporally causative

Pilot studies such as this one are needed because parasitism's role in regulating animal populations is often dismissed. Experimental studies are few and the host parasite relationship is often considered to be neutral or benign due to host-parasite co-evolution (Tompkins et al. 2001; Bordes and Morand 2009).
Moreover, most research on factors that regulate performance in large mammal

populations has focussed on mechanisms driven by predation, competition or resource limitation (Tompkins et al. 2001). These mechanisms also remain the focus of managers of black rhino (Emslie 2001; Fanayo et al. 2006). Subclinical effects illustrated as negative relationships between parasite abundance and host body condition have been difficult to quantify in the wild (Irvine 2006). Expediting species recovery increases pressure to understand what factors, parasites or otherwise, impact most on the population performance of a critically endangered species.

Resource limitation due to overpopulation of HiP's black rhino population is most often attributed for apparently poor performances (Emslie 1999, 2001; Reid et al. 2007). However, if the inverse temporal signal between LS and BC was being driven by resource limitation, this might explain why HiP rhino have both extremely severe lesions and below average body condition. However, if resource limitation was a driver of the temporal signal between LS and BC, there ought to be some evidence of seasonal fluctuations (i.e., > LS and < BC in winter when food is scarce and < LS and > BC in summer when food is more abundant). Data from this study shows females presented with larger average lesion areas (i.e., LS, LH and ELA) than male rhino. Males, however, appeared to have more variable lesion area and almost double the severity in summer than winter compared to females where lesions were similarly severe between seasons. Thus, the results from this study do not support resource availability as a potential driver of this temporal association because seasonal fluctuations are not evident. Something else may be the main causal factor for the relationship and further investigation is essential for true understanding. Alternatively, a third factor as the driver of the temporal correlation between LS and BC may not be involved. Both LS and BC could be affecting each other equally. Or the time scale of causality could be much quicker, or longer, compared to my actual observation time intervals. Finally, the measures of BC and LS may not be scaled finely enough to pick up a strong temporal causal signal (i.e., too crude a technique).

One of the most interesting findings from this study was the summer and winter differences in LS and BC between males but not females (Table 1). The mechanisms driving this are unclear but could be due to breeding age females having to partition resources to calve production. Analysis showed that female black rhino's lesions were on average larger than males but also of similar severity between seasons, whereas lesion appeared to heal in males during the winter months. In other animals, digital dermatitis, a contagious disease of cattle (*Bos taurus*), had greater risk of developing lesions in mid to late lactation than non-lactating females (Nielsen et al. 2011). Moreover, BC in black rhino males varied seasonally with higher scores in summer with better habitat quality, whereas remained static on average for females. There is some evidence that reproductive pressures do have an impact on BC in captive black rhino (*D. b. michaeli*). Edwards et al. (2014), for example, demonstrated that nulliparous female black rhino had a higher BC scores than parous females.

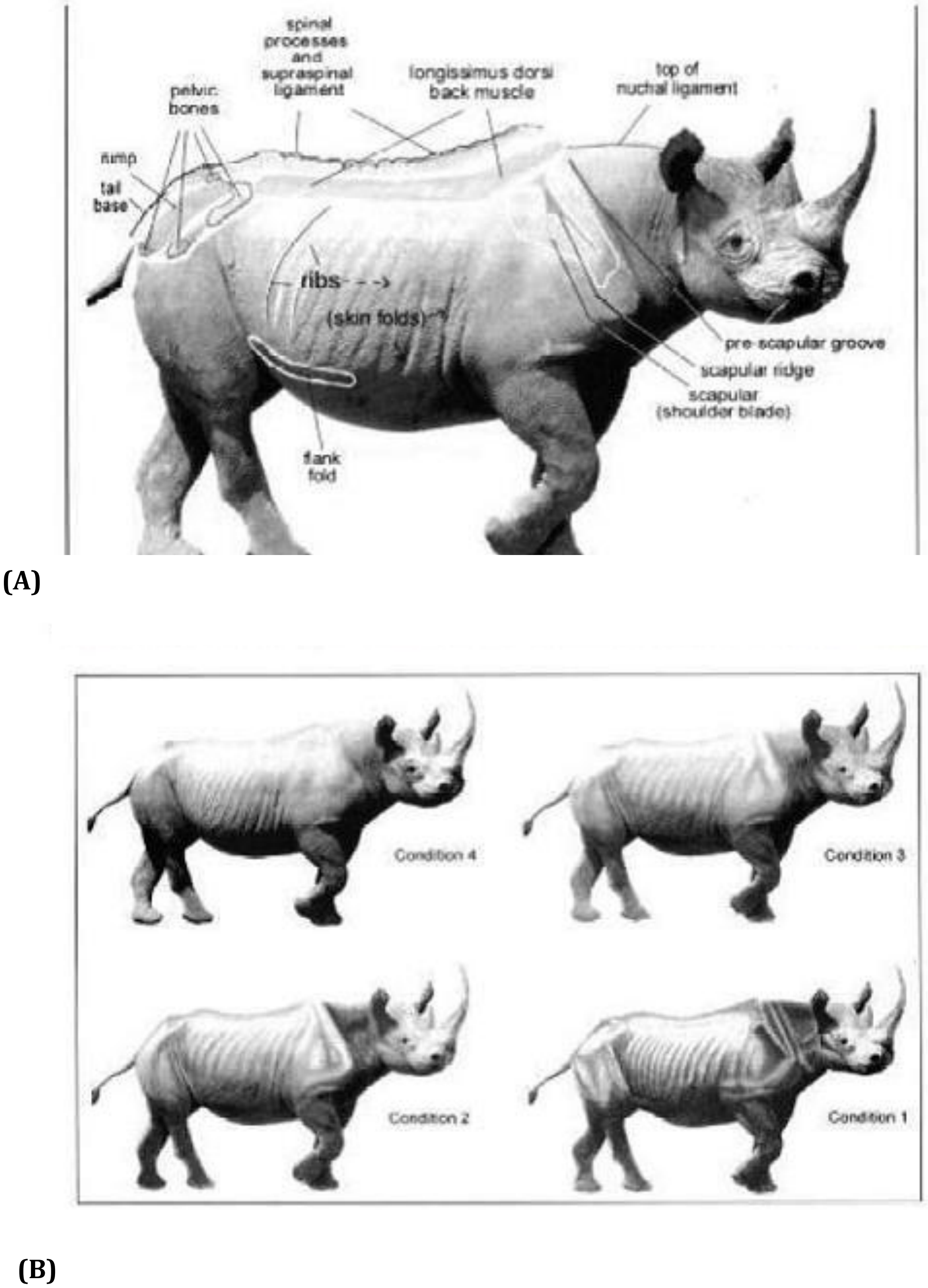
Distribution of filarial parasitism and lesions across Africa

Populations of black rhino are scattered across sub-Saharan Africa but not all host *S. dinniki.* Filarial lesions are restricted to regions in east and southern Africa: the Kenyan Highlands and North-east South Africa and Swaziland. It is not known for certain why lesions are restricted to these two regions, however, the suitability of their climate, in particular, is likely to be influenced biogeographically by several factors pertinent to the limitations of the nematodes and fly vectors life cycles.
Rainfall or humidity and temperature for the parasites Dipteran vector is likely to play an important role (Lehane 2005). The Kenyan highlands and eastern South Africa are mesic and warmer than the arid climates of other rhino reserves.

The absence of filarial lesions may also be a consequence of local extinctions and reintroductions of filarial free black rhino across Africa. Drastic fluctuations in rhino populations due to human poaching and relocation efforts over the last century are likely to have altered the current distribution of *S. dinniki*. Rhino in Tsavo and Amboseli National Parks in southern Kenya historically had lesions (Tremlett 1964), however, are now at much lower densities and no longer present with lesions. Also, Amboseli N.P. black rhino are now locally extinct. Moreover, rhino became locally extinct in Kruger National Park (KNP), South Africa, and Swaziland in the 1930s (Skinner and Smithers 1990) with no known historical account of lesion presence. However, rhino and the nematodes fly vector (*R. dutioti*) have been re-introduced to KNP from HiP and rhino do now present with lesions. Thus, as far as is ascertainable, lesion occurrence appears to have contracted in East Africa, while expanding to its probable former range in the south. Beyond this it is impossible to know for sure the former distribution of *S. dinniki*.

Future management considerations

Identifying that a temporal signal between LS and BC exists, in conjunction with a BC and novel lesion measuring technique, allows black rhino managers the potential to predict if and when the population is about to be, or was, under stress. I was not able from the results in this study to conclude that LS and BC are causing the temporal correlation on each other. To improve our understanding this study needs to be repeated in other populations and expanded upon to consider other aspects such as the effect that different time lags have on changes in LS and BC. Rhino, like many wild animals are harvested and critically endangered and management have to consider how this integral source population might be managed for parasitic disease. Poor population performance of recently translocated black rhino is mostly attributed to the age and sex demographics of the translocated rhino (Linklater et al. 2012). However, lesions and filarial parasitism often recedes or vanishes from HiP black rhino when moved to new populations. If rapid population growth rates and improved BC of relocated HiP rhino reflect, in part, the absence of filarial lesions requires investigation. It might not be possible for black rhino populations with lesions like those observed in HiP to grow as fast as populations where they are absent. Comparisons of the growth rates of infected and non-infected black rhino populations would help to clarify this. There is much that needs to be investigated about filarial parasitism, not least the role that other agents have on LS. This pilot study provides a reliable field measurement technique and an updated filarial lesion distribution map that will allow for comparisons between populations. It is my hope that this preliminary study will act as a baseline for comparative research into *S. dinniki's* role in Africa's black rhino population.



Adapted from Reuter and Adcock (1998)

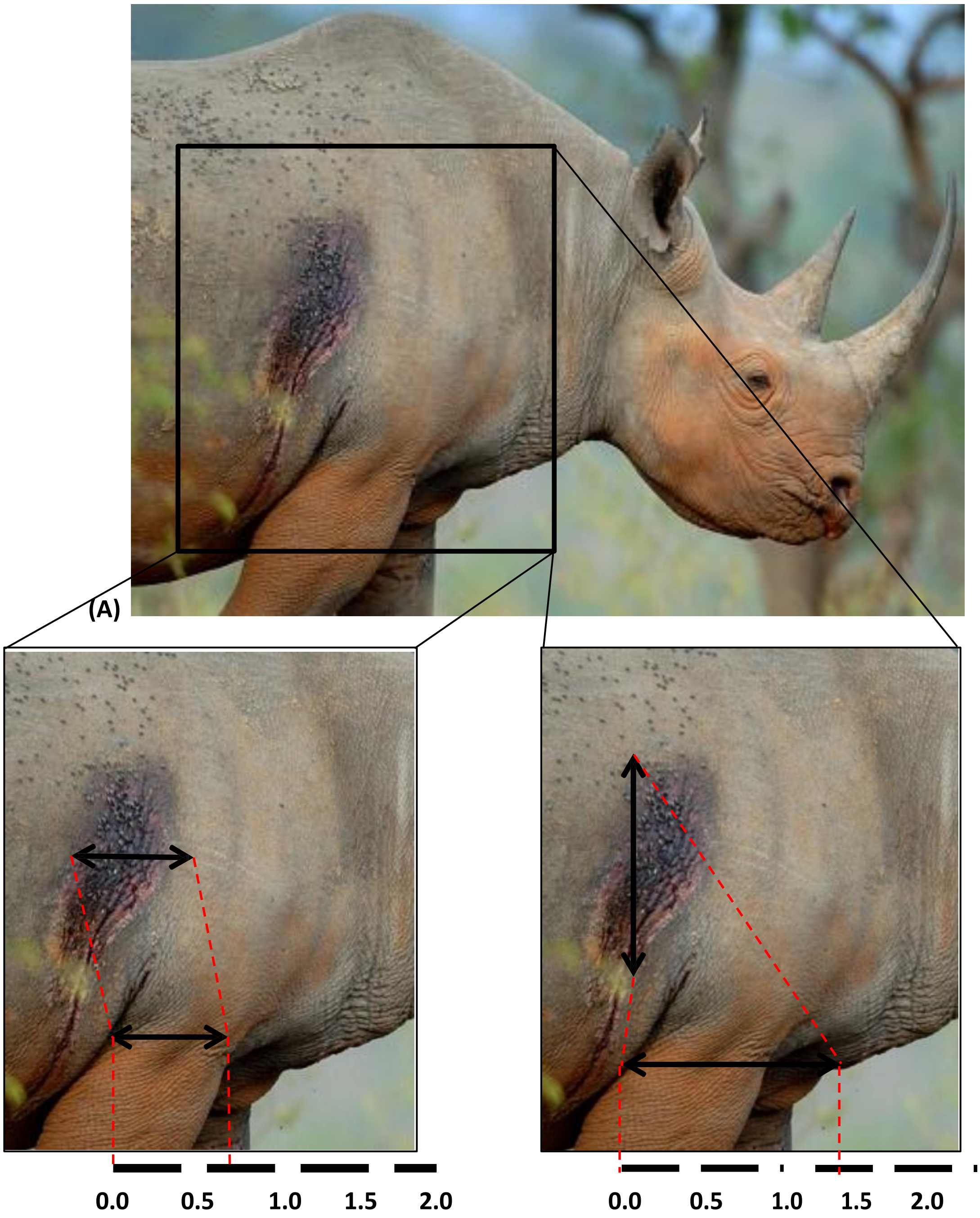
Figure 1 (A). The body regions and specific anatomical features to be observed when assessing a rhino's condition and **(B)** The appearance of black rhino for all body condition scores. Note that I used 0.5 interval scores whenever I deemed a condition score to be between whole number condition categories.

Entire Lesion Area (ELA) using area of an oval) = (W*L)*0.8
= (22cm) x (27cm) x 0.8
= (20.8cm) x (36.4 cm) x 0.8
= **± 594 cm^2**

Proportion (%) of lesion estimated haemorrhaging (PH) = 60%

Lesion Severity (LS) = ELA: 594cm^2 x PH: 0.6
= **356cm^2**

Figure 2. Example of a direct measurement of the right filarial lesion of a breeding age female black rhino in Hluhluwe-iMfolozi Park, South Africa (Photograph by Roan Plotz).



(B) Width (W) = estimated as 0.8

(C) Length (L) = estimated as 1.4

Entire Lesion Area (ELA) using area of an oval) = (W*L)*0.8
= (0.8 x26cm) x (1.4x26cm) x 0.8
= (20.8cm) x (36.4 cm) x 0.8
= **± 606 cm^2**

Proportion (%) of lesion haemorrhaging (PH) = 80%

Lesion Severity (LS) = ± 80%
= 0.8 x 606 cm^2 **= 486 cm^2**

Figure 3. Diagram showing how the novel method for attaining remote estimates of lesion area (cm^2) was used to estimate entire lesion area (ELA), proportion of the lesion haemorrhaging (PH) and lesion severity (LS) (Photographs by Dale Morris).

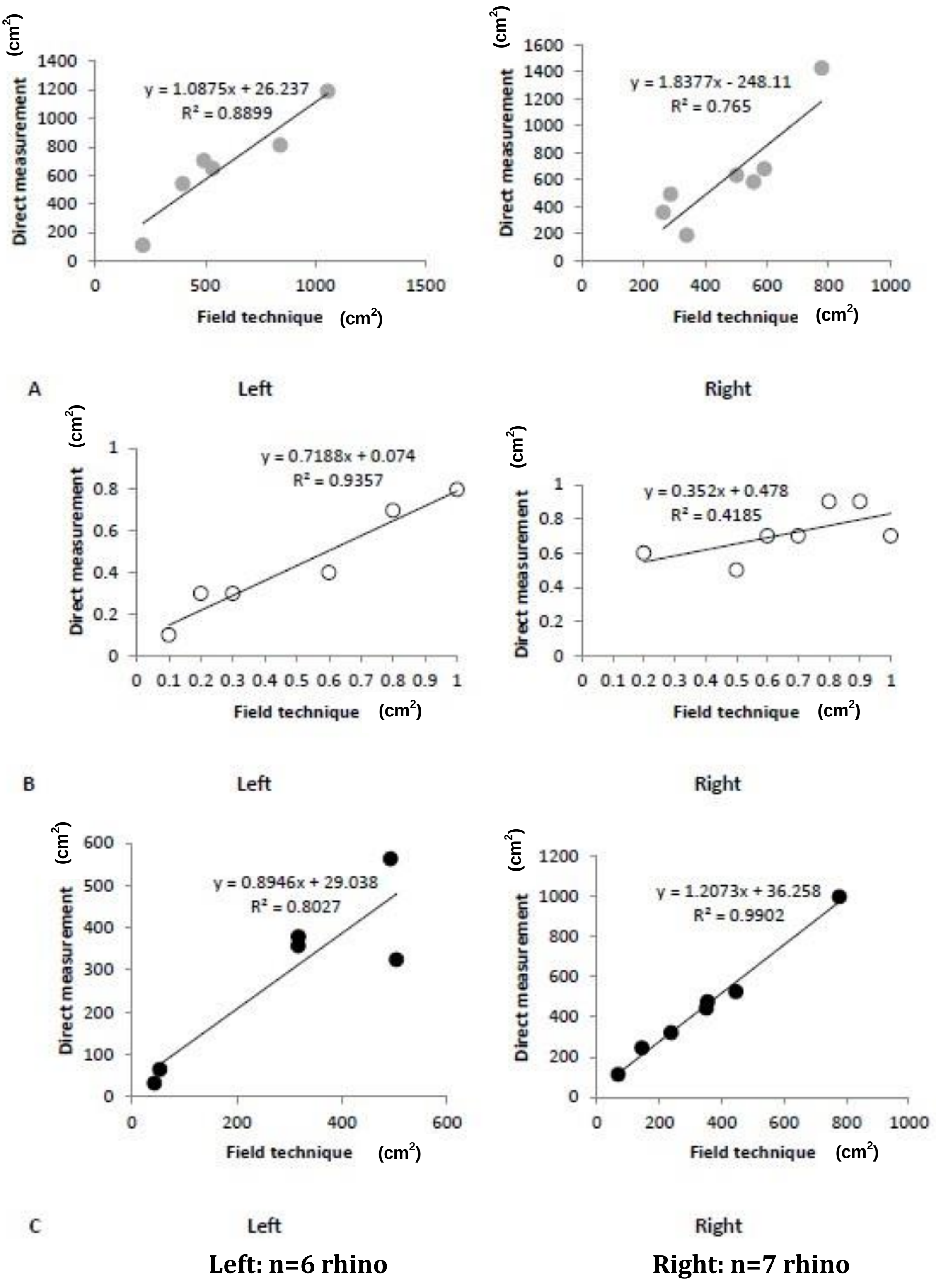


Figure 4. Comparisons between the left (n=6) and right (n=7) anterior flank filarial lesion estimates using direct (ruler measured) and the novel field based technique to calculate **(A)** entire lesion area (ELA), **(B)** estimated percentage that the lesion was haemorrhaging (%) and **(C)** lesion severity (LS), calculated as the area of the ELA (lesion severity = lesion area * % haemorrhaging).

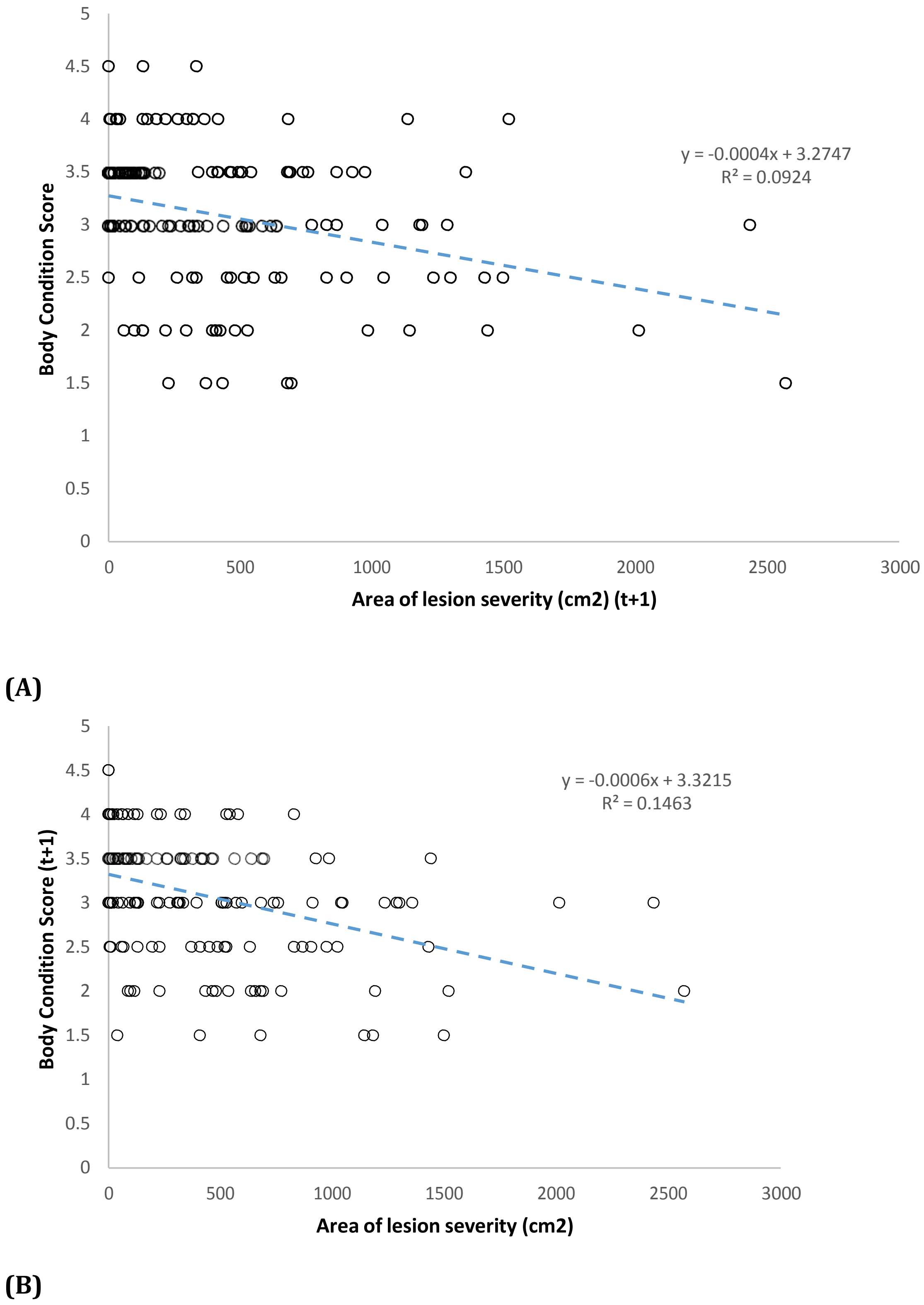


Figure 5. The temporal correlation between **(A)** filarial lesion severity estimates in future (t+1) with previous estimates of body condition (t) and **(B)** body condition scores in future (t+1) with previous estimates of lesion severity (t) in adult (≥ 6 years) black rhino.

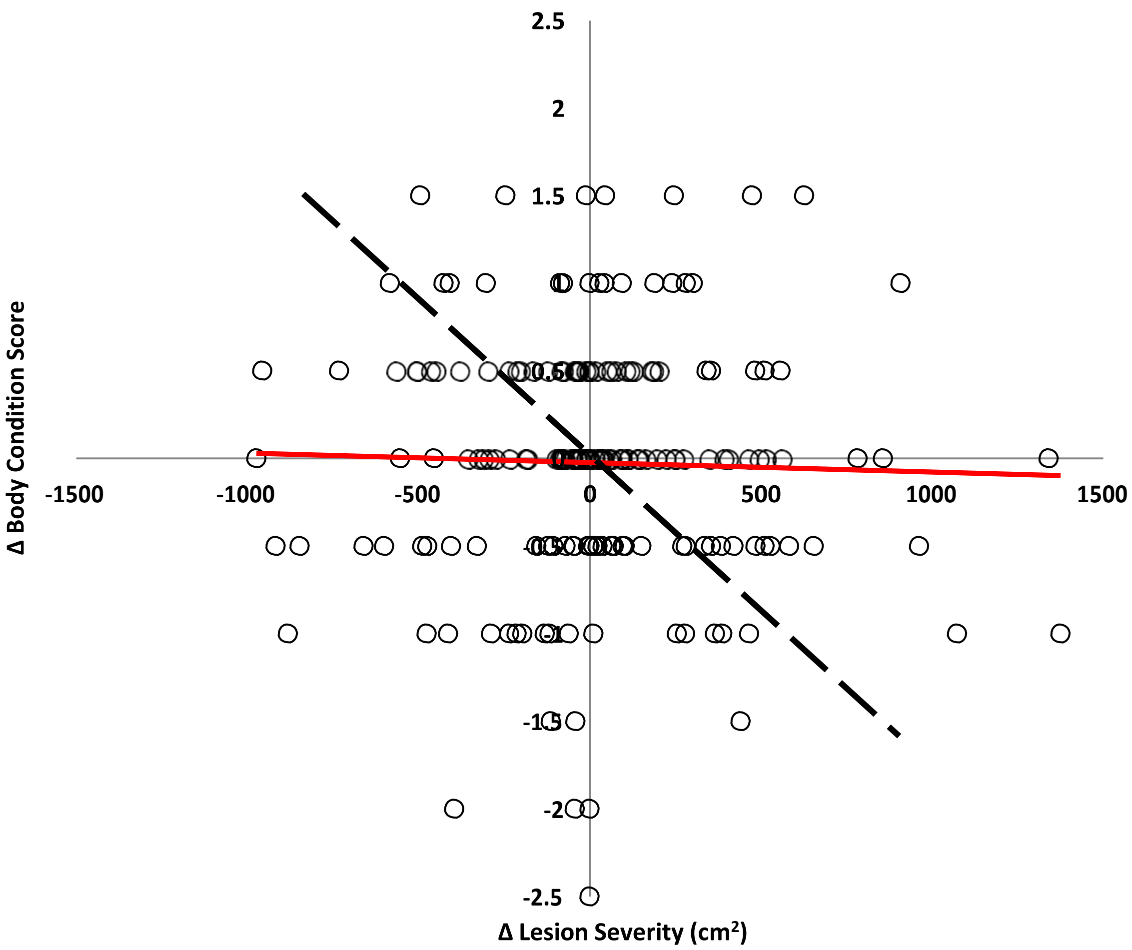
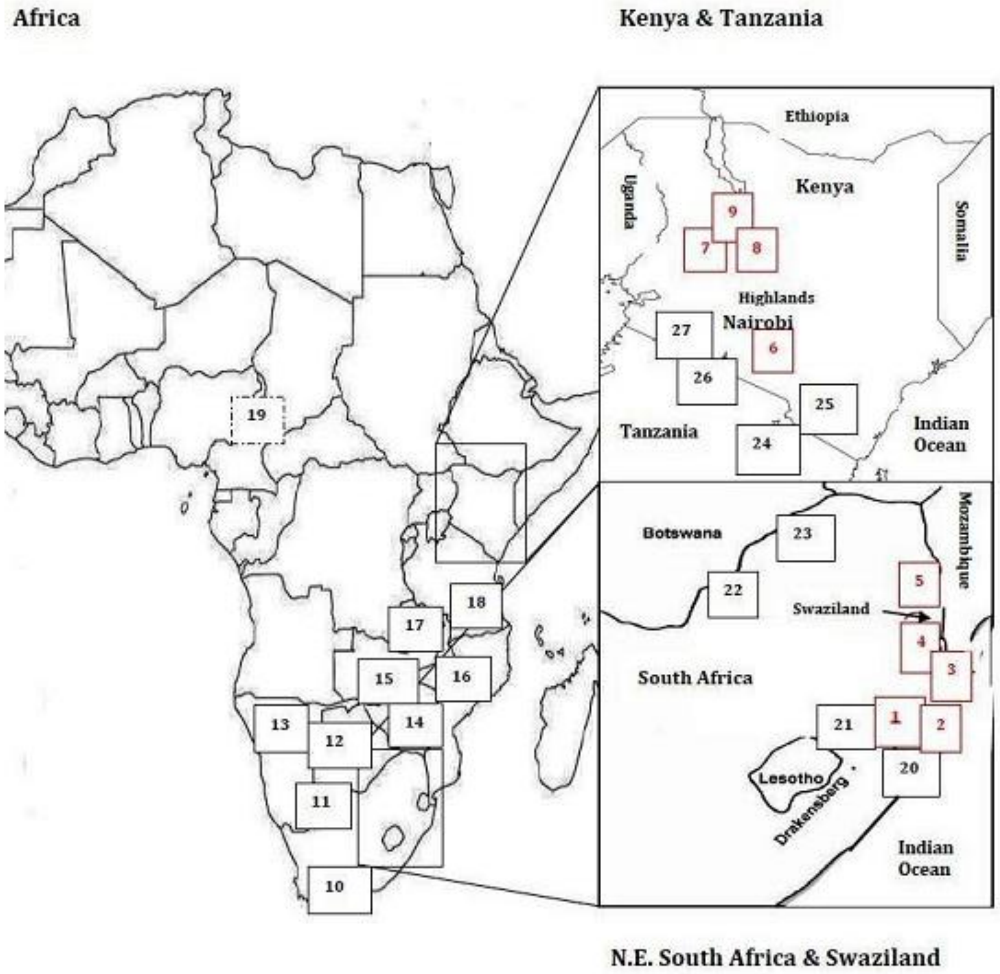


Figure 6. The correlation between changes (positive or negative) in body condition against concurrent changes (positive or negative) in filarial lesion severity.
Note the dashed black line is the relationship I predicted to see if one factor (i.e., LS or BC) was having a significant effect in change on the other. The red line indicates the relationship I determined and suggests that neither factor are associated with significant change over the other.



Current black rhino reserves / sanctuaries with:

Map/Key	**Filarial Lesions Present:**
1	Hluhluwe-iMfolozi Park, Zululand [b,c,d,e,h,j,q,s,v,x]
2	uMkhuze G.R.[b], Phinda-Munyawana Conser., Pongola G.R., several private reserves E. KZN, Thanda G.R. & Zululand Rhino Reserve[v], Zululand [c,d,e,q,s,v,x]
3	Ithala, Ndumo & Tembe G.R.'s, Zululand [c,d,k,q]
4	Mkhaya G.R., Swaziland [d]
5	Kruger N. P. (southern section), Mpumalanga [d,e,f]
6	Nairobi N.P., Highlands [a,p]
7	Aberdares & Lake Nakuru N.P. [a,p]
8	Solio, Laikipia Dis. & Mt Kenya N.P, Highlands [a,p]
9	Meru N.P. & Lewa W. Conser., Highlands [d,p,w]
	Filarial Lesions Absent
10	Addo E.N.P., Great Fish River R., Karoo N.P., Kwandwe & Shamwari P.G.Rs., E. & W. Cape [e,h,i,k,s]
11	Augrabies Falls N.P., Tswalu Kalahari R., & Vaalbos N.P., N. Cape, South Africa [j,k]
12	Botswana Reserves [d]
13	Damaraland, Etosha N.P. & Kakaoland/Kunene Region, Namibia [d,f,q,x]
14	*Chirisa Safari Area, Hwange N.P.*[l] *Matabeleland*, Imire Safari Ranch [l,t] Malilangwe Priv. Wild. R.[t,u] of S.E. lowveld, Zimbabwe
15	*Matusudona N.P.*[l,t]*, Lower Zambezi River, Zambezi Valley, Zimbabwe,* [d,g,t]
16	Majete Wildlife Reserve, Malawi [m]
17	North Luangwa N.P., Zambia [f,j,n]
18	Selous G.R., Tanzania [o]
19	Bouba Ndijida N. P., Cameroon [r-EXTINCT]
20	Eastern Shores, iSimangaliso W. P., Zululand [c,k]
21	Weenen G.R., Midlands, KZN [c,d,u]
22	Madikwe G.R. & Pilanesberg N.P., N.W. Province [c,f]
23	Lapalala Wilderness, Marakele N.P., Sable Ranch, Thabo Tholo G.F., Limpopo Province, South Africa [d,h]
24	Nkhomazi G.R., Tanzania [d,h]
25	*Tsavo East & West Ecosystem, Kenya* [a]
26	Ngorongoro C.A. & Serengeti N.P., Tanzania [a,d,h,j,p]
27	Masaai Mara N.R., Kenya [h]

Figure 7. Map of current filarial lesion distribution in black rhino populations. Study Reserve underlined and reserves with lesions historically or uncertainty about filarial are listed under absent and highlighted in italics. Several reserves in same area are sometimes listed under one number and associated superscript letters link the verification sources.

Figure 7 source verification (references for map key): **a:** Mihok et al. 1996; R. Kock, pers. comm.; **b:** Shulz and Kluge 1960; Schulz 1961; Hitchins and Keep 1970; Skinner and Smithers 1990; **c:** D. Cooper, pers. comm.; **d:** P. Hitchins, pers. comm.; **e:** Authors, pers. obs.; **f:** M. Hofmeyr, pers. comm.; **g:** Kock, A.M. and Kock (1990); **h:** E. Smidt; **i:** P. Lent, pers. comm.; **j:** J. Shaw, pers. comm.; **k:** K. Buk, pers. comm.; **l:** C. Foggins and P. Law, pers. comm.; **m:** Craig Reid, pers. comm.; **n:** E. Sayer and N. Leader-Williams, pers. comm.; **o:** F. Alpers and Kes Smith, pers. comm.; **p:** P. Morkel, pers. comm.; **q:** Skinner and Smithers 1990; **r:** Lagrot et al. (2007); **s:** A. Stringer, pers. comm.; **t:** R. du Toit, pers. comm.; **u:** S. Clegg, pers. comm.; **v:** D. Airton, pers. comm.; **w:** Mutinda et al. 2012; Ndeereh et al. 2012; **x:** W. Linklater, pers. comm.

Additional reference notes for each region / reserve (numbers correspond to key in Fig. 6):

1 – 9: Filarial lesions in Kenya (*D. b. michaeli*) have different appearance to those in the southern populations (*D. b. minor*) (this chapter of thesis; P. Hitchins & P. Morkel; pers. comm; Hitchins and Keep 1970 cf. Ndeereh et al. 2012; Mutinda et al. 2012). Lesions are generally smaller and less severe in Kenya populations (e.g., typically 5cm wide) compared to 30 cm wide or more in HiP, South Africa (this chapter and Hitchins and Keep 1970). **1:** Filarial lesions first identified as such in Hluhluwe Game Reserve by Shulz and Kluge (1960). HiP black rhino have the largest and most severe filarial lesions of any reserve in which they currently occur (D. Cooper, pers. comm.; this Chapter of thesis; Hitchins and Keep 1970; S. Clegg pers. comm). Malilangwe Wildlife Reserve, in south eastern Zimbabwe, imported 28 black rhino from KZN between July and September 1998. These rhino came from a number of areas including Hluhluwe, iMfolozi- Masinda and Ithala. Almost all the rhino showed some filarial scarring. Most prominent lesions were seen in HiP- Masinda animals. **2:** Authors pers. obs: Lesions present on black rhino in this nearby region typically less severe than HiP black rhino (see this chapter and photograph of lesion on Phinda black rhino (Chapter 6). **3:** S. Clegg (pers. comm): Malilangwe Wildlife Reserve, in south eastern Zimbabwe, imported black rhino from KZN between July and September 1998. These rhino came from a number of areas including Itala. Almost all the rhino showed some filarial scarring. Most prominent lesions were seen HiP- Masinda animals and less significant lesions were seen in the Itala animals. **4:** Photograph by Nico J. Van Strien of an adult black rhino in Mkaya Game Reserve., Swaziland, with filarial lesion on left flank behind shoulder [online access: http://www.rhinoresourcecenter.com/images/Black-Rhino-Mkhaya-Swaziland_i1200176681.php] **5:** Black rhino and fly vector *R. dutoiti* were locally extinct in K.N.P. (and the old Transvaal) by 1936 (Penzhorn 1971; Skinner and Smithers 1990). *R. dutoiti* was re-introduced with the dung of translocated female black rhino from HiP, proliferating throughout southern K.N.P. from Pretoriuskop to Mooiplaas (Skinner ad Smithers 1990). **6 – 9:** The only areas in Kenya where one can still see large clouds of *Rhinomusca brucei* flies on rhino.

Mihok et al. (1996) also discovered previously thought to be southern African specific filarial vector *R. dutoiti* in Nairobi N.P. & Laikipia District Highlands (i.e., Solio Ranch). They confirmed it against Zumpt's (1950) museum samples of *R. dutoiti* and *R. bruscei*. **8** (and **25**)**:** Laikipia District black rhino (Solio Ranch) had their filarial skin lesions clear up shortly after being relocated to Lugard Falls in Tsavo (Mihok et al. 1996). **14:** R. du Toit and S. Clegg (pers. comm.): Zululand (KwaZulu-Natal) black rhino had their filarial skin lesions clear up within 1-year after being relocated to Malilangwe Private Wildlife Reserve (i.e., within 1-year). P. Law (pers. comm.): in Sinamatella I.P.Z. of Hwange N.P. saw possible filarial lesion on only one black rhino just before October rains. Noted this to be unusual because no other black rhino's had such a wound, probably not filarial (e.g., intraspecific fighting wound). R. du Toit, (pers comm): Black rhino from Chitake region Zambia, with pink saucer sized lesions of unknown cause, lost these lesions when translocated to Zimbabwe lowveld. **15:** R. du Toit (pers. comm.): Currently, re-introduced black rhino into Matusudona N.P. do not have lesions.

To prevent local extinction from intense poaching led to the relocation of the Matusodona population to Zimbabwe Lowveld from 1989 – 1991 (Baudron et al. 2011). Kock and Kock (1990) recorded supposed filarial skin lesions on the necks of black rhino in this population but no typical behind the shoulder lesions were detected (Silberman and Fulton 1979; Skinner and Smithers 1990). Some adult filarial nematodes (unidentified sp.) found in a few tissue biopsies but not in rhino blood samples. **17:** N. Leader-Williams (pers. comm.): observed rhinos closely in Luangwa Valley, Zambia, for 5 years, and never saw the characteristic filarial wounds along the flank the rhinos. Also mentions that some rhinos did occasionally have a circular pink patch of skin on their neck from unknown cause. R. du Toit (pers. comm.): In the Chitake area of the Zambezi Valley, which is relatively more humid compared to some other areas of the Zambezi Valley, black rhinos typically had circular pink lesions on their chests at the base of the throat and never saw any on their flanks. The chest lesions were about the size of coffee mug's base. **18:** F. Alpers (pers. comm.): during 2000-2005 headed the Selous black rhino protection and research project. During intense tracking, flying to find the last several remaining rhinos, saw around 5 different individuals and recalled no filarial lesions. Also Kes Smith (over 3 years) over the same period says that there were no filarial lesions on the black rhino. **19:** *D. bicornis longipes*: probably extinct (Lagrot et al. 2007; IUCN 2013). Photographs in Lagrot et al. (2007) from 1977 showed no lesions on flank (black and white photograph). Also, colour photograph (cover of Pachyderm vol. 27) by Dr Hubert Planton (Wildlife Veterinarian, Cameroon) of female in same park without lesions on either side of anterior flank.

21: P. Hitchins (pers. comm.): Confirms absence of black rhino host specific blood sucking fly *Rhinomusca dutoiti,* the vector for *S. dinniki* (Zumpt 1964). **25:** Historically, Tsavo and nearby Amboseli N.P. had black rhino with filarial skin lesions (Shulz and Kluge 1960; Spinage 1960; Schulz 1961; Parsons and Sheldrick 1964; Tremlett 1964) and the fly vector - East African blood sucking fly (*Rhinomusca bruscei*) (Parsons and Sheldrick 1964). Subsequent lesion disappearance coincided with dramatic population reductions from mass poaching, large scale habitat changes and local extinction of *R. brucei* (Mihok et al. 1996). Round (1964) first identified the pathology of the filarial nematode as *Stephanofilaria dinniki* from Tremlett's (1964) lesion biopsies in Tsavo. Black rhino in Amboseli National Park, Tanzania, are now locally extinct (R. Kock, pers. comm.).

Table 1: Mean direct (16 samples) and field estimates (208 samples) of entire lesion area (ELA), severity (LS) and healed area (LH) according to season and sex of rhino. Note: w=width and h=height.

Direct Measurements		**LS (cm^2)**	**ELA (cm^2)**	**BC**
Female (n=14)	*Winter*	262 ± 40	441 ± 36	_*
			Range (cm): w=11-37; h=18-47	
Field Estimates				
Male (n=11)	*Summer*	342 ± 125	383 ± 129	3.7 ± 0.04
	Winter	181 ± 38	288 ± 49	3.3 ± 0.09
Female (n=24)	*Summer*	338 ± 54	474 ± 60	3.0 ± 0.10
	Winter	412 ± 43	540 ± 47	3.0 ± 0.07

* *BC scores were not dependably obtainable from sedated rhino that were lying down (see Reuter and Adcock 1998).*

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5.

Interactions between Red-billed Oxpeckers and Black rhinoceros in Hluhluwe-iMfolozi Park

A red-billed oxpecker feeds on the filarial lesion of a black rhinoceros in Zululand, South Africa (Photograph: Louise van Stuyvesant Meijn)

ABSTRACT

The degree of parasitism or mutualism between species can depend upon the biotic and abiotic environment. Different or changing environments alter the behaviour of interacting species and make the nature of interspecific relationships conditional. Although the conditionality of oxpecker-ungulate interactions has been demonstrated in captivity it remains to be tested in the wild. Field observations were conducted comprising 782 instantaneous samples (52.1 hrs) of the interactions between red-billed oxpeckers (*Buphagus erythrorhynchus*) and black rhino (*Diceros bicornis*) with large haemorrhaging anterior flank filarial (*Stephanofilaria dinniki*) lesions in Hluhluwe-iMfolozi Park, South Africa. Oxpeckers preferentially occupied rhino's lesions to feed and spinal area to perch more than three times as much as areas of tick attachment. I also show black rhino to be extraordinarily tolerant of oxpeckers – the only known wild host, even when they fed upon their lesions. Rhinos may tolerate oxpeckers parasitism because the birds are also sentinels, but this remains to be quantified. Oxpeckers use of filarial lesions during winter when tick abundance is low appears to reflect recent findings that ectoparasite abundance controls the conditional nature of oxpeckers tick versus blood foraging habits. Further research is needed to determine if oxpeckers actually provide black rhino with increased vigilance from sentinel behaviour. If oxpeckers sentinel behaviour was found to benefit black rhino, it raises an intriguing possibility. Oxpeckers might be using this additional benefit to ameliorate the cost of lesion feeding and manipulate black rhino's tolerance thereof.

KEYWORDS: conditional mutualism, parasitism, filarial lesions, ectoparasites, *Diceros bicornis minor*, *Buphagus erythrorynchus*, Ixodid ticks, *Stephanofilaria dinniki*, interspecific interactions, seasonal tick variability.

INTRODUCTION

The benefits and costs of inter-specific interactions can, and often do, vary depending on the ecological setting (Holland *et al*. 2002). Changes in temperature, rainfall and resource availability can influence the behaviour of interacting species and the outcome of their interaction. Circumstances where the outcomes of the interspecific interaction are context-dependent have been termed conditional (Bronstein 1994 a, b). At any given time or place many interspecific relationships may fall into one category, but conditionally shift along a dynamic continuum from mutualism to commensalism to parasitism when conditions change (Cheney and Cote 2005; Plantan 2009).

A well-known example of an interspecific interaction that exhibits conditional outcomes is Africa's oxpecker (*Buphagus* sp.) – ungulate 'cleaner' relationship. Some studies of oxpecker parasitic feeding behaviour (Weeks 1999; 2000) are at odds with other studies that report oxpeckers to mainly be cleaner mutualists, removing ectoparasites from hosts (Nunn et al. 2011). Some studies report red-billed oxpeckers (*B. erythrorynchus*) conditionally feeding on the blood and tissue of host species rather than ectoparasites at a cost to their hosts (Keet et al. 1997; Plantan 2009; Plantan et al. 2012). Animals with open wounds and sustained blood loss risk secondary infections and suffer immune system and body condition suppression (Anderson and May 1981). It is unlikely that that a stable mutualistic relationship can be maintained if oxpeckers revert to parasitism, even if occasionally (Bronstein 1994a, b). In response, hosts control parasitic oxpeckers by adopting several oxpecker displacement behaviours (intolerance) such as running, shaking, horning, rolling and lying down (Watkins and Cassidy 1987; Keet et al. 1997; Plantan 2009; Bishop and Bishop 2014).

Oxpeckers, however, also have the potential to employ their own behaviours to avoid conflict during interactions such that net positive benefits are maintained. For example, anti-predator alarm calling behaviour by oxpeckers has frequently been reported by Africa's indigenous peoples and modern hunters (Craig 2009). Oxpeckers that reliably alarm call at hosts' predators may reduce or even mitigate host intolerance towards costly blood feeding by oxpeckers. The use of behaviours other than ectoparasite removal to mitigate conflict and costs in cleaning interactions is not uncommon. Cleaner wrasse (*Labroides dimidiatus),* for example, adopt pre-conflict behavioural strategies (e.g., tactile stimulation) that allows them to avoid conflict during interactions with coral trout (*Plectropomus leopardus*) (Bshary and Wurth 2001; Grutter 2004).

Studies have so far been unable to quantify whether oxpecker foraging behaviour is unambiguously mutualistic or parasitic (cf. domestic cattle; Weeks 1999, 2000; Plantan 2009). This appears, in part, to be due to a historically narrow research focus. Previously, studies have almost explicitly focussed on one question: are oxpeckers targeting ticks or blood on their hosts (e.g., Hart and Hart 1990; Weeks 1999, 2000; Nunn et al. 2011)? Plantan's (2009) study provides insights which highlight why the outcomes of the oxpecker-ungulate relationship remain ambiguous. Plantan (2009) manipulated tick levels on a captive host to show that oxpeckers favoured ticks as long as they remained abundant, gradually switching to blood as ticks became scarce. Moreover, Plantan (2009) went on to observe that several wild host species were highly intolerant towards oxpeckers that tried to target their wounds. Hosts appeared to use rejection behaviours to shift negative parasitic interactions with oxpeckers towards a mainly mutualistic relationship with net positive benefits.

Field experiments in a captive setting, while illuminating, do not account for the plethora of variables that form part of oxpecker-ungulate interactions in the wild. For example, tick abundance fluctuates considerably in the wild (Randolph 2008) and some hosts may be better than others at rejecting blood feeding oxpeckers. Some hosts might also gain increased vigilance from oxpeckers sentinel behaviour, while others have no need for it. The potential for conditional outcomes in any one oxpecker-ungulate interaction remains enormous.

Unravelling the true conditional nature of any one oxpecker – ungulate interaction in a wild setting will require the ability to concurrently investigate host tolerance towards oxpeckers while factoring in all known costs and benefits. This remains a difficult prospect because oxpecker hosts are large fast moving mammals that range over large distances (Weeks 2000).

HiP black rhino, however, may be the ideal oxpecker host to test the conditional nature of oxpeckers interactions. Observing whether oxpeckers forage on ticks or blood is made easier by the fact that black rhino have three main sites of tick attachment (nostrils, anogenital region and ears) (Penzhorn et al. 1994) and chronic lesions caused by the filarial nematode *Stephanofilaria dinniki* (Schulz 1961; Hitchins and Keep 1970). Black rhino are also the oxpecker host most associated with oxpeckers sentinel behaviour (Leslie 1876; Schenkel and Schenkel-Hulliger 1969; Craig 2009). Finally, accounting for tick abundance is also made easier because HiP occurs in the Northern KwaZulu-Natal (KZN) region where Ixodid ticks undergo a reproductive diapause that for the most part makes them absent during the cool dry winter months (i.e., April to October; Mushi et al. 1997; Walker et al. 2000; Horak et al. 2003, 2009). Thus, HiP occurs in the southern fringes of red-billed oxpeckers distribution where tick abundance can, to a reasonable extent, be reliably estimated.

For oxpeckers blood has similar nutritional benefits to ticks (Plantan 2009). Therefore lesions offer a significant resource opportunity for oxpeckers to target (Spinage 1960). Oxpeckers that are sympatric with black rhino populations that have lesions could gain significant nutritional advantage if they increased their time and energy towards providing sentinel behaviour that mitigates conflict if and when they target lesions. Ostensibly, oxpeckers that target lesions might also to a certain extent divide their time utilising rhino's spinal region, as it is well documented to be the location on rhino that oxpeckers gather as sentinels and alarm call (Leslie 1876; Schenkel and Schenkel-Hulliger 1969; Weeks 1998; Authors pers. obs.).

Determining whether or not red-billed oxpeckers are mutualists or parasites with black rhino will depend upon whether there is a net positive benefit or cost respectively to the host. There are two possible benefits i.e., 1. removal of ectoparasites and 2. increased vigilance (sentinels). There is one cost i.e., feeding on lesions (parasitism). This study aims to be the first step in understanding how oxpeckers utilise black rhino in a region with seasonally fluctuating tick abundance and in turn how black rhino respond to this utilisation. To this end I compared the proportion that red-billed oxpeckers utilised regions of tick attachment (*benefit 1*), filarial lesions (*cost 1*) and the spinal region (*benefit 2*) during the cool dry winter months when ticks were scarce. To understand whether black rhino might be mitigating costly foraging by oxpeckers I also recorded black rhino's tolerance towards visiting oxpeckers. I present results from more than 50 hours of observations of black rhino-oxpecker interactions, the largest data set of its kind.

MATERIAL AND METHODS

Details about the study site, study populations, radio transmitter installation and capture techniques including approvals are described in **Chapter 1** and the material and methods section of **Chapter 2** of this thesis. For this study, 10 adult female black rhino in HiP's southern and central regions (Mbhuzane, Masinda and Nqumeni), eight accompanied by calves and two without calves, were fitted with horn implant radio-transmitters installed during May of 2007 and 2008 and then released. Juvenile black rhino (< 6 years) that did not yet have filarial lesions were excluded from sampling.

HiP's 218 (Clinning et al. 2009) black rhinoceros are the favoured hosts of red-billed oxpeckers (Sutterheim 1980). Yellow-billed oxpeckers are locally extinct (*B. africanus*) (Stutterheim and Brooke 1981). HiP black rhino display 100% prevalence of lesions on both anterior flanks approaching adulthood (> 6 years) (Hitchins and Keep 1970 and **Chapter 4** of this thesis).

Oxpecker Utilisation Patterns

Oxpeckers interactions with the 10 focal rhino were observed fortnightly from May 2007 to July 2009 during the cooler dry winter months (Apr-Sep).
Field observations were made using Nikon 8 x 40 binoculars and/or a Bushnell field spotting scope (20 x 60). Observations were typically conducted between 50 to a 100 m from the rhino. Study rhino were selected for observation between dawn and dusk in random sequence without replacement and tracked using VHF radio-telemetry and a TR-4 receiver (Telonics, Inc., Mesa, AZ, USA). Direct sightings were achieved by initially obtaining a signal from high elevation and walking up towards each rhino on foot until the focal rhino was sighted. While tracking, I also obtained sufficient fortuitous observations of an additional 17 female and 9 male rhino because they had unique ear notches (Hitchins 1978).

Samples were evenly distributed throughout the daylight hours and all weather conditions except during heavy rain. Sampling included instantaneous scan samples (ISS) (Altmann 1974) every four minutes for at least one hour or until the rhino moved irretrievably out of view.

In order to compare the proportion that oxpeckers utilised different areas of black rhino, I divided each individual rhino into five distinct body regions and tallied oxpeckers presence or absence for each ISS. The five regions were: 1=the left and right anterior flank filarial lesions, 2= the area perceived as most suitable for sentinel behaviour- spine and head; 3=three tick attachment sites of ears, anogenital region and nostrils; 4= upper body region (rest of upper half of body) and 5=lower body region (rest of lower body region) (Fig. 1B).

For every ISS the number and location of red-billed oxpeckers (Fig. 1A) on each black rhino were recorded. The locations oxpeckers selected on rhino for each ISS were assigned to the three rhino body regions associated with the three oxpecker activities I was interested in: (1) tick foraging that occurs mostly from the three main tick attachment sites around the anogenitals, ears and nostrils (Penzhorn et al. 1994), (2) tissue and blood parasitism that occurs mostly from anterior flank filarial lesions and (3) sentinel behaviour, if it occurs, would occur best from elevated areas like the head and spine from neck to rump. For comparison, locations of oxpeckers were also recorded as being on the upper or lower body.

Accounting for the visibility of body regions

Attempting to compare oxpeckers utilisation of each of the five body regions I designated created a dilemma for subsequent analysis. For instance, black rhino are very large and mobile mammals. Although conspicuously large mammals, in reality each of the black rhino's five designated body regions were not evenly visible across the entire 782 ISSs completed. For example, an oxpecker might be seen visiting a lesion during one ISS, but this could not be determined for the next because the rhino had moved and vegetation had blocked the view of the lesion. When not visible, any of the black rhino body regions could have had oxpeckers utilising it but remain undetected. If this bias was not taken into account then the higher, more visible region of black rhino, like the spine, might seem to have higher rates of oxpecker utilisation mainly because it was easier to observe the spinal region and see visiting oxpeckers than it was for rhino's lower regions (e.g., legs). Thus, for every ISS I recorded whether each region was entirely visible to me and whether oxpeckers were present or absent at each visible region.

Black rhino intolerance behaviour

During ISS I recorded whether or not black rhino were intolerant towards oxpeckers as has been observed for black rhino in captivity, buffalo with lesions in the wild, and several other wild ungulate species (Keet et al. 1997; McElligot et al. 2004; Plantan 2009; Bishop and Bishop 2014). Any observed rejection attempts by rhino towards oxpeckers was also recorded. In McElligot's et al. (2004) study of black rhino in captivity, as well as other ungulates, the use of tails, shaking ears or head or stomping their legs, shaking their flanks, spinning around or running away whenever oxpeckers perched on or near these body parts or lesions were evidence of host intolerance (Keet et al. 1997; Weeks 1999). Intolerance behaviour by rhino was assigned according to oxpeckers' location and, thus, the three oxpecker activities I was investigating: cleaners (i.e., tick preference), lesions (i.e., blood-parasitism) and or sentinels (i.e., along spine).

Estimating Tick abundance

In southern Africa the favoured tick species by oxpecker undergo seasonal (winter) reproductive diapause due to fluctuations in temperature and rainfall (Tyson and Dyer 1975; Berkeley and Linklater 2010) and are less available (Mulilo 1985; Mushi et al. 1997; Horak et al. 2003, 2009; Randolph 2008). HiP is at the southern fringe of oxpeckers' distribution and occurs in a region where Ixodid tick populations in Northern KZN are well documented to be absent during the cool dry winter months (i.e., April to October; Mushi et al. 1997; Walker et al. 2000; Horak et al. 2003, 2009). Thus, seasonal tick availability can to a certain extent be estimated.

Analyses

A total of 69 sampling periods covering 57 hr 06 mins (i.e., 856 ISS's) were made. I excluded 5 hours comprising 75 ISS's because rhino were entirely obscured by vegetation or moved out of sight during sampling. Therefore, 52 hours of observations were used for analyses, averaging 2 hours per rhino (n=26). As already mentioned, rhino body regions were not equally visible during sampling periods. To illustrate the inconsistency in visibility during ISSs, I analysed the number of ISS's a region was visible to me, regardless of whether or not an oxpecker was present, and divided it by the total number of ISSs conducted (i.e., 782 = 52 hrs) (Fig. 2). The proportion that each of the five designated body regions were utilised by oxpeckers (i.e., oxpecker present), relative to its visibility, was calculated and tested for significance using Chi-square tests. Tests were two-tailed with a significance level of $p<0.05$ (SPSS Statistics v. 16.0). In summary, I calculated oxpecker utilisation for each body region using this formula: The total number of ISSs where oxpeckers were observed to be present at a body region divided by the number of ISSs that the region was visible (i.e., it could be observed whether or not oxpeckers were present at the region) (Fig. 3).

Finally, to test the hypothesis that oxpeckers lesion-feeding should elicit host intolerance (McElligot et al. 2004; Plantan 2009; Plantan et al. 2012; Bishop and Bishop 2014), I recorded each dislodgement attempt of oxpeckers by rhino (i.e., intolerance) and related it to where the oxpecker was when intolerance behaviours were initiated. The proportion of response behaviours that were tolerant responses and rejection responses were calculated and tested for significance using Chi-square tests.

RESULTS

Visibility of black rhino body regions

As a proportion (%) of ISSs there was considerable variation in the level of visibility for each of the five black rhino body regions. Location visibility in descending order: Spine and hump for sentinel behaviour 78% (i.e., 37 of 52hrs), upper body 55% (i.e., 29 of 52hrs), tick sites 46% (i.e., 24 of 52hrs), lower body 26% (i.e., 14 of 52hrs) and filarial lesions 20% (i.e., 11 of 52hrs) (Fig. 2).

Oxpecker utilisation patterns relative the visibility of each body region

Oxpeckers were observed to be present on rhino for a total of 6 of the 52hrs (11%). Proportionate to a body regions visibility, filarial lesions were more than three times more likely to be visited by oxpeckers than all other locations on a rhino's body. Oxpeckers utilised black rhino body regions over 6 hours in descending order: filarial lesions 15% (i.e., 2 of 11hrs), spine and hump 5% (i.e., 2 of 37hrs) which were utilised more than expected based on their visibility to the observer (χ^2=102.3, df=4, p=0.0). The three tick attachment sites 4% (i.e., 1 of 27hrs of anogenital region, 1%; ears, 2%; nostrils, 1%), upper body 2% (i.e., 1 of 29hrs) and the lower body region 1% (1 of 14hrs) were all utilised significantly less than expected based on their visibility to the observer (Fig. 3).

Black Rhino Intolerance Behaviour

Evidence of rhino intolerance towards oxpeckers, even when oxpecker foraged at rhino's lesions, was never observed in the 52 hours and 782 ISSs of behavioural observations obtained. The only intolerance behaviour by black rhino towards a bird I witnessed was directed at three Cape glossy starlings (*Lamprotornis nitens*) that attempted to feed at the right filarial lesion of an adult female black rhino. Oxpeckers were absent at the time and the rhino raised and stamped her right foreleg repeatedly, twitched and shook her flanks and spun her body around in a circle.

DISCUSSION

For a symbiosis that is normally regarded as a classic example of a cleaner mutualism (Koenig 1997; Nunn et al. 2011), the significantly lower rate of tick than lesion foraging in this oxpecker-black rhino partnership is startling. From the oxpecker's perspective, blood was clearly the main resource as foraging efforts were almost entirely directed at black rhino's filarial lesions. In the absence of comparative studies in other wild settings and species, it is uncertain whether such overt blood exploitation by oxpeckers is specific to rhino or predominates among all of its wild hosts. What I do know, however, is that black rhino's tolerance of parasitic oxpeckers is rare amongst the more than 20 other wild oxpecker hosts (Keet et al. 1997; Plantan 2009; Bishop and Bishop 2014).

Johnstone and Bshary (2002) and Plantan (2009) showed that in both marine and terrestrial cleaning symbioses, client hosts control the relationship by terminating interactions with cleaners that are exploitative (parasitic). For example, Plantan (2009) reported that several ungulate host species were highly intolerant of blood feeding oxpeckers. Similarly, buffalo in Kruger National Park (KNP), South Africa that also developed large chronic filarial lesions (caused by *Parafilaria bassoni*), use their horns to vigorously displace oxpeckers away from their lesions (Keet et al. 1997). Black rhino in HiP were tolerant while African buffalo (*Syncerus caffer*) in KNP were intolerant of parasitic oxpeckers. Buffalo appear to be very effective at preventing oxpeckers from gaining access to lesions in ways also available to rhino (Keet et al. 1997). Thus, free-ranging black rhino appear to be unusually tolerant of avian parasitism and the reason requires further investigation.

Results from this study also appear to confirm that oxpeckers clearly alternated time on black rhino between occupying locations on rhino that afford greatest sentinel capabilities and feeding at lesions (Fig. 3). Oxpeckers have well documented alarm calls (e.g., *Krsss*, Weeks 1998). Whether they are alternating lesion foraging with sentinel behaviour to promote tolerance requires an understanding of whether black rhino actually receive increased vigilance from hosting oxpeckers. Some studies have been unable to determine if oxpeckers increase vigilance for domestic cattle (Weeks 1998). It may be that only rhino respond and benefit from oxpeckers alarm calls as they are more visually impaired and asocial than most other species and exposed to greater human and non-human predation pressure (Schenkel and Schenkel-Hulliger 1969; Plotz and Linklater 2009; Beech and Perry 2011). The results of this study suggest that oxpeckers appear to be mitigating the costs of their parasitic foraging behaviour by increasing the anti-human vigilance for black rhino. The fact that free-ranging black rhino appear to be the only known species (McElligot et al. 2004; Plantan 2009; Bishop and Bishop 2014) that entirely tolerates parasitic feeding behaviour by oxpeckers adds weight to this argument.

Evidence for the conditionality of mutualisms

My results appear to substantiate the variability of cleaner mutualisms based on ectoparasite abundance (i.e., conditional mutualisms; Becker and Grutter 2005; Cheney and Cote 2005). Although seasonal tick densities are well documented in KZN, my results were limited by the fact that I was unable to measure tick densities on rhino. I also could not confirm whether oxpeckers time on the spine and head truly reflected sentinel behaviour by the birds. To be certain that seasonal fluctuations of ticks are conditionally regulating parasitic and sentinel behaviour by oxpeckers, tick densities should be measured in future (cf. Plantan 2009). Also, to determine whether oxpeckers are manipulating black rhino's tolerance of their parasitic feeding behaviour requires further investigation. Experiments which test for improvements in predator detection distances and tolerance levels of oxpeckers other host species is also needed.

The key to understanding the variable nature of the African oxpecker-ungulate cleaning symbioses appears to be the environmental mechanisms that drive temporal and geographical variation in tick abundance (cf. Bansemeer et al. 2002; Cheney and Cote 2005). These mechanisms are not well understood but may also vary according to host's tick levels that are affected by body condition, nutritional quality affecting immunity and thus rates of tick infestation (Gallivan and Horak 1997).

Future areas of research: is blood a bridging resource for oxpeckers?

Oxpeckers might have used blood from lesions, in part, as a bridging resource to meet their nutritional requirements during a period of seasonal tick scarcity. Tick density and distribution is regulated by seasonal rainfall patterns in KZN (Mushi et al. 1997; Horak et al. 2003, 2006, 2009; Randolph 2008). In the more temperate climes of southern Africa, like KZN, ticks undergo a reproductive diapause in winter, when conditions are unfavourable to tick development (i.e., colder and drier; Randolph 2008). In light of this, HiP's location and rainfall patterns are likely to make it a marginal habitat for tick-feeding red-billed oxpeckers. Moreover, Walker et al. (2000) and Horak et al. (2009) indicate that in North-East KZN, where HiP is located, preferred oxpecker tick species of *R. appendiculatus* and *R. (Boophilis) decloratus*, are at best only sparsely present or displaced all together by *B. microplus* - a much less favoured tick species by oxpeckers (Plantan 2009). Oxpeckers are known to be especially reliant on ticks during the summer months in South Africa, when the birds have their breeding season (Stutterheim 1982; Craig 2009; Plantan 2009). Our results suggest that black rhino and their filarial lesions may be a bridging resource allowing red-billed oxpeckers to persevere in an otherwise marginal habitat for the ectoparasites preferred by oxpeckers. To understand this better will require this study to be repeated in the wet summer months (October to March) to see if a period of greater tick abundance shifts oxpeckers foraging habits back towards tick feeding. Lesions may also be too valuable a resource for oxpeckers to ignore especially when black rhino tolerate such behaviour.

In summary, our results may explain oxpeckers differential foraging behaviours between hosts (Hart et al. 1990; Weeks 1999, 2000; Nunn et al. 2011) and why oxpeckers on hosts in drought conditions or in captivity, where tick abundance is lower or absent, are seen to parasitise more than tick forage (e.g., lowveld region Zimbabwe, Weeks 1999, 2000; captive zoo, McElligot et al. 2004).

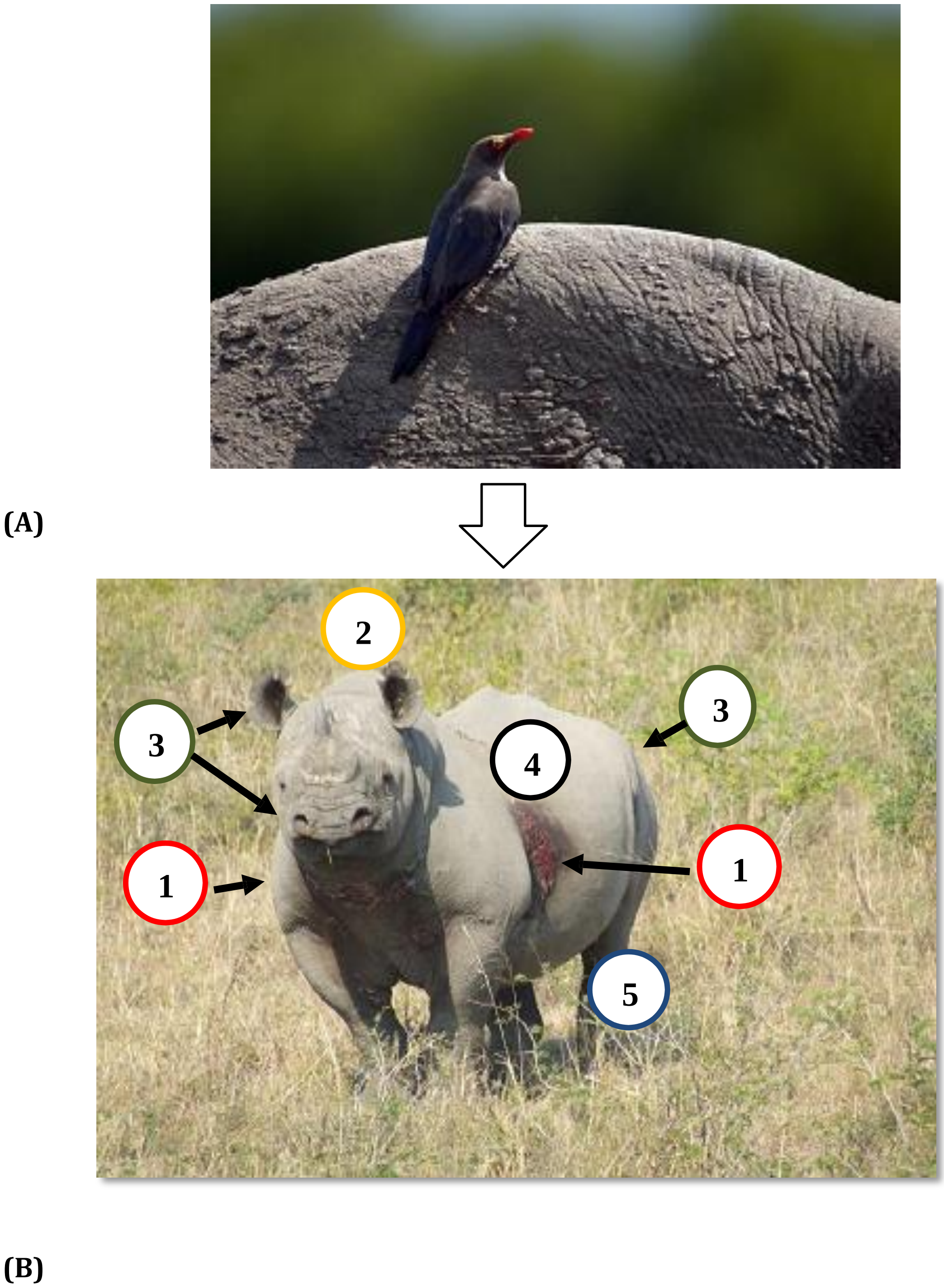

Figure 1 (A). Red-billed oxpecker on the spinal region of black rhino in Hluhluwe-iMfolozi Park, a useful location to act as sentries (photograph by Dale Morris). **(B)** Oxpeckers seen visiting rhino were marked as present in one of these five body regions (as marked in Fig. 1 A): 1=the left and right anterior flank filarial lesions, 2= the area perceived as most suitable for sentinel behaviour- spine and head; 3=three tick attachment sites of ears, anogenital region and nostrils; 4= upper body region (rest of upper half of body) and 5=lower body region (rest of lower body region) (photograph by Roan Plotz).

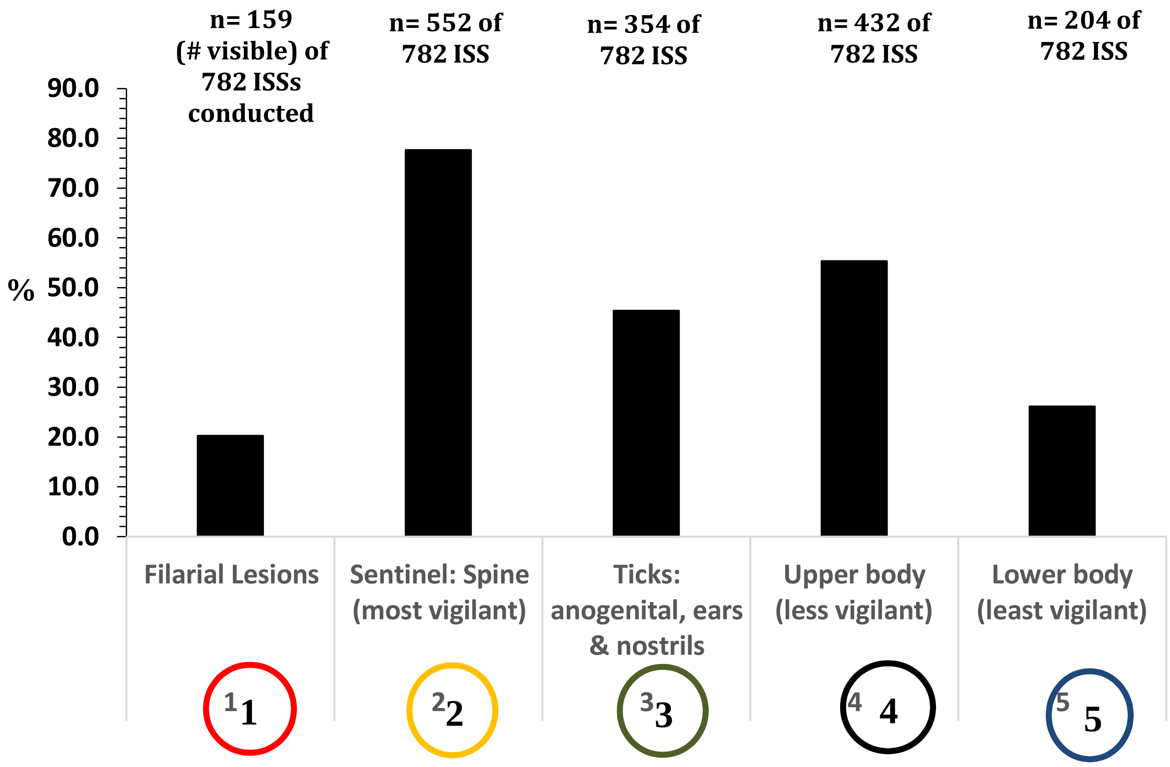

Figure 2. The proportion (%) of total instantaneous scan samples (ISSs) that each of the five selected rhino body regions were visible to the observer (i.e., # ISS samples location visible divided by 782 ISSs - the total observation time). Note that each of the five regions are presented as the proportion (%) that each was visible out of the 782 samples conducted (e.g., 159/782 samples means that this region was visible 20 % of ISSs).

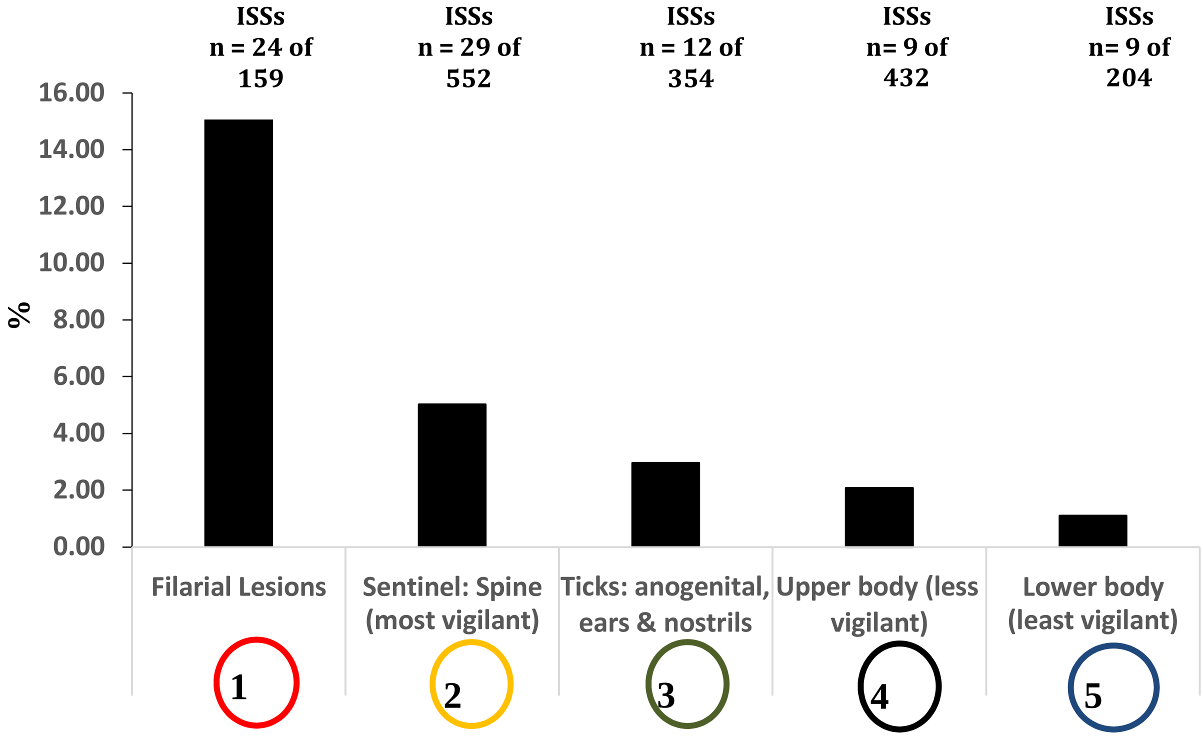

Figure 3. The proportion (%) of instantaneous scan samples (ISSs) that oxpeckers were observed at each black rhino body region, relative to each body regions visibility (e.g., at filarial lesions oxpeckers were seen for 24 ISSs out of the 159 ISS where lesions were visible to the observer – other body regions were more visible: see Fig. 2 for relative visbilities of each body region). Although oxpeckers presence at all five black rhino's body regions are represented together on one graph, proportions do not collectively add up to 100%, as measures for each regions are independent of each other due to their varying levels of observability.

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6.

The Rhino's Guard

Black rhino adopting a characteristic alarm response (ears and head up facing downwind) after red-billed oxpecker alarm calls (Photograph by Jed Bird)

ABSTRACT

Africa's oxpeckers (*Buphagus* sp.) are suspected of sentinel behaviour where their alarm calls are thought to warn their ungulate hosts to approaching predators. Anecdotal reports from human (*Homo sapiens*) hunters propose that oxpeckers regularly alerted grazing animals to their approaches as well. In fact, the Swahili name for the red-billed oxpecker (*B. erythrorynchus*) is "*Askari wa kifaru*" and translates as the rhinos' guard. Hence, I tested the widely held but unproven belief that red-billed oxpeckers warn black rhino (*Diceros bicornis*) of approaching predators. Eighty-four unconcealed approaches by a person to seven marked adult female black rhino were monitored. I recorded detection probability and approach distances that could be related to the presence- absence and number of oxpeckers resident on the rhino and corresponded to their alarm calling. When oxpeckers were absent black rhinos were able to detect the person on 23% (11of 48) of occasions at an average detection distance of 23 ± 2 m (average 1 SE). However, oxpecker presence increased the rhino's detection rate to 100% (36 of 36) and more than doubled detection distance to 59 ± 6 m. The 36 detections were an immediate response to an oxpecker alarm call. There was a significant positive relationship between increasing number of oxpeckers on a rhino's back and detection probability and distance. Finally, I recorded that black rhino alerted by oxpecker's alarm calls typically re- orientated to face in a downwind direction (34 of 36). Thus, I show experimentally that oxpeckers acted as sentinels for rhino against a human predatory threat but that rhino also covered their sensory blind spot i.e. downwind, where they cannot smell and from where humans stalk rhino. This study validates the traditional name of the red-billed oxpecker as the rhino's guard.

KEYWORDS: conditional mutualism, parasitism, sentinels, *Buphagus erythrorynchus*, *Diceros bicornis minor*, *Homo sapiens*, approach trials, tolerance, vigilance

INTRODUCTION

"Black rhino can only see what is immediately before it, so if one hunts downwind of it, it is not difficult to approach within a few paces. But the tick bird who sees all the better…alerts the rhino by a shrill warning cry…"Leslie (1876)

Mutualism and parasitism are not static conditions of an interspecific relationship but extremes of a dynamic continuum (Herre et al. 1999; Del-Claro 2004). The degree of parasitism or mutualism between species can depend upon the biotic and abiotic environment (Bronstein 1994; Bronstein and Barbosa 2002). Changes in temperature, rainfall and resource availability can influence the symbiotic behaviour of interacting species. Apparently mutualistic cleaning relationships, where an organism removes a third species (e.g., ectoparasite) from the host, are prone to become parasitic when conditions change (Cheney and Cote 2005). Such relationships involving three or more species are for this reason progressively termed "conditional mutualisms" (e.g., cleaner – client fish- gnathiids, Cheney and Cote 2005; oxpecker-ungulates-Ixodid ticks, *Buphagus* sp.; Plantan 2009). However, the role of a third or more species as the condition which modifies a mutualism has received little attention (but see Cheney and Cote 2005; Plantan 2009; Plantan et al. 2012).

The apparently mutualistic oxpecker (*Buphagus* sp.) - ungulate relationship is folklore but a largely untested hypothesis. Oxpeckers on ungulates are thought to be feeding on ectoparasites, particularly ticks and blood-sucking flies.

Oxpeckers are also suspected of sentinel behaviour where their alarm calls warn ungulates of danger (Alexander 1836; Leslie 1876; Schenkel and Schenkel- Hulliger 1969; Dean and MacDonald 1981; Craig 2009). Human (*Homo sapiens*) hunters report oxpecker alarm calls alerting grazing animals to their approach (Craig 2009). Alternatively, herders regarded oxpeckers as the killers of domestic stock for opening and feeding from the ungulate's wounds, hence the origin of their genus name *Buphaga* – Latin for ox-eater (Attwell 1966; Craig 2009). Thus, whether oxpeckers are mutualists or parasites of ungulates is debated (Weeks 2000; Nunn et al. 2011).

Mutualisms are characterised by net positive benefits to participant species (e.g., cleaner fish, *Labroides dimidiatus*; Grutter 1999). Central to the uncertainty about the oxpecker-ungulate relationship has been that the bird's supposed anti- parasitic cleaner benefits to ungulates (i.e., ectoparasite removal, Nunn et al.

2011) might be secondary to their own parasitism because they also feed on host tissue and blood, especially from extant wounds (Keet et al. 1997; Weeks 1999, 2000; Plantan 2009). Moreover, oxpecker sentinel behaviour and anti-predator benefits to their hosts have largely been inferred from anecdotal observations (e.g., van Someren 1951; Pitman 1956; Spinage 1962; Attwell 1966; Schenkel and Schenkel-Hulliger 1969) and the only empirical test was inconclusive (e.g., Weeks 1998). A major challenge, therefore, has been to quantify whether oxpeckers benefit their ungulate hosts.

In the cleaner-client fish mutualistic association cleaner fish cooperate by gleaning ectoparasites from client fish. But cleaners actually prefer to cheat by feeding on tissue and mucus (Bshary et al. 2008). Mutualisms that are subject to such exploitation lead to conflicts of interests between partner species that disrupt the relationship (Bronstein 2001). Although such conflicts of interest are common in interspecific associations, they are generally controlled (Douglas 2008). Client fish jolt their bodies or terminate interactions by swimming away in response to cheating behaviour (Bshary and Grutter 2002; Bshary et al. 2008). Similarly, when oxpeckers turn to wound-feeding, hosts will adopt rejection behaviours to deter exploitation and reinforce the mutualistic tick-feeding actions of oxpeckers (e.g., Keet et al. 1997; Plantan 2009; Bishop and Bishop 2014). Several large herbivores, for example, will run through the bush, use their horns, kick their legs, swing their tails, and roll on the ground to dislodge the birds (Watkins and Cassidy 1987; Keet et al. 1997; Weeks 1999; Bishop and Bishop 2014). Another factor that may control conflict and a host's tolerance verse intolerance behaviour are additional services. For example, in order to promote interspecific tolerance for their otherwise costly klepto-parasitic foraging behaviour, fork-tailed drongos (*Dicrurus adsimilis*) will specifically alarm call at predators that threaten their host but not themselves to cause hosts to flee a food source to gain access to additional resources (e.g., dwarf mongoose,

Helogale parvula; Ridley et al. 2007). Sharpe et al. (2010) even observed drongos go so far as to assist mongooses in the mobbing of puff adders (*Bitis arietans*) and an African civet (*Civettictis civetta*), neither of which posed a threat to drongos.

Are wound feeding oxpeckers that alarm call able to gain access to a typically intolerant host's wounds? The critically endangered (IUCN 2012) black rhino is a favoured oxpecker host (Stutterheim 1980) and most associated with oxpeckers' anti-predator alarm calling behaviour, especially towards people (Alexander 1836; Leslie 1876; Schenkel and Schenkel-Hulliger 1969; Goddard 1970, 1973; Skinner and Smithers 1990). Moreover, black rhino (*Diceros bicornis*) appear to remain tolerant of oxpeckers that predominately feed at lesions (See **Chapter 5**). Despite their large size (i.e., *c.* 1000kg; Owen-Smith 1988), black rhino are solitary living animals with poor eye sight easily stalked undetected (e.g., Leslie 1876; Goddard 1970). Indeed, organised groups of humans with projectile weapons like spears began successfully hunting rhino from the late Pleistocene (i.e., < 50 000 years; Leslie 1876; Klein 1977; Owen- Smith 1987; Diamond 1997). However, in the last 150 years, people with rifles hunted rhino to the brink of extinction from over 1 million to *c.* 2100 by 1992 (Emslie 2008). Despite fenced reserves and paramilitary protection of rhino populations, both illegal and legal hunting of rhino still occurs (Nelson 2006; Beech and Perry 2011). In comparison, adult black rhino are largely immune to non-human predation (Owen-Smith 1987), although young calves remain vulnerable, e.g.; lion, *Panthera leo*, and spotted hyena, *Crocuta crocuta*; Plotz and Linklater 2009). Oxpeckers anti-predator alarm calls could therefore be directed at both human and non-human predators.

The Swahili name for oxpeckers: "*Askari wa kifaru*" translates to 'the rhino's guard'. Experienced observers describe being able to walk undetected to within a few paces of black rhino without oxpeckers in attendance and when approaching from downwind (Leslie 1876; Goddard 1970, 1973). In contrast, others report black rhino becoming alert and orientating downwind in an apparent response to red-billed oxpeckers (*B. erythrorynchus*: hereafter oxpeckers) alarm calls (described as hissing *Krsss* by Weeks 1998) directed at humans (e.g., Alexander 1836; Leslie 1876; Schenkel and Schenkel-Hulliger
1969). Humans have never been known to hunt oxpeckers (Craig 2009).

Nonetheless, oxpeckers may significantly improve black rhino's anti-human vigilance (i.e., detection rate and distance) to promote tolerance in black rhino for improved access (i.e., host tolerance) to the remarkable resource that is the filarial lesion.

Parasitism generally imposes a cost to their victims, yet many victims appear to tolerate their parasites (Radford et al. 2011). I suggest that in the case of the black rhino-oxpecker interaction this may be because oxpeckers (parasites) provide black rhino (hosts) with the mitigating benefit of increased predator vigilance even though they appear to predominately parasitise their lesions (see **Chapter 5**). I designed this study to define one aspect of the complex African oxpecker-black rhino relationship that has not been looked at before i.e., increased vigilance from sentinel behaviour. I hypothesised that if rhino respond to oxpeckers alarm calls, then they ought to orientate towards their sensory blind spot (i.e., downwind: as suggested by Schenkel and Schenkel-Hulliger 1969). To this end, an anti-human vigilance approach trial was implemented. A field experiment that improved upon Schenkel and Schenkel-Hulliger's (1969) more subjective observations was conducted to test for the mutualistic sentinel behaviour of oxpeckers on black rhino. Human approaches to individually known black rhino were made and the influence of oxpecker alarm calling on rhino vigilance and human-predator detection evaluated. In this work I tested whether oxpecker sentinel behaviour improves black rhino's anti-human vigilance such that human detection rate and distance is enhanced.

Determining whether or not red-billed oxpeckers are mutualists or parasites with black rhino will depend upon whether there is a net positive benefit or cost respectively to the host. There are two possible benefits i.e., 1. removal of ectoparasites and 2. increased vigilance (sentinels). There is one cost i.e., feeding on lesions (parasitism). In **Chapter 5** I demonstrated that oxpeckers targeted lesions but were tolerated by black rhino while doing so. In this study I focussed on whether oxpeckers increased the vigilance of black rhino (*benefit 2*), which has yet to be investigated. This benefit has not yet been looked at before. To achieve this I conducted multiple field approach experiments where I, as an observer, monitored the approaches of a human 'threat' such that I could determine whether oxpecker presence made a significant impact on the approach distances achievable by the human threat.

MATERIAL AND METHODS

Study site and population

Approximately 200-300 black rhino (*D. b. minor*) (Clinning et al. 2009) are sympatric with red-billed oxpeckers in HiP (Stutterheim 1980). HiP's red-billed oxpecker population size is not known but they are regularly seen foraging on several ungulates, including black rhino and their lesions (Hitchins and Keep 1970; Stutterheim 1980). Yellow-billed oxpeckers (*B. africanus*) are locally extinct (Stutterheim and Brooke 1981). Incessant hunting of rhino by humans with rifles during the 19th century motivated the proclamation of the then separated Hluhluwe and iMfolozi Game Reserves in 1875. HiP now holds one of only two remaining endemic *D. b. minor* populations the other being nearby Mkhuze Game Reserve.

HiP's spotted hyena population (excluding cubs) has been estimated at 321 individuals (Graf et al. 2009). The average spotted hyena density in HiP is relatively high for southern Africa, but intermediate if compared to East African areas (Graf et al. 2009). Following local extinction in 1958 the first lone male lion re-entered the iMfolozi Game Reserve (Southern half of HiP), followed by two females in 1965 (Anderson 1981; Grange et al. 2012). By the 1980s approximately 60 lions had been recorded (Maddock et al. 1996). Between 2003 and 2004, the total lion population declined from 80 to 61 (Trinkel et al. 2008), but had rebounded to 114 by 2008 and reached an estimated 200 individuals in 2010 (Grange et al. 2012). Unchecked human hunting of all ungulates in HiP resumed for thirty years (*c*. 1920 to 1950) after de-proclamation and the black rhino population was as low as *c.* 85 individuals by 1935 (Emslie 2001). Since re- proclamation illegal rhino poaching in HiP has been sporadic but has increased again since 2008 (Beech and Perry 2011; Coniff 2011; Swart 2011). Hunting for live capture and translocation has occurred for both black and white rhino since 1961 when animals were chemically immobilised by tranquilizer dart delivered initially on foot, horseback or vehicle and more recently from a helicopter (Keep et al. 1969; Hitchins et al. 1972, Hitchins 1984; Emslie 2001).

For this study, ten adult female black rhino (eight with calves and two without) in HiP's southern and central region were chemically immobilised from a helicopter and had horn implant radio-transmitters installed (five rhino in May of 2007 and 2008 received combinations of Sirtrack Pty Ltd., NZ or Telonics, USA models installed using techniques described in Shrader and Beauchamp 2001; Linklater et al. 2006) and were then released. EKZNW Game Capture Team, including wildlife veterinarian, administered capture and drug protocols using chemical immobilisation from a helicopter (described in detail: Morkel and Kennedy-Benson 2007). This study made use of standard approved techniques to capture, monitor and approach black rhino the research methods were approved by Victorian University of Wellington, New Zealand (AEC) and EKZNW ethics approval (research permit number: ZC/ 101/1).

Human Approach Trials

Trials consisted of unconcealed human approaches to rhino and sampling by a stationary distant observer to quantify the influence of oxpeckers on rhino vigilance and human-threat detection. To improve the probability that human approaches were unconcealed and observations uninterrupted trials were only carried out in open habitat. Typically, open habitat was grassland or savannah with short to medium grass. Rhino were selected in a random sequence and located via radio-telemetry triangulation (see methods in Chapter 2). Approach trials began immediately after a black rhino was first sighted. The following attributes recorded by a stationary observer included the date, time, rhino identity and if they were alert (i.e., head and ears raised in vigilance posture; Schenkel and Schenkel-Hulliger 1969). Also, the number of oxpeckers resident on rhino and if alarm calls (e.g., *Krsss*; Weeks 1998) were heard. Finally, the observer recorded the wind direction and rhino's initial and alert orientations relative to prevailing wind directions (i.e., up, down or cross-wind – see Fig. 1). The orientation of a rhino was the direction anterior shoulders were facing. The wind directions and rhino orientations were recorded by envisaging 12 points of an analogue clock encircling the rhino with the static observer always at 6 o' clock. The following attributes were determined by the person approaching the rhino (hereafter threat). The distance attained to rhino before it was either alerted or it was unsafe for the threat to go any closer but they remained undetected by the rhino. Distances were measured by the threat using a Rangefinder (Leica Pty Ltd.). Each approach by the threat had the following sequence (Fig. 1 for illustration). First, the observer with a field spotting scope remained static at a fixed location (i.e., 6 o' clock). The threat starting from the observer at 6 o' clock moved at a constant walking speed in a wide arc to the left or right of the observer until they reached a position approximately perpendicular to the observer-rhino axis (i.e., 3 or 9 o' clock). From here the threat moved in a straight line toward the rhino. If at any point during a recording session the rhino became alert the suspected reason was recorded (i.e., oxpecker alarm call or noise or scent of threat) and the rhino's selected orientation after becoming alerted was recorded (Fig. 1). Schenkel and Schenkel-Hulliger (1969) report anecdotally that East African black rhino (*D. b. michaeli*) alerted by oxpeckers' alarm calls orientated downwind (i.e., facing where the wind was blowing towards), the direction that rhino predators are most likely to successfully stalk rhino. Human hunters typically approach rhino from downwind to remain undetected by rhino for longer. To determine whether a downwind orientation was selected preferentially or rhino with resident oxpeckers were able to

distinguish the exact direction of the approaching threat, the threat alternated 36 approach starts to individual rhino between 18 downwind and 18 crosswind (i.e., perpendicular to wind direction) directions. If during the approach the threat was not visible to the rhino, the distances to the observer too large to hear oxpecker alarm calls, or oxpeckers flew onto the rhino during the trial such that they had an aerial view of the threat the approach was not used in analyses.

Statistical Analyses

I conducted 85 approaches to rhinos, 48 without and 36 with oxpeckers resident on the rhinos. I analysed the percentage of occasions and average distance (m) the threat was detected by rhino. Similarly, the distance attained by the threat to each rhino with and without oxpeckers was related to the number of oxpeckers resident on rhino at the time of approach using a GLM ANOVA with a Log_{10} transformed data to compensate for significant positive skew in dependent variable distance and oxpecker frequency. Levene's test for equality of variances was performed to determine data normality.

The percentage proportion that black rhino selected a downwind orientation when oxpeckers were absent and present pre- and post- alarm call were calculated and tested for significance using Chi-square tests. Tests were two-tailed with a significance level of $p<0.05$ (SPSS Statistics v. 19.0).

RESULTS

Oxpeckers consistently alarm called during 36 threat approaches and rhino consistently reacted immediately to the calls. The dominant rhino response was to adopt an alert standing posture (36 of 36 approaches) regardless of prior position (e.g., lying) and direct flight in one of 36 approaches. Oxpeckers always came together on the hump and spine of black rhino immediately after alarm calls.

When oxpeckers were absent, black rhino detected (i.e., adopted alert posture) the approaching threat on 23% (11 of 48) of occasions with an average detection distance of 23 ± 2m. However, when oxpecker were present and alarm called, the rhino's human threat detection rate improved to 100% (36 of 36) at an average detection distance of 59 ± 4m. Oxpeckers always alarm called before their rhino hosts detected the approaching threat. Rhino without oxpeckers that detected the approaching threat appeared to do so acoustically (i.e., 6 heard the threat approach) and olfactory (i.e., 5 direction reversals and spoor detection by rhino). For each occasion that rhino detected the approaching human, the rhino orientated directly at the threat.

There was a significant positive relationship between the number of oxpeckers resident on rhino at the time of the approaching threat and the dependent variable detection distance ($R^2 = 0.6$; $n=85$, $F_{1,84}=12$, $p<0.0$; Fig. 2).

The interaction between the variables rhino identity (n=85, $F_{1, 9}$=0.3, p=0.1) and the number of oxpeckers resident on rhino was not significant (n=85, $F1_{1, 38}$ =0.8, p=0.7).

The dominant wind orientation selected by rhino after an alarm call was downwind (e.g., 94 %, 34 of 36) rather than crosswind (6 %, 2 of 36) or upwind (0%, 0 of 36), which was utilised significantly more than expected (χ^2=50.167, df =2, p=0.0; Fig. 3). Rhino faced the threat only when approaching from directly downwind (18 of 36) and never when approaching from crosswind (18 of 36; i.e., at right-angles to the observer rhino-axis). Also, black rhino typically selected to orientate in a downwind direction after they were alerted by the alarm calls of resident oxpeckers. Downwind orientations were selected considerably more by alert rhino compared to un-alert rhino when oxpeckers were absent, or when resident but had not yet alarm called.

DISCUSSION

Human approach trials demonstrate that red-billed oxpeckers significantly increase black rhino human-threat detection more than four-fold (i.e., number of detections) and more than doubled detection distance. Detection probability and distance also improved with increasing numbers of oxpecker. Black rhino responded to oxpecker's sentinel behaviour by directing their vigilance behaviour to their sensory 'blind-spot' (i.e., 95 % of post-alarm call alert postures orientated downwind). Clearly oxpeckers alarm calls do not include information about the direction of the threat.

Predation risk has been an important natural selection influence on animal behaviour. Mega-herbivores immune to large predators are nevertheless vulnerable to human predation – more so than smaller mammal species (Owen- Smith 1987, 1988). They are large conspicuous animals with a slow recruitment rate. The kind of anti-predator weaponry (e.g., size, horns and behaviour) to defend immature calves against carnivores would be ineffective against organised groups of humans hurling projectile weapons (Owen-Smith 1987).

Non-human predators, however, cannot be ruled out also contributing to the oxpecker-black rhino relationship especially because calves remain vulnerable to lions and spotted hyenas (Plotz and Linklater 2009).

Given the tendency for black rhino to orientate downwind after oxpecker alarm calls raises the question as to why? Humans are well known rhino predators known to hunt prey consistently from downwind (Leslie 1876; Owen- Smith 1987; Lamprecht 2009). Lions, contrary to popular belief, do not appear to take as much notice of wind direction when hunting and stalking ungulate prey. Schaller (1972), for example, documented over 300 hunts by Serengeti lions that approached from upwind as readily as they did from crosswind or downwind.

Proximity to vegetation cover appeared to determine the direction from which lion stalk prey. However, there is no data on the tactics lions use to hunt large and dangerous prey like rhino. Lions may hunt from all wind directions to disorientate rhino so that calves become easier to separate from their mothers. There is also no evidence that oxpeckers alarm call at non-human predators. All this remains to be tested before the findings of this study can be placed in its true context.

One inconsistency with the human hunter induced oxpecker-black rhino vigilance response remains: why do black rhino not flee immediately when they hear an oxpecker's alarm call? Rhino flee after detecting human scent but not the presence of other large predators (Owen-Smith 1987). When offered an oxpecker alarm call I found that black rhino stood alert facing downwind but only fled once.

Lion and spotted hyena density has been high enough to exert significant predation pressure to drive the evolution of black rhino-oxpecker anti-predator vigilance interactions (Graf et al. 2009; Grange et al. 2012). It therefore remains a possibility that that this oxpecker-black rhino vigilance interaction can also be explained by a role for other large non-human predators. Whether the oxpecker- black rhino mutualism is in response to long term or more recent intense human predation pressure in the last 150 years is unknown. Nevertheless, human overkill where numbers were reduced by 96% in the last 150 years raises the intriguing possibility (Beech and Perry 2011).

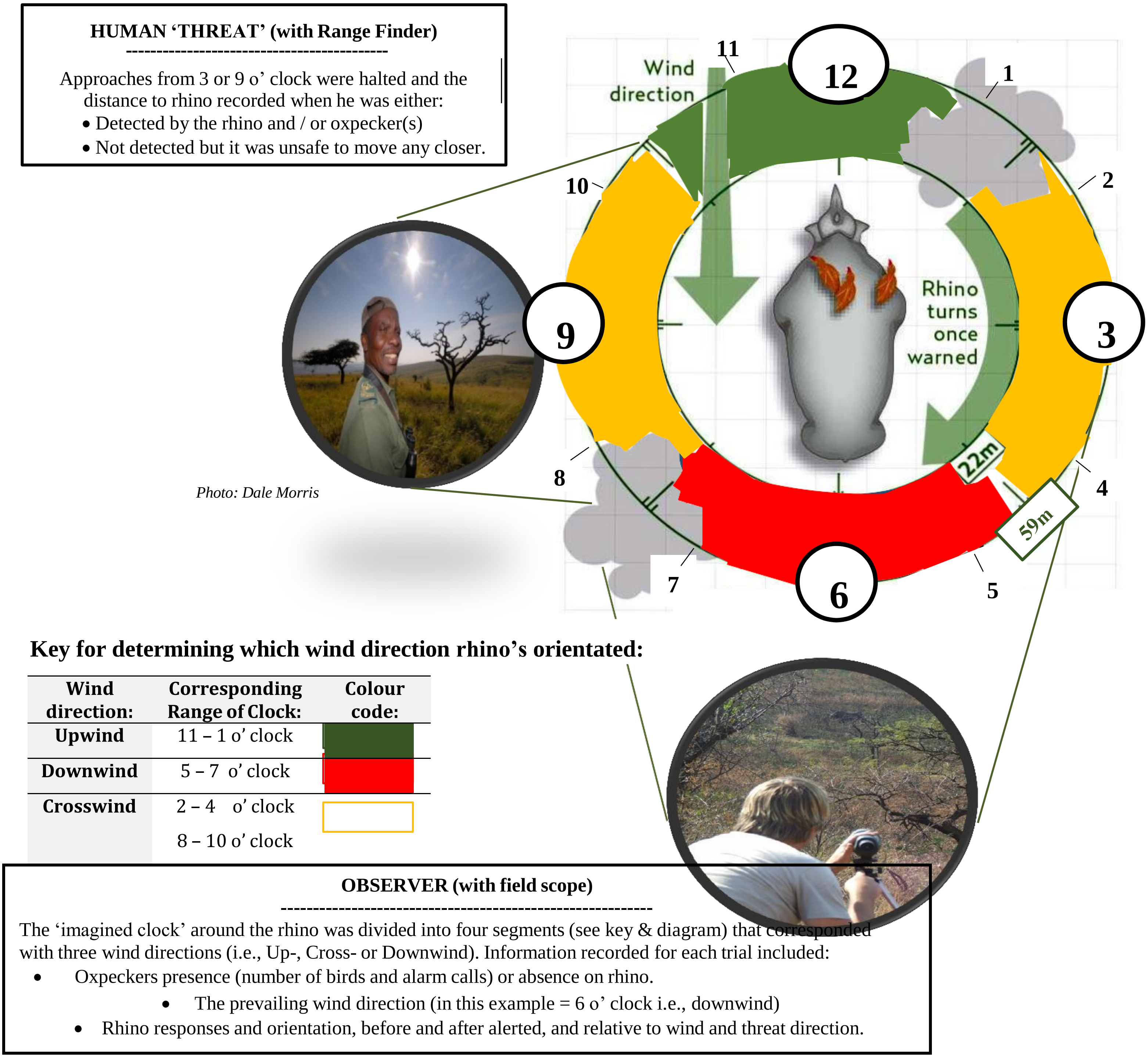
Mutualisms can develop between a bird and ungulate in less than 100 years. Recently introduced banteng (*Bos javanicus*) in have developed a cleaning

mutualism with the Torresian Crow (*Corvus orru*) in Northern Australia (Bradshaw and White 2006). However, a second inconsistency is the magnitude of the human detection distance improvement for black rhino. It is difficult to imagine that a 59m on average improvement has consequences for a modern hunter's ability to shoot a rhino, especially a rhino seemingly reluctant to flee after an oxpeckers alarm call. It is entirely possible that oxpeckers, resident on black rhino or in the air, alert black rhino to human presence at greater distances than I was able to quantify. The results of my human approach trials are likely to be conservative as trials were limited by my ability to accurately hear alarm calls and observe oxpecker-rhino-human interactions (i.e., typically not greater than 150m's). Whether oxpeckers provide black rhino with greater increases in detection rate and distance to humans and if it actually increases a rhino's
overall fitness (i.e., survival), still needs to be quantified.

CONCLUSION

My results in this chapter raise the intriguing possibility that rhino tolerate oxpecker parasitism (**Chapter 5**) because they are provided with increased vigilance. If this were so this relationship appears to provide benefits to both participants – blood for oxpeckers and increased vigilance for rhino. My findings involving wild co-evolved hosts are an important confirmation of recent research on the oxpecker-ungulate relationship in captivity which showed that the outcomes of oxpecker-host interactions were indeed highly variable and conditional (Plantan 2009; Plantan et al. 2012).

The oxpecker-ungulate interaction is inherently more complex than currently represented in text books – even those which acknowledge oxpecker parasitism (Craig 2009). Interspecific interactions, such as this apparent cleaning symbiosis, may therefore not be definable under a single definition. Any given interaction is likely to be conditional upon the ratio between costs and benefits that will be mediated by the species interacting, time and place.



HUMAN 'THREAT' (with Range Finder)

Approaches from 3 or 9 o' clock were halted and the distance to rhino recorded when he was either:

- Detected by the rhino and / or oxpecker(s)
- Not detected but it was unsafe to move any closer.

Photo: Dale Morris

Key for determining which wind direction rhino's orientated:

Wind direction:	Corresponding Range of Clock:	Colour code:
Upwind	11 – 1 o' clock	🟩
Downwind	5 – 7 o' clock	🟥
Crosswind	2 – 4 o' clock 8 – 10 o' clock	🟨

OBSERVER (with field scope)

The 'imagined clock' around the rhino was divided into four segments (see key & diagram) that corresponded with three wind directions (i.e., Up-, Cross- or Downwind). Information recorded for each trial included:

- Oxpeckers presence (number of birds and alarm calls) or absence on rhino.
  - The prevailing wind direction (in this example = 6 o' clock i.e., downwind)
- Rhino responses and orientation, before and after alerted, and relative to wind and threat direction.

Photo: Roan Plotz

Figure 1. Schematic of human-rhino approach trials. Imagining an analogue clock with the rhino at the centre, the observer (me) remained at 6 o' clock, while the human 'threat' (Bom) walked around to approach at right angles (at 3, or in this example 9 'o clock). Thus orientations selected by rhino relative to three wind directions could be determined (i.e., Up, Cross and Down-wind), both before (i.e., at first sighting) and during approaches. Typically rhino's noticed the threat at about 22m, but this increased to about 59m with rhino's turning to face downwind when oxpeckers were present to give the alarm. Diagram adapted from Plotz (2012, **App. 6**).Grey shapes at 1 and 7/8 o'clock represent vegetation.

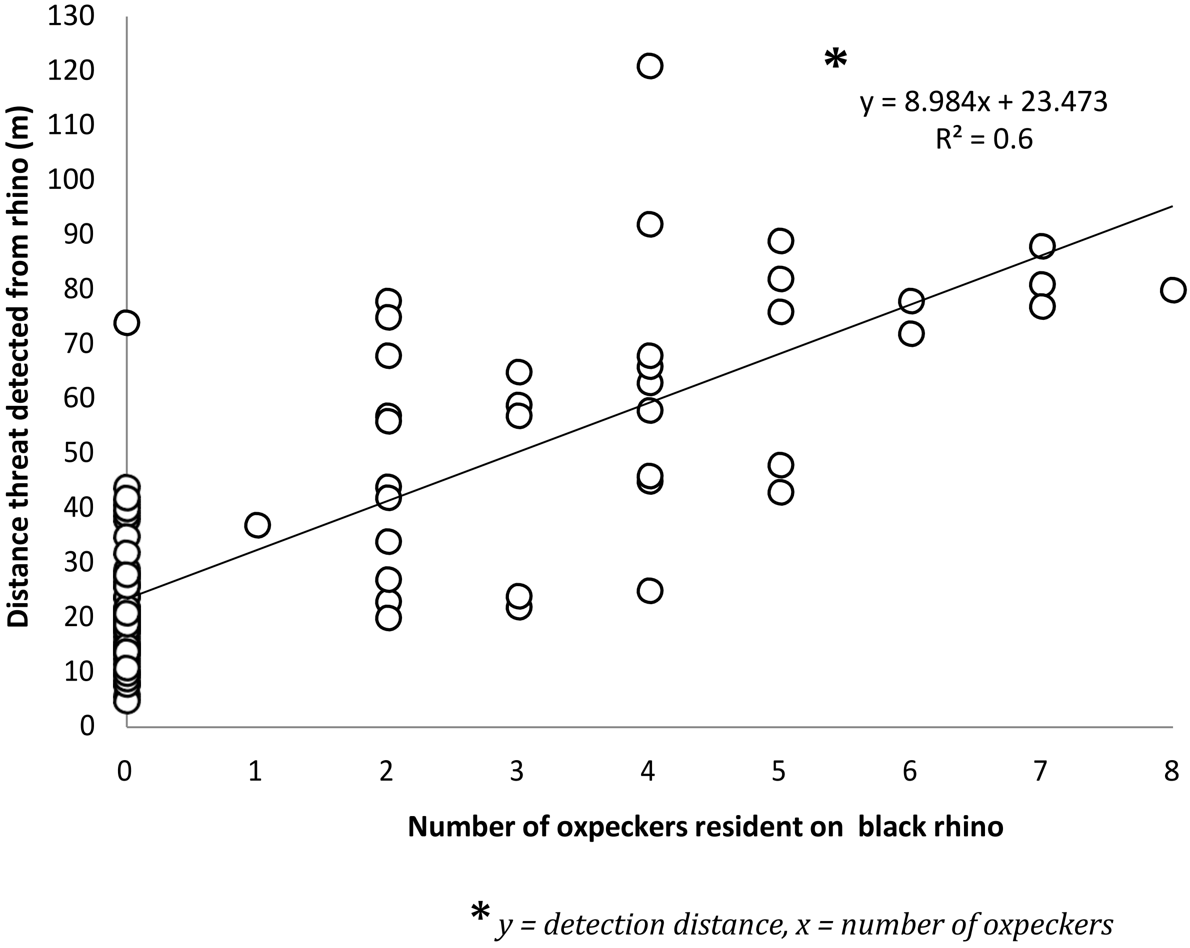


Figure 2. The relationship between the number of oxpeckers resident on black rhino and the distance the approaching human threat was detected by rhino.

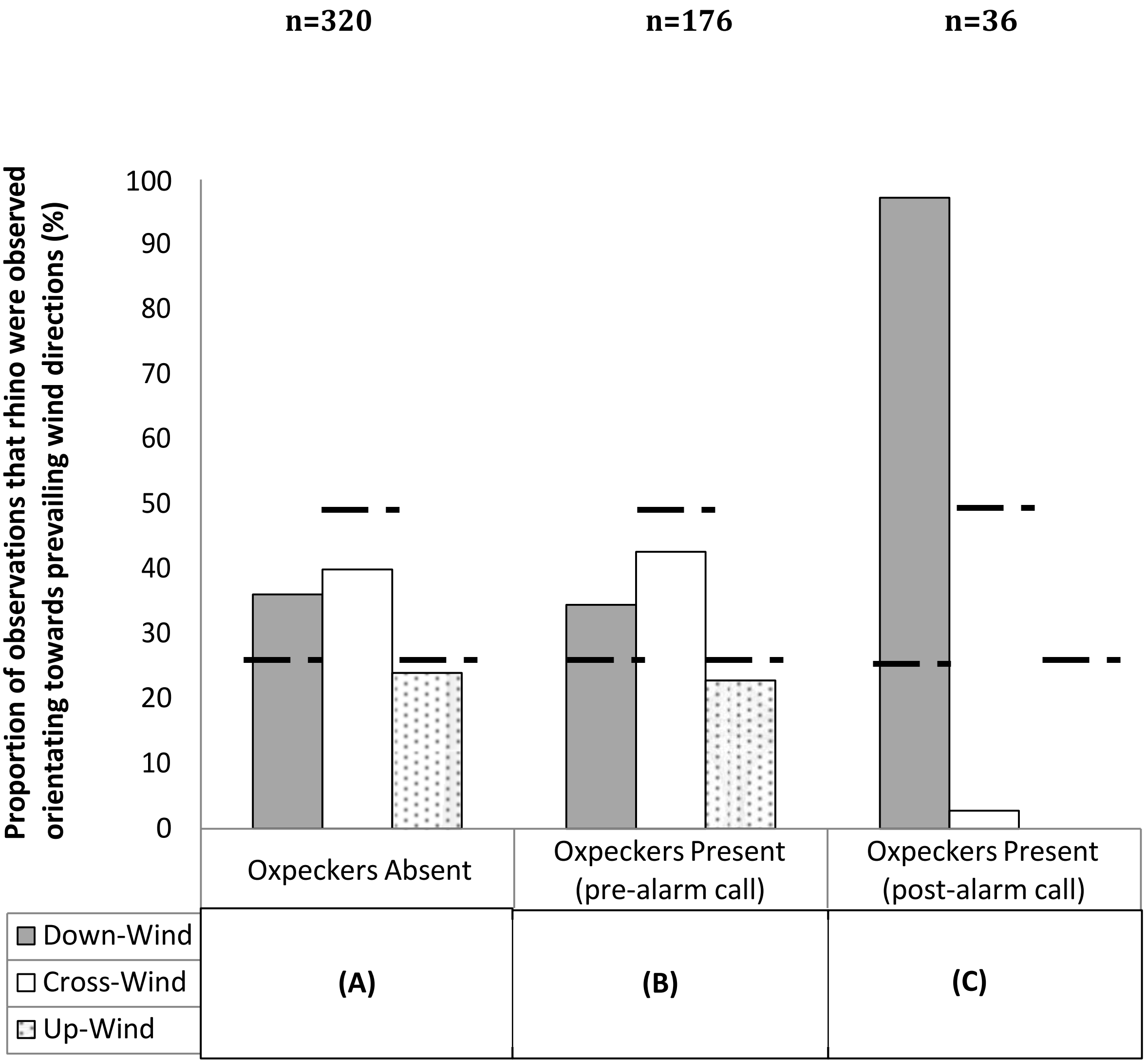


Figure 3. The relationship between the orientation (i.e., direction of head and chest) selections of un-alert black rhino (at first sighting) relative to the prevailing wind directions (i.e., Down-, Cross- and Up-Wind) when: **(A)** oxpeckers were absent and **(B)** oxpeckers were present but had not yet alarm called. **(C)** Represents the orientation a rhino turned towards immediately after responding to an oxpecker's alarm calls (note: after an approach by the human threat). The horizontal dashed lines are the expected levels if rhino were making random selections when orientating. Note that rhino had two options for making orientations that faced cross- wind (i.e., 90 degrees to up or cross wind, hence, 50% expected selection level). In contrast, rhino only had one option if facing Up- or Down-wind , hence the 25% expected level for each. Also, the observer used the 'imagined clock' method to determine the relative prevailing wind directions and the orientations of the rhino at the time they were first sighted and after becoming alerted by oxpecker alarm calls (see key and schematic in Fig. 1).

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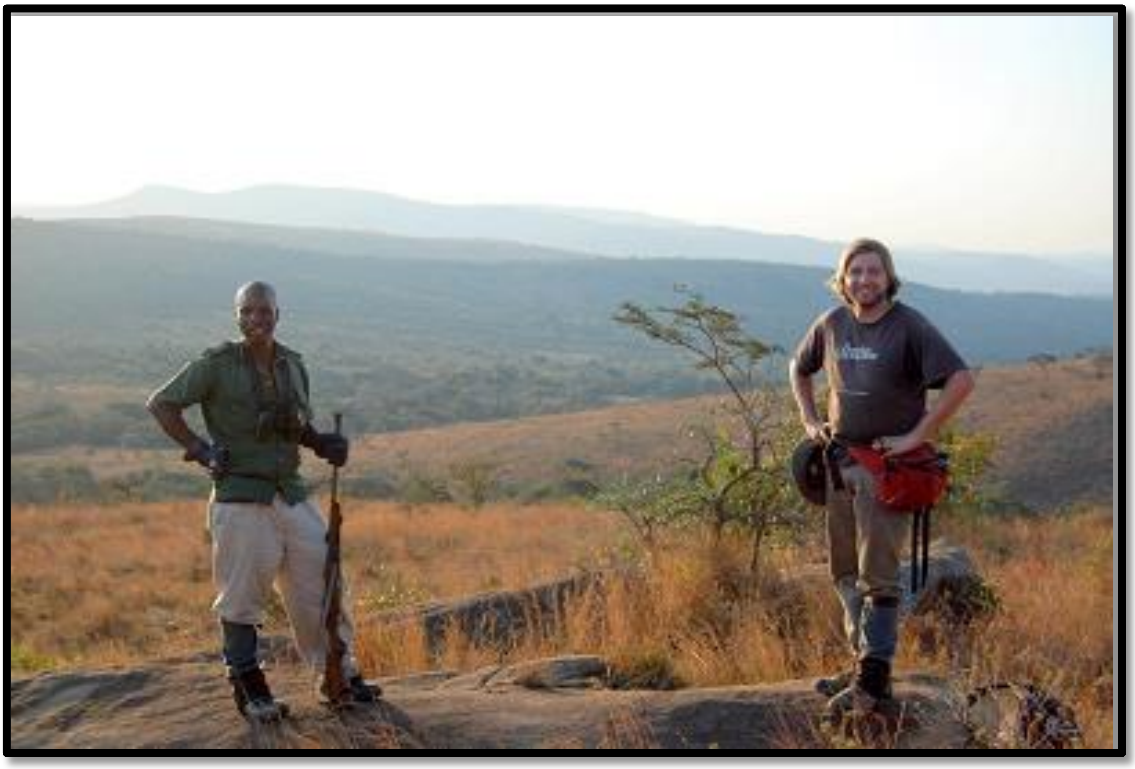
Supplementary:

Table 1: GLM ANOVA table for detection distance (Log transformed) (DF = degrees of freedom, F= F-value, P = statistical significance: P<0.05)

	DETECTION DISTANCE (Log10 transformed data)		
	DF	F	P
Individual rhino	9	0.328	0.957
Number of oxpeckers	8	11.455	0.000
RhinoID x Number of Oxpeckers	21	0.774	0.734
Levene's Test	df1=38, df2=46	0.992	0.5

7.

DISCUSSION



Last day in the field with the well trodden Nqumeni Area behind us (in picture: Bom Ndwandwe, left, and myself, right; photograph by Andrew Stringer).

Thesis Summary and Applications

7.1 Introduction

This thesis examined aspects of the reproductive performance and behavioural ecology (i.e., interspecific relationships) of an apparently poorly performing black rhino (*Diceros bicornis minor*) population in Hluhluwe-iMfolozi Park (HiP), South Africa. Combining spatial and behavioural analyses provides the most comprehensive insight into the home range and relationship with predators and between filarial lesion severity and body condition for black rhino in Hluhluwe-iMfolozi Park (HiP) to date. In particular I investigated the variously mutualistic and parasitic relationship between the red-billed oxpecker (*Buphagus erythrorynchus*) and *D. b. minor* in greater detail. I revealed that oxpeckers are both mutualists and parasites to black rhino. Rather than ectoparasite removal (i.e., cleaner mutualist), red-billed oxpeckers in HiP provided the benefit of increased vigilance (i.e., sentinels). However, oxpeckers were also predominately parasitic lesion foragers (i.e., cost). The benefit of increased vigilance may explain why I found black rhino to be unusually tolerant of parasitic oxpeckers, compared to several other ungulate hosts (Plantan 2009; Bishop and Bishop 2014). Oxpecker's role in providing hosts with increased vigilance has not really been investigated before this PhD study (but see Weeks 1998), particularly for wild co-evolved hosts like rhino. The intriguing interplay between the net costs versus benefits in the oxpecker-rhino interaction illustrates the need for research that covers the range of variations in cost- benefit ratios across varying spatial and temporal scales.

7.2 Summary of major findings

Despite some authors reporting a 306% increase in average home range sizes, my study suggested that black rhino home range sizes have not significantly increased over the past 40 years within HiP (**Chapter 2**). Moreover, regular observer monitoring over a 6-year period did not significantly inflate black rhino home range sizes either. Nevertheless, observations obtained via radio-telemetry triangulations had the potential to significantly inflate black rhino home range size, especially when readings were taken from greater than one kilometre from individual rhino. Managers can therefore be confident that home range studies of black rhino that use radio-telemetry monitoring provide relatively accurate estimates of home range size as long as care is taken when triangulating positions. This study provides an essential baseline for future research that both managers and researchers can use for meaningful comparisons of home range size and structure.

Black rhino calf depredation was proposed by management as one of several suspected causes of apparently low calf survival in HiP. Evidence has been restricted to anecdotal observations of juvenile black rhino attacked by lions and spotted hyenas. For this reason black rhino with missing ears and tails are often cited as direct evidence of failed predation attempts. Nevertheless, a direct causal link (i.e., observation) remained elusive and was debated such that the phenomenon could not continue to be ignored when designing population management and policy (Fanayo et al. 2006). This study identified an 8-month-old black rhino calf that succumbed to severe anogenital and flank and neck wounds inflicted by a lion (**Chapter 3**). Most significantly the associated tail amputation confirmed that tail, and perhaps ear, loss in calves can indeed be caused by failed depredation attempts. Managers ought to consider the role that predators might have when managing black rhino populations for improved performance as populations with high predator densities might not be capable of growing as fast as those that have low densities of predators.

This study found that HiP black rhino suffer from the largest and most severe filarial lesions yet recorded. Chronic lesions in some animals can cause poor body condition (Sutherst et al. 2006). However, the relationship between filarial parasitic lesions and reduced body condition in black rhino had yet to be determined. I found significant inverse relationship between lesion severity and body condition but neither factor was driving this relationship. An as yet unknown factor or factors were implicated (**Chapter 4**). Finally, to facilitate research into the role that filarial lesions might play in black rhino welfare I mapped the current known locations of populations known to present with lesions. Filarial lesions are localised to two distinct regions in east and southern Africa. It was apparent that an understanding of what other factors might drive lesion severity in black rhino requires investigation.

Factors other than body condition appear to be driving lesion severity for black rhino. Early 20th century observers suspected that oxpeckers caused filarial lesions but their suspicions were forgotten. Oxpeckers were believed to forage on ectoparasites (e.g., ticks) of rhino and other ungulates and their role as cleaner mutualists gained credence. Most other ungulates are intolerant of wound feeding oxpeckers and deter such parasitic activities when they occur.

My investigations challenged the notion of oxpeckers as classic examples of terrestrial mutualists, however in Chapter 6, I found that the birds significantly favoured feeding from filarial lesions over other sites of tick attachment on black rhino and that black rhino were wholly tolerant of their parasitic feeding.

Further analysis determined that lesion preferences by oxpeckers were seasonal. Oxpeckers significantly favoured lesions over ticks in winter while in summer the preferences were reversed. These results add evidence to the developing idea that cleaner (i.e., ectoparasite removalists) mutualists are conditionally mutualistic depending on ectoparasite abundance. They also raise the possibility that oxpeckers depress black rhino body condition and population performance.

It remained unclear to me how a seemingly predominately parasitic relationship between black rhino and oxpecker (Chapter 6) persisted unless other benefits were accrued by rhino from the relationship. Rhino have been subjected to substantial overkill by humans and oxpeckers are, anecdotally, reported to alert rhino to human approach through their distinct shrilling alarm calls. In order to untangle the apparent complexity within the oxpecker-rhino association I conducted human approach trials to test whether the birds' sentinel alarm calling behaviour actually benefitted HiP's black rhino. I discovered that oxpeckers afforded black rhino three and four fold increases in human detection distance and rate respectively. Moreover, black rhino responded by facing most often in the direction of downwind (i.e., with the direction of the wind) that suggested a potential evolutionary response to downwind hunting approaches by humans. In sum, I propose a new understanding of the oxpecker-rhino relationship – a conditional mutualism-parasitism that is driven by filarial lesion and tick availability and human overkill providing the impetus for a new anti-predator cooperation and greater lesion parasitism by oxpecker.

7.3 Implications and applications

Using animal population indicators to evaluate conservation achievement is widely practised, yet seldom empirically tested (Hoare et al. 2013). Measuring conservation goals for black rhino recovery is a prime example of this tendency. As already mentioned, several authors have concluded that HiP's black rhino population is in rapid decline i.e., exceeded its carrying capacity (i.e., 'crashing': e.g., Emslie 1999, 2001; Reid et al. 2007; Adcock 2009; Slotow et al. 2010). The term carrying capacity (hereafter CC), however, is widely used yet frequently misunderstood (Morgan et al. 2009). Originally adopted by agricultural scientists (e.g., sheep, *Ovis aries*) the CC was equated to optimal stocking rate, the population density giving maximum yield of animal products for money. For ecologists, in contrast, it is the zero growth density (i.e., births match deaths).

Moreover, the density level at which births match deaths is limited by any factor(s) changing birth or death rates. Predation can thus affect the density level attained, as can harvests. For black rhino in reserves like HiP with high densities of large predators and ongoing annual harvesting makes it inherently difficult to be confident of CC levels (e.g., Morgan et al. 2009).

Further complicating the matter is that for large mammals, density dependence arising largely from exploitative competition may not become effective until population density exceeds some threshold level. In other words the vital rates, defined as the overall change in births and deaths per 1000 individuals, are density vague for black rhinoceros (Owen-Smith 2001).

Therefore, vital rates of animal populations relative to increasing density, rather than being a linear relation projected by a simple logistic model are convex (e.g., human populations: slow decline in vital rates that increases at high densities) or concave downwards (e.g., small mammals: rapid decline in vital rates as soon as densities increase). Black rhino do not reach the same high vital rates that small and even large mammal populations at low densities are able to and for this reason crash quickly after an unknown density threshold is reached (Fig. 1).

Thus, the relationship between black rhino populations' vital rates and its density and subsequent range size may be ramp-like with no obvious indication that vital rates and habitat are deteriorating along with increasing range sizes until the threshold is reached. For this reason caution is advised when trying to use my or other studies findings as evidence of population status and performance. Although, I discovered that range sizes have not changed (**Chapter 2**), calf predation does occur (**Chapter 3**), lesion severity is temporally linked with black rhino body condition (**Chapter 4**) and oxpeckers are conditional parasites that target lesions over tick sites in periods of low tick density (**Chapter 5**) but that black rhino might tolerate this due to increased vigilance benefits (**Chapter 6**). This study's major conservation application therefore is that it is the first systematic monitoring of HiP's black rhino population in over forty years. Being confident in the meaning of my findings and detecting changes in this population's status and ongoing performance will require similar studies to be repeated in the future. Nevertheless, knowing that radio-triangulation home range studies are reliable and home range size does not appear to have increased significantly over the last forty years (**Chapter 2**) ought to encourage conservation managers and researchers to be more discerning when using historical black rhino home range studies to infer reductions in CC (e.g., Reid et al. 2007). Further, research into how black rhino respond spatially to habitat changes would benefit our understanding of **Chapter 2's** results and basic black rhino spatial dynamics.

Another concern for apparent population decline has been predators (Fanayo et al. 2006). Research has shown that overall lion: prey ratio within HiP around the time of this study (i.e., 2010) had actually increased markedly from historically low densities (Grange et al. 2012). Thus, the black rhino calf depredation attempt I recorded (**Chapter 3**) might be a reflection of recent increases in predator density. A concurrent decline in alternative prey such as kudu and buffalo (Grange et al. 2012) might be driving lion to seek unusual prey such as black rhino calves. Conservation managers, however, rarely factor predation in their management plans or projections but perhaps they ought to regularly monitor predator/ prey densities when managing black rhino for
improved performance.

Body condition is above average (i.e., average score > 3.0; Reuter and Adcock 1998) for black rhino in HiP (**Chapter 4**). The severity of the management challenge at hand and the danger of misleading conservation policy requires the systematic monitoring of unbiased sample of individuals and their habitat through time (Linklater et al. 2010). Despite the remarkably severe filarial lesions observed on HiP black rhino, lesions themselves do not appear to drive poor body condition that might impact on rhino fecundity. Discerning whether this is likely has significant implications as it will allow us to determine if HiP's below desired population performance might be due to the occurrence of filarial parasites. Black rhino's exposure to human overkill and greater than realised calf depredation might have made them unusually tolerant towards overt lesion feeding by oxpeckers. To be certain future studies ought to conduct concurrent measures of tick densities that are repeated in other black rhino- oxpecker sympatric populations with filarial lesions of varying severity (e.g., southern and east Africa; Stutterheim and Brooke 1981; Stutterheim 1982a; Craig 2009) and different human exposure histories. **Chapter 4** also provides a map of locations that enables such comparisons in future. Therefore, the results of this thesis can be applied toward improving our understanding of black rhino welfare in several ways (also see Linklater et al. 2010) and act as preliminary baseline studies for additional conditional parasitism-mutualism investigations in future.

7.4 Directions for future research

This thesis has answered some of the questions regarding factors suspected of being driving the poor performance of HiP's black rhino population. Throughout the course of this research many new questions have arisen. The groundwork has now been laid for more empirical investigations into other current performance indicators (e.g., inter-calving intervals, calving rates) frequently used to measure the conservation success of this critically endangered species (Emslie 2001). Further, investigations into the role that oxpeckers play as rhino 'parasites' themselves, will hopefully tease apart the inherent complexity of Africa's most well-known terrestrial cleaner mutualism.

If oxpeckers are mainly targeting black rhino's lesions, while providing sentinel benefits, it might actually be detrimental to black rhino welfare especially in the cooler drier winter months when ticks are absent and habitat conditions are poorer. It will then be necessary to determine how much anti-predator vigilance benefits provided by oxpeckers (**Chapter 6**) increases rhino fecundity and whether it actually mitigates the negative effects of lesion exploitation. To better understand the interspecific evolutionary ecology of black rhino and encourage others to expand on my work I use the current literature to speculate below on **Chapters 4, 5** and **6** as presented in this thesis.

7.4.1 Is the oxpecker-black rhino interaction an example of a conditional mutualism?

No evidence previously existed for oxpeckers foraging preferences of wild free-ranging black rhino. Oxpeckers apparent predilection for blood (Keet et al. 1997; Weeks 1999, 2000; McElligot et al. 2004; **Chapter 5**) over ticks has challenged the view that oxpecker-host interactions are a classic example of a cleaner mutualism (Weeks 2000; Nunn et al. 2011). Plantan (2009) and Plantan et al. (2012) recently demonstrated that oxpeckers appear to be conditional cleaner mutualists that alternate mutualistic tick verse parasitic blood foraging depending on the availability of a handful of favoured Ixodid ticks (e.g., *R. appendiculatus*, and *R. (B) decloratus*). Seasonal tick density and distribution is heavily regulated by rainfall patterns in KwaZulu-Natal (KZN) (Tyson and Dyer 1975), South Africa (Short et al. 1989; Gallivan and Horak 1997; Mushi et al. 1997; Horak et al. 2003, 2006; Randolph 2008). In KZN and the more temperate climes of southern Africa, ticks undergo a complete diapause in development in the cold dry season i.e., winter (Madder et al. 2002; Randolph 2008). Moreover, Walker et al. (2000) and Horak et al. (2009) indicate that in North-East KZN, where HiP is located, that *R. appendiculatus* and *R. (Boophilis) decloratus* are at best only sparsely present or displaced all together by the tick species (i.e., *B. microplus*). Oxpeckers are especially reliant on ticks during the summer months in South Africa, when the birds have their breeding season (Stutterheim 1982b; Craig 2009). Indeed, ticks contain more than 10 times the selenium and other minerals necessary for eggshell production and moulting (Plantan 2009). In light of this, HiP's location and rainfall patterns are likely to make it a marginal habitat for red-billed oxpeckers. Black rhino only host one of oxpeckers two favoured species of ticks (i.e., *R. appendiculatus*; Baker and Keep 1970), further limiting ectoparasite availability for visiting oxpeckers. Nevertheless, our discovery that red-billed oxpeckers in HiP seasonally alternated the amount of time spent foraging at filarial lesions verse tick sites on black rhino supports the recent literature and lays the foundation for further investigations into the black rhino oxpecker relationship and the conditionality of mutualisms in general (cf. Cheney and Cote 2005).

An obvious limitation to **Chapter 5**, however, was my inability to concurrently measure tick densities on black rhino or in the surrounding habitat. Therefore, to be certain that seasonal fluctuations of ticks are conditionally regulating parasitic behaviour by oxpeckers, tick densities should be concurrently measured. Moreover, if tick availability was the driver of oxpeckers parasitic activity than I speculate that in central equatorial Africa, where tick densities do not significantly change across seasons (Madder et al. 2002; Randolph 2008), oxpeckers ought to predominately favour tick sites over black rhino's filarial lesions at all times (cf. **Chapter 5**). This pan-African disparity in tick abundance might explain why black rhino in central Africa have less severe filarial lesions (Mutinda et al. 2012) compared to infected black rhino in southern Africa. Oxpeckers might spend less time foraging and exacerbating lesions of black rhino (*D. michaeli*) in central African reserves when tick abundance remains level throughout the year.

7.4.2 Is the novel mutualism between black rhino and oxpeckers triggered by the barrel of a gun or non-human predators?

Humans have hunted rhino since the late Pliocene and in recent times driven black rhino to the brink of extinction (Beech and Perry 2011).

Unsurprisingly therefore, rhino's rapid fleeing behaviour is restricted to humans (i.e., scent) and is not seen when similarly exposed to non-human predators (Schenkel and Schenkel-Hulliger 1969; Owen-Smith 1987). For this reason, perhaps, available evidence suggests that oxpeckers do not actually alarm call at the non-human terrestrial predators of their hosts (e.g., lions; Weeks 1998). However, without empirical testing we cannot rule out a role for non-human predators in the potential anti-vigilance behaviour between oxpeckers and black rhino and research into this possibility is needed.

The fact that black rhino predominately faced downwind during the human approach trials raises the possibility of an adaptive response to human hunters, who unlike lions (Schaller 1972), always approach from downwind. Lions however, are known to deliberately scatter prey via scent and have other members of the pride available to attack (Skinner and Smithers 1990). **Chapter 6** raises the possibility that the vigilance benefits afforded to rhino might be in exchange for tolerance of lesion exploitation (**Chapter 5**). Understanding whether humans have driven this adaptive response will require further investigation into oxpecker's reaction to non-human predators and comparing oxpecker-black rhino interactions in reserves where lesions do not occur. Where black rhino do not have lesions, oxpeckers might have less incentive to provide black rhino without lesions with the same time constraining sentinel benefits.

Also, black rhino in areas not as exposed to human hunters or non-human predators might not be as responsive to parasitic sentinel oxpeckers and so determining the conditionality of various scenarios requires investigation.

In closing the rhino-oxpecker relationship may be a consequence of a wider web of inter-specific relationships – filarial nematodes, ectoparasitic ticks and human hunters – and as such inter-specifically conditional.

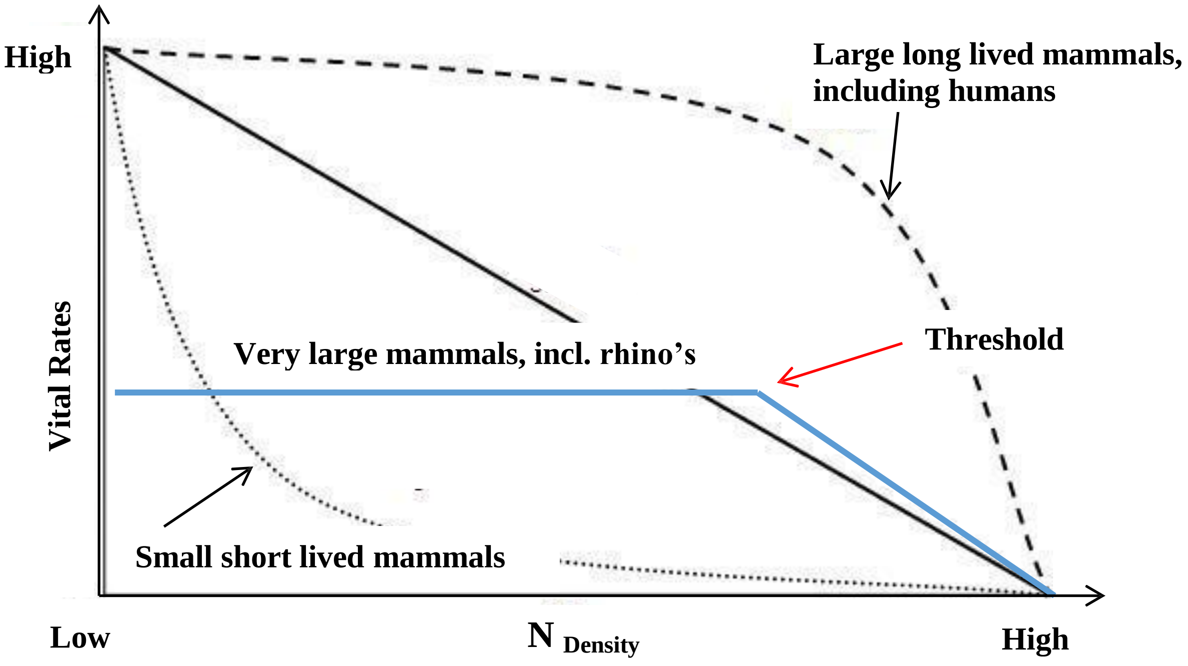


Figure 1: Diagram showing the relationship between increasing density (n) and vital rates for small short lived, large and very large mammals. For large mammals, density dependence arises largely from exploitative competition and may not become effective until population density exceeds some threshold level i.e., vital rates are density vague (see red arrow). Therefore, vital rates of animal populations relative to increasing density, rather than being a linear relation projected by a simple logistic model are convex (e.g., human populations: slow decline in vital rates that increases at high densities) or concave downwards (e.g., small mammals: rapid decline in vital rates as soon as densities increase).

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APPENDICES

Me searching for bhejane (Zulu for black rhino) up a Marula tree

(Photograph by Liana Cahill)

Appendix 1: Morris, D.R. (2011). The Rhino Man of iMfolozi. South African Country Life Magazine. December: 30-34.

THE RHINO MAN OF IMFOLOZI

WILD EARTH

COUNTRY LIFE

TEXT AND PICTURES DALE MORRIS

KWAZULU-NATAL

Roan Plotz has dedicated his life to studying black rhino. DALE MORRIS stepped nervously into the wild with him

ROAN PLOTZ TWIDDLED WITH HIS telemetry receiver and adjusted the position of the antenna he was holding in his hand. I could hear the soft clicking of a signal emanating from his headphones, and as he moved the antenna round the sound became ever so slightly louder. Roan raised his eyebrows, sighed and removed the phones.

"I think she's over there," he told me, "but I'm not a hundred percent sure. The signal is weak. Still, let's go and take a closer look. If we're lucky she won't see us coming." He pointed to a grove of trees about a kilometre from where we were standing in a grassy area in the heart of KwaZulu-Natal's Hluhluwe Imfolozi Park.

"Keep your eyes peeled, Dale," he said as we walked off in single file. "We wouldn't want to surprise yet another rhino now, would we?"

The question was, of course, rhetorical …

I had been tracking black rhino with Roan and his field assistant, Bom Ndwandwe, for five straight days and during that time had been charged on numerous occasions. I had discovered that black rhino can travel at 56km/h, that their sense of smell is phenomenal and that they tend to charge at the faintest whiff of danger.

I had also discovered, through bitter experience, that black rhino consider scientific researchers and journalists potentially dangerous, and that it is nigh impossible to get a usable photograph of a rhino while running, climbing, hiding, panicking or pooping oneself.

"The ability to climb quickly is a prerequisite for anyone wanting to study black rhino," Roan had told me on one occasion when all three of us had been driven to the top of a spiky acacia. "But don't worry. Unlike elephants, rhino rarely try to extract you from a tree."

Rarely!

Of course, if this story was ever to make it into the pages of this magazine I would have to a) survive in order to write it and b) get at least one passable photo of a rhino. However, things had not been going all that smoothly. We were down to my last day in the park and all I had to show for my efforts was a pile of abstract photos showing large grey smudges and out-of-focus branches.

I had seen rhinos hurtling across the landscape towards the horizon and I had seen rhinos »

□ A black rhino lurking with intent. You have a better chance of seeing a wild rhino in Hluhluwe Imfolozi than almost anywhere else on the planet.

Opposite:

□ Roan Plotz at work in his 'office,' searching for black rhino with his radio telemetry equipment.

Country Life December 2011 31

□ Hluhluwe-Imfolozi Park is a mosaic of grasslands and forested hills.

□ A game capture team working on an anaesthetised and blindfolded black rhino.

>> hunting towards us. I had seen rhinos hidden in grass and hidden behind bushes. I had even seen a few of them at night. What I hadn't seen, though, was a rhino willing to stand still in a photogenic manner for more than a millisecond.

Thankfully, Roan had been markedly more successful as far as his personal mission was concerned. When I met up with him he was in fact just finishing off three years of field observations of 14 radio-tagged Imfolozi black rhino.

"Few people study black rhino intensively," Roan told me. "Probably because it's not easy to approach and watch them undetected." (This was something I'd discovered for myself on numerous occasions in the preceding days.) "White rhino are far less skittish or aggressive, so you find more research papers on them. However, there are many gaps in our knowledge of black rhino and this really has to change."

Rhino (both black and white) are a prime target species for poachers because of the value of their horn, which is used in traditional Asian medicine for conditions ranging from headaches to the Little Willie syndrome, and in Yemen for making ceremonial dagger handles. So any information from research projects such as Roan's could be invaluable to organisations striving to protect the creatures from extinction.

"What I'm doing," said Roan, "is looking closely at their pregnancy rates, infant survival rates, territorial behaviour, habitat requirements and interaction with other species. It's basically to do with how many rhinos should be kept in a fenced reserve, and I very much hope my data will be useful to those who make decisions regarding their conservation, not just here in Imfolozi but wherever black rhino are managed."

Those who stand to benefit most would include national parks and reserves, captive breeding institutions, conservation organisations, field researchers and, of course, the black rhino themselves.

In order to track and observe black rhino in the wild, Roan had to enlist the help of Imfolozi's legendary game capture unit, a dedicated team of rugged gentlemen who regularly tackle rhino in the name of conservation. I was fortunate to be in the park during a black rhino darting operation, and even more fortunate that they let me tag along.

I sat waiting with the ground crew on the back of a 4x4 vehicle, watching a nearby lion nibbling on a porcupine, while up above the team's vet surveyed the park from a helicopter, dart gun at the ready. Less than 15 minutes later we received a call saying a black rhino had been darted and we sped off into the bush to intercept the creature. The lion barely looked up from its feast while I clung on for dear life to the vehicle's roll bars.

When we arrived at the downed rhino the vet was already checking its vital signs, the helicopter's rotor blades still slowing to a standstill. A drill was produced, a hole was made in the animal's horn, a radio transmitter was inserted and the hole was sealed with dental acrylic paste. Finally the antidote was administered so the rhino could recover. That was our signal to leave … quickly.

"I found my first game capture very exciting," Roan admitted, "and I still find them exciting."

I could easily understand why. Zipping around the bush in specially designed 4x4 vehicles, grappling with huge beasts and flying in helicopters is thrilling indeed. But the excitement doesn't end when the game capture crew depart. In fact, as far as Roan is concerned, that's when the fun really begins.

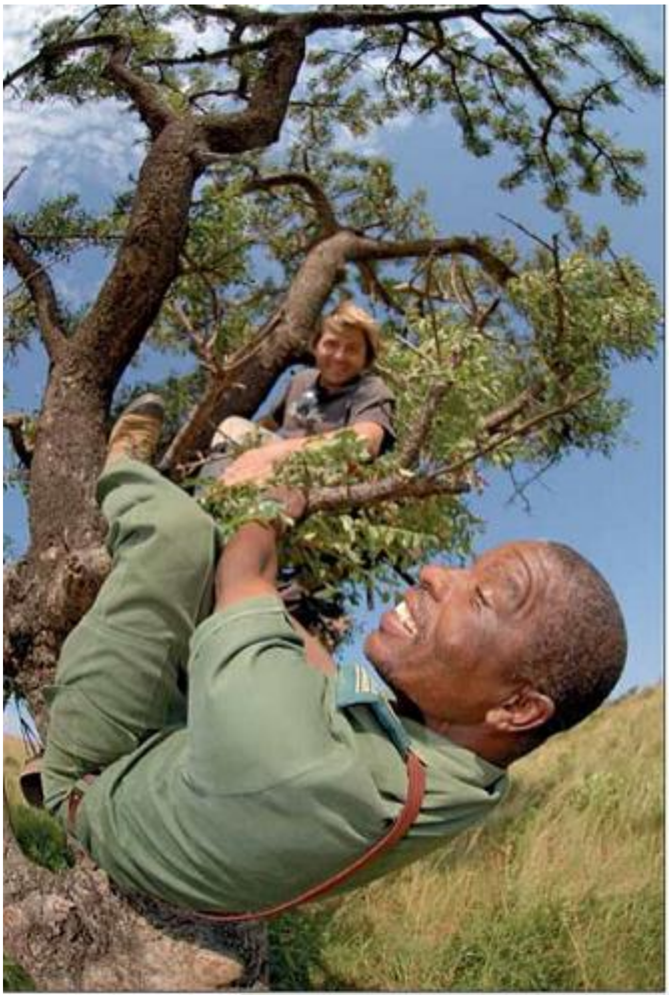
Every day Roan and Rom find their way on foot through herds of buffalo and other potentially dangerous creatures (such as lions, hyenas, leopards and tourists) to keep track of and collect data from their study animals. It's a risky undertaking, but after a while, or so Roan told me, you begin to know intuitively when things are getting risky. >>

□ Rhinos are short sighted.

□ Oxpeckers often see an approaching human long before the rhino and sound the alarm.

□ Mother and daughter black rhino pose for the camera on the last afternoon of our five-day visit.

□ Sometimes it can be a long run to the nearest tree.



□ Roan and Bom escaping from a perturbed rhino

□ White rhino, distinguished by their square lip, are far less aggressive than black. .

>> "Sometimes I just get a gut feeling," he said as we crept towards where we hoped the rhino we were after might be resting, "and when that happens – when the hairs on the back of my neck stand up – I follow my instinct and head off in a different direction.

"Lions will rarely, if ever, attack people. You can escape a buffalo or rhino by climbing a tree. But if you somehow insult an elephant, well, there isn't a tree in the park that it couldn't knock down or pull you out of."

Suddenly Roan signalled us to remain silent – a signal I had long since learned to obey. He beckoned me to lower myself as much as I could and then motioned for Bom to lead me a little way uphill from the grove of trees at which we'd just arrived. I followed Bom until we reached a low and sturdy acacia tree into which, under instruction, I quietly climbed.

It was almost dark and this was my very last opportunity of encountering a rhino with Roan, but I couldn't see a darn thing – just leaves and branches and hills and rocks and things. Then all of a sudden, out of the shrubbery trotted two huge black rhino (a mother and daughter, I was later told). I held my breath and prayed that the creatures would turn towards me for a photograph. The light was perfect and the animals were beautiful, but I was still looking at nothing more than a pair of oversized bottoms.

Then, as if on cue, they turned and ambled slowly straight towards me, passing directly beneath the branch I was on. 'Suddenly they caught my scent (or heard my heart thumping, I'm not sure which), snorted, and hurtled away like a pair of runaway trains.

But I'd got my photos and could now leave the park a happy man. Roan was happy for me too, but I'm sure he was happier still when, several weeks later, he completed his project and went home to 'civilisation' and to marry his fiancé.

The data he'd collected and the scientific papers that have resulted from his hard work and risk-taking will no doubt play an important role in the survival of the species.

And as for the rhino themselves? Well, I truly hope they continue to breed and find a sanctuary in the Hluhluwe-Imfolozi Park. □

Map reference D8
see inside back cover

WILD EARTH
COUNTRY LIFE

Ezemvelo KZN Wildlife
www.kznwildlife.com

Appendix 2: Morris, D.R. (2009). Black and white survival. Wild Magazine 7, Winter: 16-28.

Black & white SURVIVAL

If Hluhluwe and Imfolozi didn't exist, rhinos would likely now be extinct. By Dale Morris

THERE'S NOTHING QUITE SO INSPIRING AS A RAMPAGING RHINO TO REMIND YOU THAT WE ARE DESCENDED FROM MONKEYS AND ARE STILL RATHER GOOD AT CLIMBING TREES. There I was, up amongst the flimsy boughs of a spindly acacia somewhere in the middle of KwaZulu-Natal's Hluhluwe Imfolozi Park with not one, but four black rhinos rumbling by below.

Two other men, Roan Plotz, a conservation biologist affiliated with the Nelson Mandela Metropolitan University, and Bom Ndwandwe, a KZN wildlife ranger, were also up there.

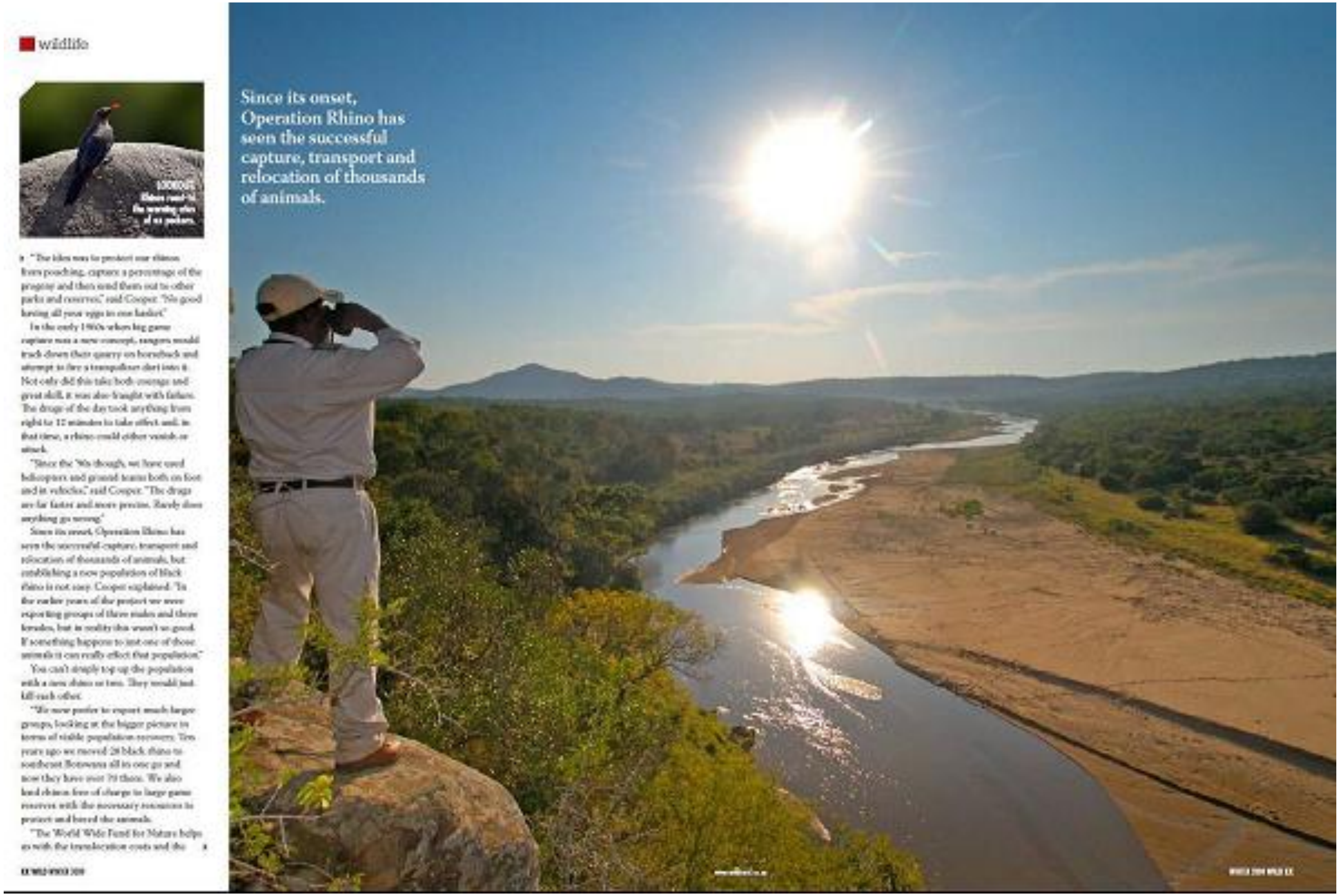
"This is one of the reasons why the species can sometimes be difficult to study," said Roan as the aptly named 'crash' of rhinos vanished noisily off into the undergrowth. "They have a tendency to charge at the slightest whiff of a human."

In this case though, the animals hadn't got a whiff of us at all. We had been approaching from down wind and had been moving silently. Ndwandwe at the front with his gun (just in case), Plotz in the middle with his tracking antenna and myself at the rear with my note book and camera. The bush had been typically woody and by rights we should have been concealed from all but the keenest of eyes.

"Rhinos are as blind as bats," continued Plotz as we dropped from the tree and dusted ourselves down. "But ox peckers aren't and rhinos have learned to respond to their alarm calls."

It's a fascinating three-way beneficial relationship. The ox pecker is tolerated by the rhino and gets to feed on parasites. The rhino gets an early warning system. And the researcher gets an excellent incentive to stay fit.

SAFE HAVEN The endangered black rhino has found a refuge in the Hluhluwe-Imfolozi Park.



wildlife

Since its onset, Operation Rhino has seen the successful capture, transport and relocation of thousands of animals.

Hluhluwe and Imfolozi became the first formal wildlife reserves on the continent, established with the goal of saving black and white rhinos.

new custodian gets to own 50 per cent of any baby rhinos born (currently worth half a million rand each). This really is a nice incentive for cooperation between private land owners to drop their fences, which in turn has a fantastic spill-over effect for all sorts of other animals such as wild dogs and elephants."

Cooper smiled and there was a discernable glint in his eye. Obviously, this is a project that makes him, and no doubt every other rhino conservator in Africa, very, very proud.

A glitch in the rhino system?

Just about every black rhino on the planet can attribute both its genes and survival to the rhinos from Hluhluwe Imfolozi. If this population is now failing without clear answers as to why, it could possibly spell disaster for rhinos everywhere.

Ongoing data collected by anti-poaching teams as well as past observational studies indicate rhino home ranges within Hluhluwe have been increasing in size since the 60s and overall numbers of rhino have dropped.

"Too many rhinos on the land is not a good thing," said Imfolozi's conservation manager David Robertson. "They would need to range further to find sufficient browse and this in turn could depress their own breeding successes. Conflict between animals would also increase."

Another worrying issue is the apparent lengthening of time between the birth of one calf and the next. Again this is something that could possibly be attributed to a lack of health within the entire population. However, few (if any) studies have been conducted on black rhinos in which a representative group of individual animals has been so precisely monitored as those being scrutinized by Plotz.

Pregnancy rates are being recorded through chemical analysis, births documented, accurate home ranges mapped through radio tracking and individual animals outside of his study group are now easy to identify due to an ongoing ear notch system. No-one knows what Plotz will find when he analyses the data, but everyone who cares about the future of the black rhino is hoping science will provide answers.

Regardless of whether the rhinos are doing well or badly due to the effects they are having on the land, there can be no debate the species is still very much in peril. A resurgence in rhino poaching has seen more than 100 killed in South Africa alone, the majority in Kruger. Organised crime syndicates are using helicopters, modern tranquilisers, legal loopholes and (some suspect) inside knowledge to get at rhinos. All the conservation work done could still be undone.

Hluhluwe's conservation manager Sihle Nxumalo remains upbeat though: "To keep the dreams of those who started the difficult task of saving the rhino is not easy. To keep that good story alive is very demanding and it costs a lot of money. I still feel hopeful for the future so long as our government and the local communities support us. Who knows what comes tomorrow. Hopefully a safe future for the rhino."

"As long as you can get yourself a few feet up off the ground you should be safe. It's rare a rhino will try to horn you out of a tree."

RISKY BUSINESS [illegible] and Plotz scramble for safety.

Many people believe ground-up rhino horn will cure all sorts of ailments, even though it's made from the same material as hair and nails. Incredibly, it can fetch up to US$3000 a kilo on the black market. You're better off eating half a kilo of toenail clippings.

RUN, RHINO, RUN They may look cumbersome, but rhinos can reach speeds of 50 km/h.

www.wildcard.co.za

Appendix 3: Kernutt, T.G. (2008). Walking with Rhinos. Weekend Australian Newspaper, April 26-27: page 6 of Travel Supplement.

JOURNEYS: THE SPIRIT OF DISCOVERY

WALKING WITH RHINOS

Tim Kernutt learns some vital lessons on a trek through the South African bush

IF you see a black rhino charging you, don't run. Try to get behind a tree. This is not the kind of advice one hears everyday. I am in Hluhluwe-iMfolozi Park in KwaZulu-Natal, South Africa, sweltering in 40C heat, while listening to a researcher talk about a particularly endangered black rhino subspecies, *Diceros bicornis minor*.

The 96,000ha reserve, a nearly four-hour drive north of Durban, is the oldest on the continent (it was established in 1895) and one of South Africa's largest. It is considered to be one of the best game parks in Africa to view black and white rhinos in their natural habitat.

I am accompanying PhD student Roan Plotz of Melbourne who is briefing me before our walk to track one of seven black rhinos that have had an electronic chip implanted in their horns. Plotz tells me the process of inserting these electronic chips is an intoxicating mix of helicopters, sedatives and drilling, which seems a far cry from the dusty science most of us are taught at school.

Black rhinos are far less docile than white rhinos. Plotz says it is as if they are aware of the danger posed by humans: after all, the black rhino population has been reduced to about 3100, although experts fear it could be less.

Plotz so passionately drills me on the perils of the African bush that I fear I may not make it out of the park alive. Anything that moves in the wilderness of Africa, seemingly, can harm humans, from the ticks you have to flick off when walking through long grass to deadly snakes such as black mambas. Then there are scorpions, spiders and the obviously dangerous big beasts. There is even a tree, the tambotie, which gives off poisonous fumes when burned.

The aim of the game is survival. A couple of nights of acclimatisation in the African wilderness proves good preparation for my walk through the bush. The basic hut in which I stay is part of a small camp area in the heart of the HiP; it does not have a perimeter fence. The thought of the dangerous animals that could be roaming about at night restricts my nocturnal walking to an absolute minimum. There is certainly not much incentive for stargazing in this neck of the African veldt.

Meet the locals: A rare sighting of a black rhino and her calf in Africa's oldest reserve

Picture: Tim Kernutt

FLASHING A TORCH I SOON MAKE OUT THE SHAPE OF A HUGE MALE ELEPHANT TAKING A MOONLIT STROLL THROUGH CAMP

While I am in the communal kitchen area of the camp one night, banging and crashing can be heard in bushes nearby. Flashing a torch, I soon make out the shape of a huge male elephant taking a moonlit stroll through camp. It pauses to feed off a plant directly at the back of my hut. Despite being about 4m tall and probably weighing four tonnes, it could charge at great speed, park workers tell me. The footprints it leaves are five times larger than mine.

When I finally venture into the bush with Plotz on a humid Monday morning, I am as prepared as I am going to be. It is March, the rainy season is just coming to an end, and the grass is at least 1m tall.

"Watch out for the ticks . . . they can give you a nasty bite. And make sure you avoid standing on a puff adder, that will send you home a little earlier than you would have hoped," Plotz warns. It strikes me that my travel insurer would have reassessed its premium if it had known I would be heading on foot into the African bush.

A ridiculous aspect of such a walk in the wild is the automatic weighing-up of risks. Suddenly those snakes that could inflict a fatal bite seem less of a threat when compared with the possibility of being skewered by a hippo or charged by a testosterone-fuelled male elephant.

It does make me feel more confident that Plotz has by his side a guard, Bhom, who carries a .458-calibre elephant gun. Bhom lives in one of the local Zulu communities bordering the park and is a self-titled champion of the *bhejane* (black rhino).

I am assured he has been walking through the South African bush for as long as I have been alive; however, I am slightly perturbed when Plotz casually mentions Bhom doesn't have "A-class hearing". I hope this is more to do with his age than overuse of his rifle.

Within five minutes of setting off across the top of a ridge in the middle of the park, we walk into one of the big five. Staring at us is a lone male buffalo; thankfully it runs off as soon as I stare at it, which gives me a mad sense of empowerment not felt since moving out of my parents' house.

It is somehow amusing to discover how difficult it is to spot black rhinos. Plotz has said he knows where to find one, but after three hours in searing heat, there's no sign of it.

With his tracking device waving in the air above him, Plotz looks as if he has more chance of tracking an unidentified flying object.

Suddenly mayhem breaks out. Plotz shouts for me to jump up and into the nearest tree while he and Bhom creep forward. No more than 40m from where we have been standing is a female black rhino with a baby calf.

I gawk like a child for a good half hour; the mother is highly protective of the calf, which is likely to have weighed a whopping 40kg at birth. Plotz has told me earlier that fully grown black rhinos can charge at 45km/h. They will charge at anything they perceive as a threat.

I am well satisfied by my first black rhino sighting and rather glad I am alive. My previous encounters with animals in HiP have paled, although I almost tread on a rock python, Africa's largest snake, on the walk back to camp. Plotz just laughs and says there's no such thing as an average day in the African bush.

Checklist

Imfolozi offers a range of self-catering accommodation, from rondavel cottages to tents. The best season is from May to October, when the weather is mild and dry and animals are easier to spot as they appear in open spaces looking for water.

- www.southafrica.net
- www.kznwildlife.com

The Weekend Australian, Travel Section, April 26-27 2008, page 6.

Appendix 4: Linklater, W. L., Plotz, R.D., Kerley, G.I.H., Brashares, J.S., Lent, P.C., Cameron, E.Z., Law, P.R. and Hitchins, P.M. (2010). Dissimilar home range estimates for black rhinoceros *Diceros bicornis* cannot be used to infer habitat change. Oryx 44: 16-18.

Letters

Dissimilar home range estimates for black rhinoceros *Diceros bicornis* cannot be used to infer habitat change

The strategically important black rhinoceros *Diceros bicornis* population in Hluhluwe-iMfolozi Park, South Africa, appears to have declined. Some suggested the population exceeded carrying capacity (Emslie, 2001a) and required increased harvest (Emslie, 2001b). Others were concerned about over-harvesting (Balfour, 2001). Reid et al. (2007) used apparently larger home range sizes in the Park than previous estimates to infer habitat deterioration, a conclusion that appears to be influencing the opinion of local managers (Morris, 2009) and may be used to support changes in the management of the Park's black rhinoceros population (Authors, pers. obs. at 36th Biannual Meeting of the KwaZulu-Natal Rhino Management Group, 5 November 2008, and Hluhluwe-iMfolozi Park Research Forum, 4 June 2009).

Home range estimates are sensitive to the method of data collection and analysis (e.g. convex polygon, kernel or grid cell), and number and period of observations (Laver & Kelly, 2008). Researchers, therefore, are rightly hesitant to compare estimates that differ in one of these ways. It is of concern, given the importance of their conclusion for the management of a Critically Endangered species, that Reid et al. (2007) compared estimates differing in all these respects.

Reid et al. (2007) compared their estimates using locations gathered over 11 years with an historical value from Adcock (1996), reported in Emslie (1999). Adcock's (1996) original calculations were from 1 km^2 grid-occupancy data incorporating a 4-year subset (1991–1994) of the Reid et al. (2007) data (1991–2002; Table 1). Lack of independence between datasets and the longer sampling period in Reid et al. (2007) will increase range estimates because individual home ranges shift inter-annually (Lent & Fike, 2003).

Home ranges may also be 40–300% larger with few locations and disjointed observations, such as those in Fig. 5 of Reid et al. (2007), when kernel techniques are applied (Downs & Horner, 2008; Huck et al., 2008; Boyle et al., 2009). Simulations suggest that ≥ 50 locations are required for accuracy (Seaman et al., 1999), and location data for some animals may require considerably more (e.g. 200–500 locations; Hemson et al., 2005). Reid et al. (2007) did not report numbers of locations but used as few as 10 per individual and thus probably overestimated range size.

Moreover, rhino locations in Reid et al. (2007) were not from standardized sampling but fortuitous sightings. Detection bias among sites and individuals may inflate range sizes because patrolled Park boundaries (i.e. fence-lines) and settlement areas (i.e. tourist camps and ranger stations) receive disproportionate observer effort. Animals in the Park's centre may be more likely detected on the periphery of their range and those living near settlements may be frequently displaced, thus inflating range size estimates. All examples in Fig. 5 of Reid et al. (2007) are along Park boundaries (A), surround a human settlement (C & D; i.e. Mbuzane Section Ranger Camp), or are adjacent to public roads (A, B and D).

Even if home range estimates were comparable, increases in ranging cannot be used as evidence of deteriorating habitat (particularly as no data on changes in habitat were provided) without accounting for inter-specific (e.g. competition and predation) and intra-specific interactions and anthropogenic effects (Schwartz et al., 2003; Morrison et al., 2006). Reduced animal density, for example, may drive larger range sizes, especially in an asocial species such as black rhinoceros where range overlap is limited by intra-sexual competition (particularly amongst males). If population size in Hluhluwe-iMfolozi Park has declined (Fig. 1 in Reid et al., 2007) home range size might have increased because of lower density and be unrelated to habitat quality.

Lastly, Reid et al. (2007) claim larger home ranges as evidence of deteriorated habitat but report smaller ranges during the dry and cold winter than during summer when resource conditions are better. They explain this as the result of more food allowing energy for greater movement and expanded home ranges in summer. This contradicts their contention that poor habitat causes increased range size. They cite more widely distributed water in summer to explain the contradiction but their results show no change in proximity to permanent (winter) water between seasons.

Home range size is not a reliable proxy for habitat quality. Understanding the dynamics of Hluhluwe-iMfolozi Park's black rhinoceros population requires systematic monitoring of the vital rates of an unbiased sample of individuals and their habitat through time. The severity of the management challenge at hand and the danger of misleading conservation policy requires that we resist the temptation to over-interpret poor quality data.

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Table 1 Historical sequence of estimates of black rhinoceros *Diceros bicornis* var. *minor* home ranges in Hluluwe-iMfolozi Park, South Africa.

Method	Focal population	Locations per rhino	Observation period	Home range size (ha)	Reference
Ground search & fortuitous observations: visual approximation using all points	2m, 4f	Not reported	1962–1963	Males: 199.9–223.0 Females: 212.5–494.9	Hitchins (1969)[1]
Radio telemetry & ground search: visual approximation using all points	10m, 4f	47–503 (twice daily)	86–396 days (Nov. 1969–Dec. 1971)[2]	Males: 170–619 Females: 460–950	Hitchins (1971); P.M. Hitchins (unpubl. data)
Fortuitous observations: 1 km^2 grid occupancy	Not reported	~6–20	c. 1991–1994	Males: 1,200–1,900[3] Females: 1,300–2,300[3]	Adcock (1996); K. Adcock (pers. comm.)
Fortuitous observations: 95% kernel	125	≥10	1991–Feb. 2002	Range: 500–5,500 Average: 2,302 ± SE 295	Reid et al. (2007)

[1] Reid et al. (2007) did not mention the earlier estimates of home range size in Hluhluwe-iMfolozi Park from Hitchin's (1969, 1971) intensive observations, including radio telemetry, although the same problems would arise in comparison.

[2] Sometimes included a broken sequence of two or three different transmitters in the same individual

[3] Represents the range of average values from five different regions of the Park. The value of 1,500 ha quoted by Emslie (1999) and cited by Reid et al. (2007) was only for the northernmost region of the Park.

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Acknowledgements

We thank Tim Bean, Laura Prugh, Emily Rubidge, Karen Weinbaum and Cole Burton for their critiques.

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Use of black rhino range estimates for conservation decisions: a response to Linklater et al.

We note the concerns of Linklater et al. (2010) regarding our conclusions for management of black rhinoceros *Diceros bicornis* in Hluhluwe-iMfolozi Park (Reid et al., 2007). Regarding their methodological issues, we pointed out potential biases in data collection and highlighted that the quality and quantity of information used reduced the quality of our analysis. The reader was therefore forewarned to be cautious in any interpretation.

We used opportunistic data collection throughout. Lack of independence would make any contrast conservative in terms of bias, and the effect of sample size on range size was the opposite to the concern of of Linklater et al. (2010) as the 95% kernel range increased significantly with sample size (regression: $F_{1,124} = 60.2$, $P < 0.001$). Using only subsets with larger sample sizes, for ≥ 30 sightings ($n = 43$ rhino) mean home range was 29.8 ± SE 1.7 km^2 and for ≥ 50 sightings ($n = 19$) 34.3 ± SE 2.5 km^2. While accepting potential data issues (and noting that we used kernel rather than minimum convex polygons), these ranges are substantially larger than those of P.M. Hitchins or K. Adcock/R.H. Emslie (Table 1 in Linklater et al., 2010). We believe it reasonable to conclude that range sizes in general have increased.

Linklater et al. (2010) state 'increases in ranging cannot be used as evidence of deteriorating habitat . . . without accounting for inter-specific interactions . . . and anthropogenic effects'. We were not the first to propose that rhino range size increased with degrading habitat (Emslie, 1999). Furthermore, we highlighted that changes in range size could be related to disruption of social networks, and that this and effects of elephants *Loxodonta africana* require further investigation (Reid et al., 2007).

Differential range use by rhino (Reid et al., 2007) and other mega-herbivores between dry and wet seasons is well documented, even in small fenced reserves (Shannon et al., 2006). It is thus not appropriate to use seasonal responses to resource variation as an argument when contrasting ranging across years, as is done by Linklater et al. (2010). They conclude that 'home range size is not a reliable proxy for habitat quality'. While there may be problems with our data this does not negate the potential for home range size to be an indicator for habitat quality, and Linklater et al. (2010) do not present any data to counter this possibility. Our conclusion that 'declining habitat quality . . . may have resulted in larger home ranges' was deliberately cautious, and we went on to emphasize the importance of more detailed work examining the potential mechanisms affecting habitat quality for black rhino.

Linklater et al. (2010) are correct that all potential explanations for changes in population productivity of a Critically Endangered species such as black rhino should be investigated. However, our purpose was not to exclude any particular explanation (such as social factors or management interventions) but rather to point out that there may be ecological aspects affecting productivity that need to be investigated. As stated in our original abstract: 'Ongoing review of stocking rates, population performance . . . and intervention strategies are necessary to manage black rhino in dynamic savannah ecosystems' (Reid et al., 2007). Simple ecological indices may not necessarily be appropriate as a framework for management planning (e.g. carrying capacity estimates should not be used for black rhino population management; Morgan et al., 2009), and incorporating individual variation in biology is critical (Morgan et al., 2009). Furthermore, interventions should acknowledge the importance of the social clusters that rhino develop (Morgan et al., 2009) and avoid any indiscriminate removal from these groups (Reid et al., 2007; S.R. Morgan, pers. comm.).

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Appendix 6: Plotz, R.D. (2012). Burdened Beast. Australian Geographic (May-June): 16-17.

TOPOGRAPHICAL

SPONSORED PROJECT

Burdened beast

Black rhinos are under threat from poachers, lions and hyenas. But one small bird is looking out for them.

ROAN PLOTZ WAS FORCED to make a desperate dash up an acacia tree during his first trip to Hluhluwe-iMfolozi Park, in South Africa, where he watched helplessly as his bags were skewered by a furious rhinoceros. "This kind of thing was a pretty regular occurrence for at least two years, to be honest," Roan says. "Until I became better at tracking, I'd see their ears go up and my adrenalin would get going." It wasn't a warm welcome, but par for the course, says the Melbourne-based ecologist. Aside from being habitually aggressive, Roan's chosen study subject is critically endangered. Its numbers have plummeted by a staggering 99.6 per cent, from an estimated 1 million in the 1850s to about 4500 today, with much of the decline due to the black market for horns. One of four rhino subspecies, the western black, was declared extinct in November last year.

With funding from the Australian Geographic Society and working alongside PhD supervisor Dr Wayne Linklater, from Victoria University in Wellington, NZ, Roan is studying an unusual relationship the rhino has developed with a bird: the red-billed oxpecker. Oxpeckers are a common sight across Africa, picking ticks off at least 20 different host species. However, their favoured meal is blood straight from lesions caused by a parasitic roundworm on rhino flanks.

The question is: why do black rhinos appear to be the only host that tolerates this parasitism from the oxpeckers? A clue might be in the Swahili name for the oxpecker, which is *askari wa kifaru*, roughly translating to "the rhino's guard". Black rhinos are known to be incredibly short sighted, and the oxpeckers may be tolerated in return for calling the alarm when danger approaches (see left). To test this, Roan and park ranger Bom Ndwandwe put themselves in harm's way, using a range-finder to measure how close they could get to rhinos on foot before being spotted. Their results showed that they were detected at about 22m when no oxpeckers were present and 58m when the oxpeckers were there.

However, Roan also noticed an even more interesting behaviour: when a rhino heard an oxpecker alarm call, it quickly orientated itself not to face him, but in the opposite direction to the wind. This is intriguing, he said, as poachers are the only rhino predators that consistently hunt from downwind. "We can't be sure it's human hunting that's causing the response, a lot more research would be needed to ascertain that," says Roan. We're now applying for grant funding to study rhino responses to lions and hyenas, which are their only other predators."

Early warning system

Researcher Roan Plotz found that rhinos typically became aware of the approach of a human on foot at 22m, but this increased to about 58m when oxpeckers were present to call the alarm.

Rhino population

Tagging along. Black rhinos (above left) and their red-billed oxpecker companions (above) are not easy to find, says Society-sponsored researcher Roan Plotz. To track them, he painlessly drilled holes (top) into the horns of 14 rhinos and inserted radio transmitters. "Rhino horns are made of hair, and grow like fingernails, so eventually the transmitters pop out," says Roan, who has studied the behaviour of 70 rhinos.

16 AUSTRALIAN GEOGRAPHIC

AG SOCIETY

Fabulous frigatebirds

Help save these quirky and endangered birds.

CHRISTMAS ISLAND frigatebirds are endemic to this Indian Ocean island, but they roam more than 4000km away in a single flight to forage for food. Each lay just one egg per breeding season and are highly vulnerable to extinction. Breeding pairs on Christmas Island have suffered from a 66 per cent decline over the past three generations, and now there are about 1200. Threats include land clearing, dust fallout from phosphate mining, overfishing, marine pollution and the invasive yellow crazy ant, which is killing the island's dominant red crabs, affecting the island's ecosystem.

Now, the Australian Geographic Society will support BirdLife Australia's Australasian Seabird Group to study the foraging behaviour of the species, helping to focus conservation efforts. "We want to establish more baseline data, especially on their feeding habits, which will help us to create cooperative management initiatives with our partners in Indonesia and other places the birds travel to," says Max Orchard, a project officer at Christmas Island National Park.

For more on the birds of Christmas and Cocos (Keeling) islands see page 62.

READ *more about the frigatebirds and donate at* **www.australiangeographic.com.au/society/campaigns**

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- **MEMBER BENEFITS** Join a hosted expedition with one of our travel partners to help raise funds for our work, or take advantage of other member-only offers.
- **DONATE** to help researchers save the Christmas Island frigatebird.

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