

AN ABSTRACT OF THE THESIS OF

Robert Steven Spaan for the degree of Master of Science in Wildlife Science presented on October 27, 2015.

Title: Dispersal Behavior in African Buffalo (*Syncerus caffer*): Trade-offs Between Nutritional Resources and Disease Exposure

Abstract approved: _____

Clinton W. Epps

Dispersal facilitates population health and maintains resilience in species via gene flow. Adult dispersal occurs in some species, is often facultative, and is poorly understood, but has important management implications, particularly with respect to disease spread. Although the role of adult dispersal in spreading disease has been documented, the potential influence of disease on dispersal has received little attention. African buffalo (*Syncerus caffer*) are wide ranging and harbor many pathogens that can affect nearby livestock. Dispersal of adult buffalo has been well documented, but ecological and social drivers of buffalo dispersal are poorly understood.

At the individual level, animals must balance the potential benefits of dispersal against its costs. Costs may be incurred in the form of risk, such as mortality or potential injury while dispersing, energetic and time costs associated with the energy and time invested in dispersing, and costs associated with lost opportunities, e.g. reduced fecundity due to unfamiliar surroundings and social groups. Disease in particular is another poorly-understood but potentially important factor influencing costs and benefits of dispersal. Dispersal from a crowded habitat may offer an escape from high pathogen and parasite exposure risk, conversely dispersing

individuals in this stressful period may have reduced immunity and consequently be more susceptible to infections. In addition, if pathogen exposure profiles differ among social groups, dispersing animals may face new pathogen challenges to which they are immunologically naïve to, when they arrive at a new social group. However, few studies have estimated dispersal costs of large mammals, particularly those with facultative adult dispersal.

First, we investigated drivers of adult buffalo dispersal to determine whether likelihood of dispersal for individual female buffalo was influenced by (1) animal traits, including age, condition, and reproductive status (2) herd membership, (3) environmental variables - season and year, (4) gastro-intestinal parasites - strongyles, coccidia and schistosomes and (5) microparasite infections - bovine tuberculosis (*Mycobacterium bovis*) and brucellosis (*Brucella abortus*). The likelihood and drivers of buffalo dispersal varied by herd, area and year. In the Lower Sabie herd younger individuals were more likely to disperse, with most dispersal occurring in the early wet season and during an unusually dry year, 2009. In the Crocodile Bridge area buffalo in poor condition were most likely to disperse. Our findings suggest that dispersal of female buffalo is driven by either seasonal (Lower Sabie), or perhaps social (Crocodile Bridge) resource restriction. We found no direct effects of infections on buffalo dispersal, assuaging fears that highly infectious individuals might be more prone to dispersing, which could accelerate the spatial spread of infectious diseases.

Second, we investigated: (1) effects of dispersal on fitness, by comparing survival, and fecundity of dispersing and philopatric (control) buffalo, as well as comparing the difference in pre and post dispersal body condition of dispersers with the change of body condition of philopatric control animals for the same period; (2) disease risks associated with dispersal, by determining whether burdens of gastro-intestinal parasites and the incidence of bacterial and

viral infections changed during dispersal. No significant difference in mortality risk or fecundity was observed between dispersing and philopatric control animals, nor did change in body condition differ. However, we detected disease consequences of dispersal that varied by location. Dispersers from the resource-limited herd suffered more bovine tuberculosis and brucellosis infections after dispersal, both of which are chronic infections with clear, long term effects on survival and fecundity, when compared to controls from the same location. Dispersers from the less resource-limited herds had increases in schistosome burdens. Schistosomes are parasitic worms with relatively minor health effects; relatively long-lived but not as long as the life of the host (i.e., buffalo can reduce their burdens). Previous work has shown that adult buffalo disperse in response to resource limitation due to seasonal forage shortages or density dependent

©Copyright by Robert Steven Spaan
October 27, 2015
All Rights Reserved

Dispersal Behavior in African Buffalo (*Syncerus caffer*): Tradeoffs Between Nutritional
Resources and Disease Exposure

by
Robert Steven Spaan

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented October 27, 2015
Commencement June 2016

Master of Science thesis of Robert Steven Spaan presented on October 27, 2015

APPROVED:

Major Professor, representing Wildlife Science

Head of Department of Fisheries and Wildlife

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Robert Steven Spaan, Author

ACKNOWLEDGEMENTS

Anna – I can't express enough, my gratitude for the opportunities you and Vanessa provided both me and Johannie. I feel very privileged to have been able to play a role in the buffalo project, getting the opportunity to return to a really special system to work with fantastic wildlife and people. Thanks for guiding me through my graduate research and for stimulating my scientific thought (helping me find my "inner nerd" as you put it). Lastly, thanks for having the foresight to have Clint advise me.

Clint –As an advisor you've really stimulated my thinking and interest in wildlife sciences. You were also amazing at guiding me through the perils of graduate research. I look forward to your continuing guidance as my advisor. I also look forward to the future hunts, adventures and general mischief.

I would also like to acknowledge the many members of the Jolles and Epps research groups, including Michael Buchalski, Jessica Castillo, Tyler Creech, Rachel Crowhust, Daniella Dekelaita, Mark Linnell, Page Minton-Edison, Katie Moriarty, Brandon Nickerson, Abby Sage, Doni Schwalm, Bree Beechler, Heather Broughton, Brian Dugovich, Caroline Glidden, Rhea Hanselmann, Abby Sage, Johannie Spaan and Hannah Tavalire for helping me grow as an individual and a scientist. Thanks also to the many different people in the Department of Fisheries and Wildlife for their support.

Thanks to both sides of my family for all their love, care and support, even if it is from across the "pond". Most of all I'd like to thank my wife, Johannie, for all her support and encouragement. Being able to share study fields is so rewarding. I look forward to our ongoing adventures to corners far and wide.

CONTRIBUTION OF AUTHORS

Robert Steven Spaan conceived the study, assisted with study design, performed field and lab work, analyzed data and drafted both the manuscripts. Dr. Anna Jolles and Dr. Ezenwa funded the project, assisted with study design, did field and lab-work, provided and analyzed data, and assisted in writing both manuscripts. Dr. Clint Epps assisted with study design, did field and lab work, provided and analyzed data, and assisted in writing the both manuscripts. Dr. Briana Beechler did field and lab work, provided data, and assisted in design of my 2nd manuscript.

TABLE OF CONTENTS

	<u>Page</u>
1 - Why did buffalo cross the Park?	1
Abstract	2
Introduction	3
Methods.....	7
Study area	7
Capturing buffalo and tracking movement	8
Definition of dispersal and analysis of spatial data	10
Sample collection	11
Diagnostics	11
Dispersal rates	12
Ethics statement	13
Results	13
Dispersal rates	13
Drivers of dispersal	15
Discussion	16
Acknowledgements.....	19
References	19
2 - Adult dispersal increases disease exposure	51
Abstract	52
Introduction	54
Methods.....	57

TABLE OF CONTENTS (Continued)

	<u>Page</u>
Study area	57
Definition of dispersal and analysis of spatial data	58
Sample collection	59
Diagnostics	59
Dispersal rates	61
Fitness costs or benefits – survival	61
Controls	62
Fitness costs or benefits – fecundity and body condition	62
Infection costs or benefits – gastrointestinal parasites, viral and bacterial infections	63
Ethics statement	63
Results	64
Dispersal rates	63
Fitness costs or benefits – survival	64
Fitness costs or benefits – fecundity and body condition	65
Infection costs or benefits – gastrointestinal parasites, viral and bacterial infections	65
Discussion	66
Acknowledgements.....	69
References	69

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1.1 Map of study area.....	38
1.2 Predictors of female African buffalo dispersal likelihood.	39
1.3 Mean body condition for buffalo showing a single season time lag in variation in mean body condition by season and seasonal rainfall	41
2.1 Map of study area.....	85
2.2 Fitness measures of African buffalo	86
2.3 Infection measures of African buffalo.....	88
S1.1 Box area from figure 1	42

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1.1 Model selection of generalized linear mixed effect models predicting dispersal likelihood of female African buffalo	33
1.2 Cumulative AIC weights for each predictor variable from every possible model across the set of predictor variables considered	35
1.3 Odds ratios and parameter estimates for variables in the best-fit generalized linear mixed effect models of factors predicting dispersal likelihood of female African buffalo.....	36
2.1 Contrasting demographic parameters (survival, body condition, fecundity, and population growth rate) of African buffalo	81
2.2 Univariate models determining whether dispersal is a significant predictor of survival of female African buffalo	82
2.3 Output from paired t-tests comparing the change in pre and post dispersal pregnancy rates between dispersers and controls.....	83
2.4 Output from paired t-tests comparing either the change in worm burden or the number of viral and bacterial infections gained in the dispersal period between dispersing and controls individuals	84
S1.1 Data available for this study	42
S1.2 Univariate models of fixed effects predicting dispersal likelihood of female African buffalo	44
S1.3 Correlation of fixed effects predicting dispersal likelihood of female African buffalo	47
S1.4 Monthly and annual rainfall of study area (mm)	49
S2.1 Data available for this study	90
S2.2 Model selection tables from Cox proportional hazards models predicting survival of female African buffalo	92
S2.3 Cumulative AIC weights for each predictor variable from every possible Cox proportional hazard model across the set of predictor variables	93

1 - Why did the buffalo cross the park? Intrinsic and extrinsic drivers of dispersal by female African buffalo (*Syncerus caffer*)

Abstract

Dispersal facilitates population health and maintains resilience in species via gene flow. Adult dispersal occurs in some species, is often facultative, and is poorly understood, but has important management implications, particularly with respect to disease spread. Although the role of adult dispersal in spreading disease has been documented, the potential influence of disease on dispersal has received little attention. African buffalo (*Syncerus caffer*) are wide ranging and harbor many pathogens that can affect nearby livestock. Dispersal of adult buffalo has been well documented, but ecological and social drivers of buffalo dispersal are poorly understood. We investigated drivers of adult buffalo dispersal during a 4-year longitudinal study at Kruger National Park, South Africa. We monitored the spatial movement of 200 female buffalo in two focal areas using satellite and radio collars, and captured each buffalo every 6 months to assess animal traits and disease status. We used generalized linear mixed models to determine whether likelihood of dispersal for individual female buffalo was influenced by (1) animal traits, including age, condition, and reproductive status (2) herd membership, (3) environmental variables - season and year, (4) gastro-intestinal parasites - strongyles, coccidia and schistosomes and (5) microparasite infections - bovine tuberculosis (*Mycobacterium bovis*) and brucellosis (*Brucella abortus*). The likelihood and drivers of buffalo dispersal varied by herd, area and year. In the Lower Sabie herd younger individuals were more likely to disperse, with most dispersal occurring in the early wet season and during an unusually dry year, 2009. In the Crocodile Bridge area buffalo in poor

condition were most likely to disperse. Our findings suggest that dispersal of female buffalo is driven by either seasonal (Lower Sabie), or perhaps social (Crocodile Bridge) resource restriction. We found no direct effects of infections on buffalo dispersal, assuaging fears that highly infectious individuals might be more prone to dispersing, which could accelerate the spatial spread of infectious diseases.

Introduction

Dispersal is an essential life-history trait in animals that functions as a mechanism for avoiding inbreeding and finding usable habitats (Kokko & López-Sepulcre 2006; Lebigre, Alatalo & Siitari 2010; Sparkman *et al.* 2012). Most studies of dispersal have explored natal dispersal, which is typically a permanent movement of juveniles away from their natal area, largely restricted to one sex within a particular species (Martin *et al.* 2008; Hanski & Selonen 2009; Liebgold *et al.* 2011; Arora *et al.* 2012). However, for some long-lived species, adults of either sex may make occasional permanent or long-term movements to different populations, habitat patches, or herds, e.g. desert bighorn sheep (*Ovis canadensis nelsonii*) (Epps *et al.* 2007), bison (*Bison bison*) (Plumb *et al.* 2009) and mountain caribou (*Rangifer tarandus caribou*) (van Oort, McLellan & Serrouya 2011). Both natal and adult dispersal are considered important in management and conservation of wild populations as they allow for recolonization of empty habitat patches (e.g. Epps *et al.* 2010; Griffiths, Sewell & McCrea 2010; Abbott 2011), demographic rescue (Forester 2011; van Oort, McLellan & Serrouya 2011; Eriksson *et al.* 2014), and maintenance

of genetic diversity through gene flow (Bowler & Benton 2005; Epps *et al.* 2005; Clark *et al.* 2010).

Adult dispersal is poorly understood compared to natal dispersal. Possible reasons for adult dispersal include density dependence, lack of food, interspecific interactions, relatedness of potential mates in the current home range (Bowler & Benton 2005), or potential for improving social status (Clutton-Brock & Lukas 2012). In moose, high population density and resource limitation are correlated with higher adult dispersal rates (Labonté *et al.* 1998). Similarly, dispersal of bison in Yellowstone National Park is density dependent and more common as bison populations reach carrying capacity (Plumb *et al.* 2009), a trend also seen in the fast-growing population of wood bison in northern Canada (Gates *et al.* 1990; Larter *et al.* 2000).

Infectious diseases are another important aspect to consider when studying adult or juvenile dispersal in wild populations, as dispersing animals may act as primary vectors facilitating the movement of parasites and pathogens across large geographic areas (Hess 1996). An example of this is the spread of chronic wasting disease (CWD) by white-tailed deer (*Odocoileus virginianus*) (Robinson *et al.* 2013; Green *et al.* 2014) with CWD positive deer dispersing greater than 60 km. The risk of disease spread via animal dispersal also has management consequences. For example, bison dispersing outside of the boundaries of Yellowstone are controlled due to their potential risk as spreaders of brucellosis to domestic cattle (Plumb *et al.* 2009). Importantly, disease may influence dispersal through direct impacts on animal behavior (Bowler & Benton 2005) or by affecting body condition (Belthoff & Dufty

Jr. 1998; Armsworth 2009; Debeffe *et al.* 2012). For example, body mass of European roe deer (*Capreolus capreolus*) is correlated with dispersal likelihood and dispersal distance, with individuals with a body mass less than 14 kg not dispersing and distance dispersed increasing with body mass (Debeffe *et al.* 2012). In the same population of European roe deer, dispersal propensity has been shown to decrease with nematode parasite burden, which is associated with a decrease in body mass (Debeffe *et al.* 2014).

African buffalo offer a unique opportunity to examine the influences of extrinsic and intrinsic factors, including infectious diseases, on adult dispersal. Buffalo are long-lived, wide ranging, and gregarious, with adult dispersal observed in both sexes (Oloff, Ritchie & Prins 2002). African buffalo have the weakest genetic structure of all African ungulates studied to date (Lorenzen, Arctander & Siegismund 2008) with high levels of diversity observed in 11 populations across southern and eastern African populations and significant differentiation only at the continental level (Simonsen, Siegismund & Arctander 1998). These findings suggest that buffalo are less philopatric than other African ungulates (Metzger *et al.* 2010). However, as populations are increasingly restricted by loss of habitat, habitat fragmentation and human-made barriers, gene flow among some populations may be decreasing (Heller, Okello, & Siegismund 2010; Epps *et al.* 2013) and thus dispersal, gene flow, and connectivity have become conservation priorities for buffalo management (Simonsen, Siegismund & Arctander 1998; van Hooft, Groen & Prins 2003).

On the other hand, African buffalo may pose a disease risk to domestic species and other wildlife, because they carry a number of diseases that are of

economic concern such as bovine tuberculosis (Renwick, White & Bengis 2007; Roug *et al.* 2014), brucellosis (Alexander *et al.* 2012; Tanner *et al.* 2014) and foot-and-mouth disease (Dion, Van Schalkwyk & Lambin 2011; Brahmabhatt *et al.* 2012; Dion & Lambdin 2012). Thus, understanding buffalo ranging behavior (Ryan, Knechtel & Getz 2006) can help to inform management decisions regarding their potential to cause spillover of disease into both wildlife populations (Bastos *et al.* 2000), domestic livestock (Michel & Bengis 2012) and people in the case of zoonotic infections (Michel *et al.* 2006; Alexander *et al.* 2012).

Observational and genetic studies suggest that almost all male buffalo disperse away from their natal herds (Sinclair 1977; Prins 1996; van Hooft, Groen & Prins 2003). Foundational behavioral studies of female African buffalo found that they form discrete herds with limited inter-herd movements (Sinclair 1977; Skinner & Smithers 1990; Prins 1996); but more recent observational and genetic work suggests that dispersal by adult female buffalo is not uncommon (e.g. Halley *et al.* 2002; van Hooft, Groen & Prins 2003). For example, Simonsen, Siegismund & Arctander (1998) found little genetic structure in either maternally-inherited mitochondrial DNA or microsatellite (nuclear) loci among buffalo populations across 11 localities in eastern and southern Africa. Furthermore, genetic studies in Kruger National Park, South Africa, estimated that female buffalo older than two years of age migrate at 5-20% per generation (van Hooft, Groen & Prins 2003).

Despite abundant evidence that dispersal is a common feature of the adult African buffalo behavioral repertoire, the social and ecological factors underlying decisions to disperse are not well understood in male or female buffalo (Halley *et al.* 2002;

Winnie Jr., Cross & Getz 2008). We therefore evaluated how animal traits, environmental conditions, and disease status affect dispersal of adult female buffalo. Specifically, we evaluate whether the likelihood of dispersal by female African buffalo is influenced by (1) animal traits such as age, condition, pregnancy and lactation, (2) herd membership, (3) season, (4) macroparasites, including strongyle nematodes, coccidia and schistosomes, and (5) microparasites, including *Mycobacterium bovis* (causative agent of bovine tuberculosis) and *Brucella abortus* (causative agent of brucellosis).

Methods

Study area

Our study took place in the Kruger National Park (KNP), South Africa, which lies between 22.5 and 25.5°S, 31.0 and 31.6°E and is ~19 485 km² in extent (Fig.1.1). The park has one wet season per year with summer rainfall (October-March) ranging north to south from 400 to 700 mm per year. KNP is located at an average altitude of 250 m (range 200-900 m) above sea level with granitic soils in the west succeeded by Ecca shale, basalt and rhyolites. The variation in moisture between seasons and soil types give rise to large regional variations in food availability. The main study area spans the landscape types of the Lebombo mountain bushveld, Marula (*Sclerocarya birrea subsp. caffra*)/Knobthorn (*Vachellia nigrescens*) savannah, Delagoa thorn

(*Vachellia welwitschii*) thickets, Sabie and Crocodile River thickets and Thornveld (Venter, Scholes & Eckhardt 2003).

The Lower Sabie (LS) and Crocodile Bridge (CB) herds utilize distinct areas within KNP with different underlying geological features, which give rise to different soils and associated vegetation (Venter, Scholes & Eckhardt 2003). Water distribution (both natural and artificial) within the areas used by the herds also varies (Gaylard, Owen-Smith & Redfern 2003). This is important since buffalo are water dependent and herd densities are associated with distance to water (Redfern *et al.* 2003).

Opportunities for dispersal also varied for the study herds, due to their position with respect to the park's boundary fence. The fence restricted movement of LS animals to the east, while the CB animals were restricted to both the south and east (Pickett, Cadenasso & Benning 2003). The CB animals are made up of two herds – Mountain and Power Line herds. We initially thought this was a single herd, but after observing the buffalo, and on inspection of spatial data we realized that there were two separate herds.

Capturing buffalo and tracking movement

In June/July and October of 2008, we captured 200 female buffalo, 100 each from two sections in the southern KNP: LS and CB. Captures were conducted from helicopters with a dart gun using a combination of etorphine hydrochloride, azaperone and ketamine. Effects of the opioids on immobilized buffalo were reversed using a combination of naltrexone and diprenorphine. Buffalo were fitted with either

a GPS ($n = 7$) or a VHF collar ($n = 193$) as part of a study investigating bovine tuberculosis and gastro-intestinal helminth interactions (Table S1, Supporting information). As part of this study, 100 randomly selected animals (50 from each section) received a long-acting anthelmintic bolus (Panacur bolus, (Intervet, UK)). We recaptured all buffalo biannually. The timing of the initial captures allowed us to alternate between the two areas twice per year. All LS animals came from one large buffalo herd, while CB buffalo were distributed amongst 2 main herds, the Mountain and Power Line herds (Fig. 1.1). Any animals that died throughout the study period were replaced with similar-aged animals from the same herd. Captures were conducted using the same immobilization method as the initial captures, except that buffalo were darted from the ground using 4 x 4 vehicles. Satellite collars provided 2 locations daily (06:00 and 18:00 local time) to establish the general location of each buffalo herd. Once a herd was located, we verified presence/absence of collared individuals and recorded date, time and GPS location. All VHF collar frequencies for the entire study area were checked in each herd to detect individuals that dispersed between herds.

Buffalo in the LS herd were monitored throughout the duration of the project. However, with the CB herds (Fig. 1.1) this was not always possible due to greater distance from our base location, at Skukuza and terrain that was difficult to navigate during the wet season. As a result, sample distribution for collar locations in the LS herd is more even throughout the year than sample distribution for the CB herds. Eleven collared buffalo left the confines of KNP; when possible those individuals were recaptured, brought back into KNP, and placed in the herd closest to the point of

exit. When individuals left KNP to unfenced adjoining private reserves relocation was not possible, so collars were removed. If buffalo crossed the fence on KNP's eastern boundary into the part of Mozambique, collars could not be retrieved.

The LS herd contained satellite collars throughout the entire duration of the project (n=4, with 1 replaced in November 2009 due to predation), but lost 2 to dispersal to different herds during the course of the study. The CB herd had 3 satellite collars throughout the project (Mountain herd, n=2; Power Line herd, n=1).

Definition of dispersal and analysis of spatial data

For the purpose of this study we defined dispersers as “individual buffalo that were recorded outside of their herd of origin's home range joined another herd and did not return to their herd of origin for at least one season”. For each herd, GPS locations from the satellite collars were mapped in ArcMap 10.1 (Environmental Systems Research Institute, Inc., Redlands CA) and home ranges estimated for each of the original herds using a minimum convex polygon (Worton 1987) in Hawth's Tools (Beyer 2004). This analysis assumed that buffalo with satellite collars accurately reflected the position of the entire herd. Home ranges were estimated separately for the wet season (October to March) and the dry season (April to September) in each year from September 2009 to August 2012.

Sample collection

Age, condition, pregnancy and lactation status were recorded for all recaptured buffalo, and the experimental individuals received the Panacur bolus. Blood was collected via jugular venipuncture into 10 ml EDTA coated vacutainer tubes, placed on ice and transported to Veterinary Wildlife Services (VWS) laboratory in Skukuza, KNP. Feces were collected rectally and transported back to the lab in a cooler with ice packs. Age was determined by tooth eruption up to 5 years and then judged by tooth wear (Grimsdell 1973; Jolles 2007). Body condition was determined by palpation of fat reserves on the ribs, spine, hips and tail on a scale of 1 (very poor) to 5 (very good) and then averaged (Ezenwa, Jolles & O'Brien 2009). Pregnancy status was determined by rectal palpation (Beechler *et al.* 2012). Lactation was determined by manually milking all four teats (Jolles, Cooper & Levin 2005).

Diagnostics

Methods we employed for macro- and microparasite diagnostics have been described previously (Ezenwa 2003; Budischak, Jolles & Ezenwa 2012; Anderson, Ezenwa & Jolles 2013; Gorsich *et al.* 2015). Fecal egg and oocyst counts were used to assess GI nematode and coccidian infection using a modified McMaster method (Ezenwa 2003). Previous work has shown GI nematode infections in this buffalo population commonly include, *Cooperia fuelleborni*, *Haemonchus placei*, *Haemonchus bedfordi*, and an undescribed *Parabronema* species and that fecal egg counts accurately reflect gastro-intestinal helminth burdens (Budischak *et al.* 2015). A strip enzyme-linked immunosorbent assay (ELISA) to detect circulating anodic

antigen (Bont, Steck & Meyer 1996) was validated for use in African buffalo (Beechler *et al. in prep*) and used to determine schistosome infection. TB was diagnosed using a whole-blood gamma interferon assay (BOVIGAM, Prionics), optimized for African buffalo with a sensitivity of 86% and a specificity of 92% (Michel *et al.* 2011). A commercial enzyme-link immunosorbent assay (IDEXX Brucellosis Serum Ab Test) was used to detect brucellosis (Gorsich *et al.* 2015).

Dispersal rates

We used generalized linear mixed models (GLMMs) with a binomial distribution (dispersal = 1; non-dispersed = 0) to examine which variables; best predicted whether female buffalo dispersed. We conducted three analyses, using: 1) all data combined (hereafter, pooled data), 2) the LS herd and 3) the herds in the CB area. We analyzed herds separately, because drivers of dispersal may differ between populations experiencing different environments.

Animal traits, season, year, treatment, gastro-intestinal parasites, and microparasite infections were included as fixed effects (Table S1, Supporting information), and animal ID was included as a random effect in all models, to account for repeated measures of the same individual buffalo. We also used herd affiliation as a fixed effect in the pooled data to test if dispersal drivers varied by herd. In analyses of the CB data we considered animal ID and herd affiliation as nested random effects (Bates *et al.* 2014) to account for the repeated measures of individuals within the multiple herds that comprise the CB population.

For all analyses, the final models were selected using forward stepwise regression eliminating non-significant variables. We then ranked all models according to Akaike's Information Criteria (AIC, Burnham & Anderson 2002) and reported the top five models (Table 1). To explore the importance of each individual predictor we summed the AIC weights for each predictor across all models to calculate each predictor's cumulative weight (Table 2) (Burnham & Anderson 2002). All statistical analyses were performed in the program R, v. 3.1.1 (R Core Team 2014), with models fitted using the `glmer` and `lmer` functions in the `lme4` package (Bates *et al.* 2014).

Ethics statement

All procedures were approved by South African National Parks Board (Reference No. SPARS914) and by Oregon State University and University of Georgia IACUC (Protocol numbers: OSU No. 2833, UGA No. A201010-190-A1).

Results

Dispersal rates

During the course of the four year study a total of 304 female African buffalo were captured and tracked: 137 in the LS herd, and 167 in the CB herds. Throughout the study period, 93 individuals (30.6%) dispersed, 54 from the LS herd and 39 from

the CB area. Thus, 39.4% of LS animals and 23.4% of CB animals dispersed throughout the study period.

Owing to mortalities and dispersal, not all animals were in the study, or in their herd of origin, for the full study period of four years. Annual dispersal rates for each herd are therefore calculated as the number of dispersers observed in each herd, divided by the number of “buffalo-years-at-risk” of dispersal from that herd. The number of buffalo-years-at-risk of dispersal is calculated by scoring, for each buffalo, the duration from its first capture until it either died or left the herd. These individual observation periods are then added up for all buffalo observed in the herd, to give the total number of buffalo-years-at-risk of dispersing. Dispersal rates thus expressed the annual per-capita “risk” or likelihood of dispersing from a given herd; analogous to incidence rates in epidemiological studies. The annual dispersal rate for the LS herd was significantly higher, at 19.2%, than the annual dispersal rate of 14.5% in the CB area (Table 3).

This is much higher than the crude estimate one would arrive at by simply dividing the fraction of animals that dispersed (here, 30.5%) by the study duration of four years, i.e. 7.6 % overall, or 9.9% and 5.9% for the LS and CB herds, respectively. These crude estimates are misleading because they erroneously assume that all buffalo, including dispersers and non-dispersers, were observed in their herds of origin.

Drivers of dispersal

Across study regions, age, herd of origin, year, season, body condition and reproductive status contributed to variation in dispersal (Table 1.1). However, the relative importance of these drivers of dispersal differed between the two study areas, LS and CB (Table 1.2). The dispersal rate for LS was higher than for CB herds. Younger buffalo were more likely to disperse (Table 1.3; Fig. 1.2a). This trend was driven by a strong, negative effect of age on dispersal rate in the LS herd. There was inter-annual variation in dispersal likelihood (Table 1.3, Fig 1.2e), but different years had high dispersal rates in two areas. Because our observation period started in July 2008 and ended in June 2012, we only had three entire years (2009-11), among which to compare dispersal rates. The driest year, 2009, stands out as having very high dispersal rates, driven by strong movement out of the LS herd (Table 1.3, Fig. 1.2e). Overall, most adult buffalo dispersal occurred in the early wet season, when buffalo are in their worst condition, following resource restriction throughout the dry season. Interestingly, this effect was driven by the LS herd, while dispersal from the CB herds peaked earlier, in the late dry season (Table 1.3, Fig. 1.2d). This corresponds to an earlier loss of body condition for buffalo in the CB area, due to differences in rainfall patterns and soil type among the two areas (Fig. 1.3). Dispersing buffalo tended to be in poorer body condition than comparable individuals that did not leave their herd. This trend was stronger in the CB herds (Table 1.3, Fig. 1.2b), where body condition is overall much worse than at LS (Gorsich *et al.* 2015) (Fig. 1.3). Finally, buffalo were less likely to disperse if they were lactating. This effect was detectable at LS, but not at CB (Table 1.3, Fig 1.2c), where overall lactation rates were much lower. None of the infectious disease variables that we tested for: gastro-intestinal parasites -

strongyles, coccidia and schistosomes, and microparasite infections - bovine tuberculosis and brucellosis had detectable direct effects on dispersal rates in adult female buffalo (Table S 1.2, Supplementary information).

Discussion

Adult dispersal was common in female African buffalo, and appeared to be driven by resource restriction. Buffalo dispersed after the dry season, following prolonged resource restriction, and individuals in poor body condition were more likely to disperse. Younger buffalo dispersed more often, whereas females currently raising a young calf were unlikely to leave their herds. By contrast, none of the infectious diseases we diagnosed directly affected dispersal decisions in adult buffalo. Buffalo thus appear to disperse as a mechanism for escaping resource limitation, which could occur due to external factors such as drought, to intraspecific competition in areas where buffalo populations are approaching seasonal carrying capacities.

We observed differing patterns in the study herds. In the LS herd, resources were abundant and young buffalo were more likely to disperse, whereas in the CB herd which was resource-poor, buffalo in poor condition were more likely to disperse. This pattern matches predictions from theoretical explorations of dispersal rates. For instance, Bonte & De La Peña (2009) argued that dispersal rates will increase for individuals with higher body condition when there is connectivity across metapopulations as well as environmental variation, and that individuals in good body

condition may disperse to take advantage of low density areas that could offer increased breeding opportunities. Young buffalo in the LS herd were in relatively good condition, but may have faced strong intraspecific competition for resources due to the hierarchical social structure of buffalo herds (Sinclair 1977; Mloszewski 1983; Prins 1989). Bonte & De La Peña (2009) further predicted that individuals in low body condition will disperse more frequently when mortality is high and there is limited variation, and Ryan, Knechtel & Getz (2007) theorized that a lack of resources associated with low rainfall years would lead to individual female buffalo becoming non-reproductive or dispersing to better habitat. This alternate pattern may explain why individuals in poor condition in the more resource-limited CB herd were willing to risk dispersal.

Animal movements such as migration and dispersal offer individuals the opportunity to flee from infected habitats and thereby avoid highly infected individuals not able to migrate or disperse (Altizer, Bartel & Han 2011; Hall, Altizer & Bartel 2014).

Conversely, it has been suggested that stressful movements, such as dispersal and migration, could potentially lower immunological function making individuals more susceptible to infection (Bonte *et al.* 2012). We found no direct effect of infectious diseases on likelihood of dispersal in our study. However, the relationship we found between dispersal and condition points to the possibility that some infectious diseases, especially chronic infections, indirectly impact dispersal as they can negatively affect body condition, e.g. bovine tuberculosis (Caron, Cross & du Toit 2003) and gastro-intestinal parasites (Budischak *et al.* 2012; Gorsich, Ezenwa & Jolles 2014; Beechler *et al. in prep.*).

Here, we have reported one of the most extensive studies on dispersal in large mammal species, recording 550 buffalo years and 93 dispersal events over a four year observation period. Our study revealed, for the first time, a tight link between resource limitation and dispersal decisions in a subtropical, social ungulate. Adult buffalo appear to disperse in an attempt to outrun unfavorable resource conditions, which can cause loss of body condition and potentially, fitness. In the context of subtropical climates, where season and interannual variation in forage availability is largely driven by rainfall patterns, our results suggest that dispersal patterns for buffalo and possibly other large herbivores may change fundamentally due to anthropogenic climate change and surface water management. Most (80%) climate projections suggest that southern Africa will have increased temperatures, reduced rainfall and later onset of rains (James & Washington 2013), which would lead to an expected increase in dispersal, disease effects (Tracey *et al.* 2014) and potential changes in genetic structure.

Future research should address actual effects of dispersal on fitness-related variables such as lifetime reproductive potential, survival, genetic diversity of offspring, and resistance to infection.

Acknowledgements

This research was supported by a National Science Foundation Ecology of Infectious Disease Grant awarded to V. Ezenwa and A. Jolles (DEB-1102493/EF-0723928 and EF-0723918). We also acknowledge the essential contributions in

animal handling and data collection by field technician Jo Spaan; veterinarians Brianna Beechler, Peter Buss, and Kristie Thompson; and veterinary technicians Jenny Joubert and Khosi Maseko. We would also like to acknowledge Dr. Sam Ferreira for assisting with the registration and support of this project.

References

- Abbott, K.C. (2011) A dispersal-induced paradox: synchrony and stability in stochastic metapopulations: Dispersal-induced paradox in metapopulations. *Ecology Letters*, **14**, 1158–1169.
- Alexander, K.A., Blackburn, J.K., Vandewalle, M.E., Pesapane, R., Baipoledi, E.K. & Elzer, P.H. (2012) Buffalo, bush meat, and the zoonotic threat of brucellosis in Botswana. *PLoS ONE*, **7**, e32842.
- Altizer, S., Bartel, R. & Han, B.A. (2011) Animal migration and infectious disease risk. *Science*, **331**, 296–302.
- Anderson, K., Ezenwa, V.O. & Jolles, A.E. (2013) Tick infestation patterns in free ranging African buffalo (*Syncerus caffer*): Effects of host innate immunity and niche segregation among tick species. *International Journal for Parasitology: Parasites and Wildlife*, **2**, 1–9.
- Armsworth, P.R. (2009) Conditional dispersal, clines, and the evolution of dispersiveness. *Theoretical Ecology*, **2**, 105–117.

- Arora, N., Van Noordwijk, M.A., Ackermann, C., Willems, E.P., Nater, A., Greminger, M., Nietlisbach, P., Dunkel, L.P., Utami Atmoko, S.S., Pamungkas, J., Perwitasari-Farajallah, D., Van Schaik, C.P. & Krützen, M. (2012) Parentage-based pedigree reconstruction reveals female matrilineal clusters and male-biased dispersal in nongregarious Asian great apes, the Bornean orangutans (*Pongo pygmaeus*). *Molecular Ecology*, **21**, 3352–3362.
- Bartel, R.A., Oberhauser, K.S., De Roode, J.C. & Altizer, S.M. (2011) Monarch butterfly migration and parasite transmission in eastern North America. *Ecology*, **92**, 342–351.
- Bastos, A.D.S., Boshoff, C.I., Keet, D.F., Bengis, R.G. & Thompson, G.R. (2000) Natural transmission of foot-and-mouth disease virus between African buffalo (*Syncerus caffer*) and impala (*Aepyceros melampus*) in the Kruger National Park, South Africa. *Epidemiology and infection*, **124**, 591–598.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) *lme4: Linear mixed-effects models using Eigen and S4*. R package version 1.1-6.
<http://CRAN.R-project.org/package=lme4R>
- Beechler, B.R., Broughton, H., Bell, A., Ezenwa, V.O. & Jolles, A.E. (2012) Innate immunity in free-ranging African buffalo (*Syncerus caffer*): Associations with parasite infection and white blood cell counts. *Physiological and Biochemical Zoology*, **85**, 255–264.
- Belthoff, J.R. & Dufty Jr, A. (1998) Corticosterone, body condition and locomotor activity: a model for dispersal in screech-owls. *Animal Behaviour*, **55**, 405–415.

- Beyer, H.L. (2004) Hawth's analysis tools for ArcGIS.
<http://www.spatialecology.com/htools>.
- Bonte, D. & De La Peña, E. (2009) Evolution of body condition-dependent dispersal in metapopulations. *Journal of Evolutionary Biology*, **22**, 1242–1251.
- Bonte, D., Van Dyck, H., Bullock, J.M., Coulon, A., Delgado, M., Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., Saastamoinen, M., Schtickzelle, N., Stevens, V.M., Vandewoestijne, S., Baguette, M., Barton, K., Benton, T.G., Chaput-Bardy, A., Clobert, J., Dytham, C., Hovestadt, T., Meier, C.M., Palmer, S.C.F., Turlure, C. & Travis, J.M.J. (2012) Costs of dispersal. *Biological Reviews*, **87**, 290–312.
- Bont, A., Steck, A.J. & Meyer, U.A. (1996) The acute hepatic porphyrias and their neurologic syndromes. *Schweizerische Medizinische Wochenschrift*, **126**, 6–14.
- Bowler, D.E. & Benton, T.G. (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews*, **80**, 205–225.
- Brahmbhatt, D.P., Fosgate, G.T., Dyason, E., Budke, C.M., Gummow, B., Jori, F., Ward, M.P. & Srinivasan, R. (2012) Contacts between domestic livestock and wildlife at the Kruger National Park Interface of the Republic of South Africa. *Preventive Veterinary Medicine*, **103**, 16–21.
- Budischak, S.A., Jolles, A.E. & Ezenwa, V.O. (2012) Direct and indirect costs of co-infection in the wild: Linking gastrointestinal parasite communities, host

- hematology, and immune function. *International Journal for Parasitology: Parasites and Wildlife*, **1**, 2–12.
- Budischak, S.A., Hoberg, E.P., Abrams, A., Jolles, A.E. & Ezenwa, V.O. (2015) A combined parasitological molecular approach for noninvasive characterization of parasitic nematode communities in wild hosts. *Molecular Ecology Resources*, **15**, 1112–1119.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York.
- Caron, A., Cross, P.C. & du Toit, J.T. (2003) Ecological implications of bovine tuberculosis in African buffalo herds. *Ecological Applications*, **13**, 1338–1345.
- Clark, R.W., Brown, W.S., Stechert, R. & Zamudio, K.R. (2010) Roads, interrupted dispersal, and genetic diversity in timber rattlesnakes: Roads and population genetics. *Conservation Biology*, **24**, 1059–1069.
- Clutton-Brock, T.H. & Lukas, D. (2012) The evolution of social philopatry and dispersal in female mammals. *Molecular Ecology*, **21**, 472–492.
- Debeffe, L., Morellet, N., Cargnelutti, B., Lourtet, B., Bon, R., Gaillard, J.-M. & Mark Hewison, A.J. (2012) Condition-dependent natal dispersal in a large herbivore: heavier animals show a greater propensity to disperse and travel further. *Journal of Animal Ecology*, **81**, 1327–1327.
- Debeffe, L., Morellet, N., Verheyden-Tixier, H., Hoste, H., Gaillard, J.-M., Cargnelutti, B., Picot, D., Sevila, J. & Hewison, A.J.M. (2014) Parasite

abundance contributes to condition-dependent dispersal in a wild population of large herbivore. *Oikos*, **123**, 1121–1125.

Dion, E., Van Schalkwyk, L. & Lambin, E.F. (2011) The landscape epidemiology of foot-and-mouth disease in South Africa: A spatially explicit multi-agent simulation. *Ecological Modelling*, **222**, 2059–2072.

Dion, E. & Lambin, E.F. (2012) Scenarios of transmission risk of foot-and-mouth with climatic, social and landscape changes in southern Africa. *Applied Geography*, **35**, 32–42.

Epps, C.W., Palsbøll, P.J., Wehausen, J.D., Roderick, G.K., Ramey, R.R. & McCullough, D.R. (2005) Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep: Highways reduce genetic diversity. *Ecology Letters*, **8**, 1029–1038.

Epps, C.W., Wehausen, J.D., Bleich, V.C., Torres, S.G. & Brashares, J.S. (2007) Optimizing dispersal and corridor models using landscape genetics: Optimizing connectivity models. *Journal of Applied Ecology*, **44**, 714–724.

Epps, C.W., Wehausen, J.D., Palsbøll, P.J. & McCullough, D.R. (2010) Using genetic tools to track desert bighorn sheep colonizations. *Journal of Wildlife Management*, **74**, 522–531.

Epps, C.W., Castillo, J.A., Schmidt-Kuntzel, A., du Preez, P., Stuart-Hill, G., Jago, M. & Naidoo, R. (2013) Contrasting historical and recent gene flow among African buffalo herds in the Caprivi Strip of Namibia. *Journal of Heredity*, **104**, 172–181.

- Eriksson, A., Elias-Wolff, F., Mehlig, B. & Manica, A. (2014) The emergence of the rescue effect from explicit within- and between-patch dynamics in a metapopulation. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 281.
- Ezenwa, V.O. (2003) Habitat overlap and gastrointestinal parasitism in sympatric African bovids. *Parasitology*, **126**, 379–388.
- Ezenwa, V.O. (2004) Interactions among host diet, nutritional status and gastrointestinal parasite infection in wild bovids. *International Journal for Parasitology*, **34**, 535–542.
- Ezenwa, V. & Jolles, A. (2008) Horns honestly advertise parasite infection in male and female African buffalo. *Animal Behaviour*, **75**, 2013–2021.
- Ezenwa, V.O., Jolles, A.E. & O'Brien, M.P. (2009) A reliable body condition scoring technique for estimating condition in African buffalo. *African Journal of Ecology*, **47**, 476–481.
- Ezenwa, V.O., Etienne, R.S., Luikart, G., Beja-Pereira, A. & Jolles, A.E. (2010) Hidden consequences of living in a wormy world: Nematode-induced immune suppression facilitates tuberculosis invasion in African buffalo. *The American Naturalist*, **176**, 613–624.
- Forester, J.D. (2011) Dispersal from the frying pan to the fire: Dispersal from the frying pan to the fire. *Animal Conservation*, **14**, 225–226.
- Gates, C.C. & Larter, N.C. (1990) Growth and dispersal of an erupting large herbivore population in northern Canada: The Mackenzie wood bison (*Bison bison athabasca*). *Arctic*, **43**, 231–238.

- Gaylard, A., Owen-Smith, N. & Redfern, J. (2003) Surface water availability: Implications for heterogeneity and ecosystem processes. *The Kruger Experience* (eds J.T. Du Toit, K.H. Rodgers & H.C. Biggs), pp. 171–188. Island Press, Washington DC.
- Gorsich, E.E., Ezenwa, V.O., Cross, P.C., Bengis, R.G. & Jolles, A.E. (2015) Context-dependent survival, fecundity and predicted population-level consequences of brucellosis in African buffalo. *Journal of Animal Ecology*, **84**, 999–1009.
- Gorsich, E.E., Ezenwa, V.O. & Jolles, A.E. (2014) Nematode–coccidia parasite co-infections in African buffalo: Epidemiology and associations with host condition and pregnancy. *International Journal for Parasitology: Parasites and Wildlife*, **3**, 124–134.
- Gorsich, E.E., Bengis, R.G., Ezenwa, V.O. & Jolles, A.E. (2015) Evaluation of the sensitivity and specificity of an enzyme-linked immunosorbent assay for diagnosing brucellosis in African buffalo (*Syncerus caffer*). *Journal of Wildlife Diseases*, **51**, 9–18.
- Green, M.L., Manjerovic, M.B., Mateus-Pinilla, N. & Novakofski, J. (2014) Genetic assignment tests reveal dispersal of white-tailed deer: implications for chronic wasting disease. *Journal of Mammalogy*, **95**, 646–654.
- Griffiths, R.A., Sewell, D. & McCrea, R.S. (2010) Dynamics of a declining amphibian metapopulation: Survival, dispersal and the impact of climate. *Biological Conservation*, **143**, 485–491.

- Grimsdell, J.J.R. (1973) Age determination of the African buffalo, *Syncerus caffer* Sparrman. *African Journal of Ecology*, **11**, 31–53.
- Hall, R.J., Altizer, S. & Bartel, R.A. (2014) Greater migratory propensity in hosts lowers pathogen transmission and impacts. *Journal of Animal Ecology*, **83**, 1068–1077.
- Halley, D.J., Vandewalle, M.E.J., Mari, M. & Taolo, C. (2002) Herd-switching and long-distance dispersal in female African buffalo *Syncerus caffer*. *African Journal of Ecology*, **40**, 97–99.
- Hanski, I.K. & Selonen, V. (2009) Female-biased natal dispersal in the Siberian flying squirrel. *Behavioral Ecology*, **20**, 60–67.
- Heller, R., Okello, J.B.A. & Siegismund, H. (2010) Can small wildlife conservancies maintain genetically stable populations of large mammals? Evidence for increased genetic drift in geographically restricted populations of Cape buffalo in East Africa. *Molecular Ecology*, **19**, 1324–1334.
- Hess, G. (1996) Disease in Metapopulation models: Implications for conservation. *Ecology*, **77**, 1617–1632.
- James, R. & Washington, R. (2013) Changes in African temperature and precipitation associated with degrees of global warming. *Climatic Change*, **117**, 859–872.
- Jolles, A.E., Cooper, D.V. & Levin, S.A. (2005) Hidden effects of chronic tuberculosis in African buffalo. *Ecology*, **86**, 2358–2364.
- Jolles, A.E. (2007) Population biology of African buffalo (*Syncerus caffer*) at Hluhluwe-iMfolozi Park, South Africa. *Africa Journal of Ecology*, **45**, 398–406.

- Jolles, A.E., Ezenwa, V.O., Etienne, R.S., Turner, W.C. & Olf, H. (2008) Interactions between macroparasites and microparasites drive infection patterns in free-ranging African buffalo. *Ecology*, **89**, 2239–2250.
- Kokko, H. & López-Supulcre, A. (2006) From individual dispersal to species ranges: Perspectives for a changing world. *Science*, **313**, 789–791.
- Labonté, J., Ouellet, J.-P., Courtois, R. & Bélisle, F. (1998) Moose dispersal and its role in the maintenance of harvested populations. *The Journal of wildlife management*, **61**, 225–235.
- Larter, N.C., Sinclair, A.R.E., Ellsworth, T., Nishi, J. & Gates, C.C. (2000) Dynamics of reintroduction in an indigenous large ungulate: the wood bison of northern Canada. *Animal Conservation*, **3**, 299–309.
- Lebigre, C., Alatalo, R.V. & Siitari, H. (2010) Female-biased dispersal alone can reduce the occurrence of inbreeding in black grouse (*Tetrao tetrix*). *Molecular Ecology*, **19**, 1929–1939.
- Liebgold, E.B., Brodie, E.D. & Cabe, P.R. (2011) Female philopatry and male-biased dispersal in a direct-developing salamander, (*Plethodon cinereus*). *Molecular Ecology*, **20**, 249–257.
- Lorenzen, E.D., Arctander, P. & Siegismund, H.R. (2008) High variation and very low differentiation in wide ranging plains zebra (*Equus quagga*): insights from mtDNA and microsatellites. *Molecular Ecology*, **17**, 2812–2824.
- Martín, C.A., Alonso, J.C., Alonso, J.A., Palacín, C., Magaña, M. & Martín, B. (2008) Natal dispersal in great bustards: the effect of sex, local population size and spatial isolation. *Journal of Animal Ecology*, **77**, 326–334.

- Metzger, K.L., Sinclair, A.R.E., Hilborn, R., Hopcraft, J.G.C. & Mduma, S.A.R. (2010) Evaluating the protection of wildlife in parks: the case of African buffalo in Serengeti. *Biodiversity and Conservation*, **19**, 3431–3444.
- Michel, A.L. & Bengis, R.G. (2012) The African buffalo: A villain for inter-species spread of infectious diseases in southern Africa. *Onderstepoort Journal of Veterinary Research*, **79**, 26–30.
- Michel, A.L., Bengis, R.G., Keet, D.F., Hofmeyr, M., de Klerk, L. de, Cross, P.C., Jolles, A.E., Cooper, D., Whyte, I.J. & Buss, P. (2006) Wildlife tuberculosis in South African conservation areas: implications and challenges. *Veterinary Microbiology*, **112**, 91–100.
- Michel, A.L., Cooper, D., Jooste, J., de Klerk, L.M. & Jolles, A.E. (2011) Approaches towards optimizing the gamma interferon assay for diagnosing *Mycobacterium bovis* infection in African buffalo. *Preventative Veterinary Medicine*, **98**, 142-151.
- Mloszewski, M.J. (1983) *The behavior and ecology of the African buffalo*. Cambridge University Press, Cambridge.
- Oloff, H., Ritchie, M.E. & Prins, H.H.T. (2002) Global environmental controls of diversity of large herbivores. *Nature*, **415**, 901-904.
- Pickett, S.T.A., Cadenasso, M.L. & Benning, T.L. (2003) Biotic and abiotic variability as key determinants of savanna heterogeneity at multiple spatiotemporal scales. *The Kruger Experience* (eds J.T. du Toit, K.H. Rodgers & H.C. Biggs), pp. 22–40. Island Press, Washington DC.

- Plumb, G.E., White, P.J., Coughenour, M.B. & Wallen, R.L. (2009) Carrying capacity, migration, and dispersal in Yellowstone bison. *Biological Conservation*, **142**, 2377–2387.
- Prins, H.H.T. (1989) Buffalo herd structure and its repercussions for condition of individual African buffalo cows. *Ethology*, **81**, 47–71.
- Prins, H.H.T. (1996) *Ecology and behaviour of the African buffalo*. Chapman & Hall, London.
- R Development Core Team (2014) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org/>
- Redfern, J.V., Grant, R., Biggs, H. & Getz, W.M. (2003) Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology*, **84**, 2092–2107.
- Renwick, A.R., White, P.C.L. & Bengis, R.G. (2007) Bovine tuberculosis in southern African wildlife: a multi-species host–pathogen system. *Epidemiology and Infection*, **135**, 529–540.
- Robinson, S.J., Samuel, M.D., Rolley, R.E. & Shelton, P. (2013) Using landscape epidemiological models to understand the distribution of chronic wasting disease in the Midwestern USA. *Landscape Ecology*, **28**, 1923–1935.
- Roug, A., Clifford, D., Mazet, J., Kazwala, R., John, J., Coppolillo, P. & Smith, W. (2014) Spatial predictors of bovine tuberculosis infection and *Brucella* spp. exposure in pastoralist and agropastoralist livestock herds in the Ruaha ecosystem of Tanzania. *Tropical Animal Health and Production*, **46**, 837–843.

- Ryan, S.J., Knechtel, C.U. & Getz, W.M. (2006) Range and habitat selection of African buffalo in South Africa. *Journal of Wildlife Management*, **70**, 764–776.
- Ryan, S., Knechtel, C. & Getz, W. (2007) Ecological cues, gestation length, and birth timing in African buffalo (*Syncerus caffer*). *Behavioral Ecology*, **18**, 635–644.
- Selonen, V., Hanski, I.K. & Mäkeläinen, S. (2012) Predictors of long-distance dispersal in the Siberian flying squirrel. *Evolutionary Ecology*, **26**, 1361–1369.
- Simonsen, B.T., Siegismund, H.R. & Arctander, P. (1998) Population structure of African buffalo inferred from mtDNA sequences and microsatellite loci: high variation but low differentiation. *Molecular Ecology*, **7**, 225–237.
- Sinclair, A.R.E. (1977) *The African Buffalo*. The University of Chicago Press, Chicago, IL, USA.
- Skinner, J.D. & Smithers, R.H.N. (1990) *The Mammals of the Southern African Subregion*, 2nd edn. University of Pretoria Press, Pretoria.
- Sparkman, A.M., Adams, J.R., Steury, T.D., Waits, L.P. & Murray, D.L. (2012) Pack social dynamics and inbreeding avoidance in the cooperatively breeding red wolf. *Behavioral Ecology*, **23**, 1186–1194.
- Stothard, J.R., Stanton, M.C., Bustinduy, A.L., Sousa-Figueiredo, J.C., Van Dam, G.J., Betson, M., Waterhouse, D., Ward, S., Allan, F., Hassan, A.A., Al-Helal, M.A., Memish, Z.A. & Rollinson, D. (2014) Diagnostics for schistosomiasis in Africa and Arabia: a review of present options in control and future needs for elimination. *Parasitology*, **141**, 1947–1961.

- Tanner, M., Inlameia, O., Michel, A., Maxlhuza, G., Pondja, A., Fafetine, J., Macucule, B., Zacarias, M., Manguela, J., Moiane, I.C., Marranangumbe, A.S., Mulandane, F., Schonfeld, C., Moser, I., van Helden, P. & Machado, A. (2014) Bovine tuberculosis and brucellosis in cattle and African buffalo in the Limpopo National Park, Mozambique. *Transboundary and Emerging Diseases*.
- Tracey, J.A., Bevins, S.N., VandeWoude, S. & Crooks, K.R. (2014) An agent-based movement model to assess the impact of landscape fragmentation on disease transmission. *Ecosphere*, **5**, art119.
- van Hooft, W.F., Groen, A.F. & Prins, H.H.T. (2003) Genetic structure of African buffalo herds based on variation at the mitochondrial D-loop and autosomal microsatellite loci: Evidence for male-biased gene flow. *Conservation Genetics*, **4**, 467–477.
- van Oort, H., McLellan, B.N. & Serrouya, R. (2011) Fragmentation, dispersal and metapopulation function in remnant populations of endangered mountain caribou. *Animal Conservation*, **14**, 215–224.
- Venter, F.J., Scholes, R.J. & Eckhardt, H.C. (2003) The abiotic template and its associated vegetation pattern. *The Kruger Experience* (eds J.T. Du Toit, K.H. Rodgers & H.C. Biggs), pp. 83–129. Island Press, Washington DC.
- Winnie Jr, J.A., Cross, P. & Getz, W. (2008) Habitat quality and heterogeneity influence distribution and behavior in African buffalo (*Syncerus caffer*). *Ecology*, **89**, 1457–1468.

Worton, B.J. (1987) A review of models of home range for animal movement.
Ecological Modelling, **38**, 277–298.

Table 1.1 Model selection of generalized linear mixed effect models predicting dispersal likelihood of female African buffalo in Kruger National Park, South Africa for the period June 2008 – August 2012, based on Akaike’s Information Criterion (AIC). We present 5 top models for the pooled data (1357 observations total; 92 dispersal observations), Lower Sabie data (654 observations total; 53 dispersal observations) and Crocodile Bridge data (705 observations total; 39 dispersal observations). Model terms included in final models included condition (continuous), age (continuous), lactating status (binary), season (categorical), year (categorical) and herd (categorical). Models were ranked according to AIC and the most parsimonious model selected.

Data set	Models	AIC	Δ AIC	AICWt
Pooled	¹ condition+age+ ² season+ ³ year+herd	636.70	0.00	0.36
	¹ condition+age+lactation+ ² season+ ³ year+herd	637.50	0.80	0.24
	age+ ² season+ ³ year+herd	638.00	1.30	0.19
	age+lactation+ ² season+ ³ year+herd	639.50	2.80	0.09
	age+ ³ year+herd	641.10	4.40	0.04
Lower Sabie	age+ ² season+ ³ year	333.50	0.00	0.44
	age+lactation+ ² season+ ³ year	334.30	0.80	0.30
	¹ condition+age+lactation+ ² season+ ³ year	336.30	2.80	0.11
	age+ ² season	338.30	4.80	0.04
	age+lactation+ ² season	338.60	5.10	0.03
Crocodile Bridge	¹ condition+age+ ³ year	298.40	0.00	0.38
	¹ condition+ ³ year	299.50	1.10	0.22
	¹ condition+age+ ² season+ ³ year	301.10	2.70	0.10
	age+ ³ year	301.20	2.80	0.09

Table 1.1 (continued)

¹ condition+ ² season+ ³ year	302.30	3.90	0.05
¹ Assessed using the residual of condition on age due to high correlation between condition and age			
² Assessed as early wet, late wet, early dry and late dry			
³ Assessed as 2008, 2009, 2010, 2011, 2012			

Table 1.2 Cumulative AIC weights for each predictor variable from every possible model across the set of predictor variables considered. Maximum cumulative weight for each predictor variable is 1; explanatory variables varied by data set but included condition, age in years, season, lactating status and herd.

Data set	Response variable	condition	age	lactating	season	year	herd
Pooled	dispersal	0.658	0.976	0.385	0.923	0.952	0.960
Lower Sabie	dispersal	0.162	0.997	0.492	0.971	0.877	na
Crocodile Bridge	dispersal	0.806	0.641	na	0.222	0.943	na

Table 1.3 Odds ratios and parameter estimates for variables in the best-fit generalized linear mixed effect models of factors predicting dispersal likelihood of female African buffalo for each of three data sets (303 buffalo for the pooled data; 136 buffalo the Lower Sabie herd; 167 buffalo for the Crocodile Bridge herds) for the period June 2008 – August 2012 in Kruger National Park. We used nested random effect of animal and herd identification in the Crocodile Bridge data and the random effect of animal identification for the pooled and Lower Sabie data set to avoid pseudo replication.

Data set	Predictor	Effect on likelihood					
		of dispersal	Odds-ratio	Estimate	SE	z-value	p-value
Pooled	condition	(↓)	-	-0.38	0.22	-1.78	0.075
	age	↓	-	-0.02	0.01	-3.47	0.001
	¹ season_late wet		1.55	-0.44	0.37	-1.20	0.229
	¹ season_early dry		1.72	-0.54	0.35	-1.56	0.119
	¹ season_late dry		1.60	-0.47	0.35	-1.34	0.180
	² year_2009	↑	2.50	0.92	0.39	2.34	0.019
	² year_2010		1.09	0.08	0.54	0.16	0.876
	² year_2011	(↑)	2.57	0.94	0.54	1.76	0.078
	² year_2012		0.46	-0.77	0.91	-0.85	0.396
	³ herd_Lower Sabie	↑	3.55	1.27	0.38	3.33	0.001
	³ herd_Mountain	↑	3.63	1.29	0.59	2.18	0.029
	³ herd_Power Line	↑	4.84	1.58	0.53	3.00	0.003
Lower Sabie	age	↓	-	-0.04	0.01	-3.31	<0.001
	¹ season_late wet	↓	3.82	-1.34	0.45	-2.97	<0.001
	¹ season_early dry	↓	2.52	-0.92	0.40	-2.32	0.020

Table 1.3 (continued)

Crocodile Bridge	¹ season_late dry	↓	9.79	-2.28	0.68	-3.37	<0.001
	² year_2009	↑	4.17	1.43	0.52	2.76	0.006
	² year_2010		1.67	0.52	0.72	0.72	0.475
	² year_2011	↑	6.47	1.87	0.67	2.79	0.005
	² year_2012		3.87	1.35	1.28	1.06	0.290
	condition	↓	-	-0.64	0.29	-2.21	0.028
	age		-	-0.01	0.01	-1.61	0.107
	² year_2009		1.47	0.38	0.63	0.61	0.541
	² year_2010	(↑)	3.08	1.13	0.64	1.75	0.079
	² year_2011	↑	5.29	1.67	0.66	2.51	0.012
	² year_2012		0.58	-0.54	1.20	-0.45	0.650

¹seasonal effects are listed in reference to the early wet season

²year effects are listed in reference to 2008

³herd effects are listed in reference to the Crocodile Bridge herd

Arrows denote significant variables while arrows in parentheses denote marginally significant variables

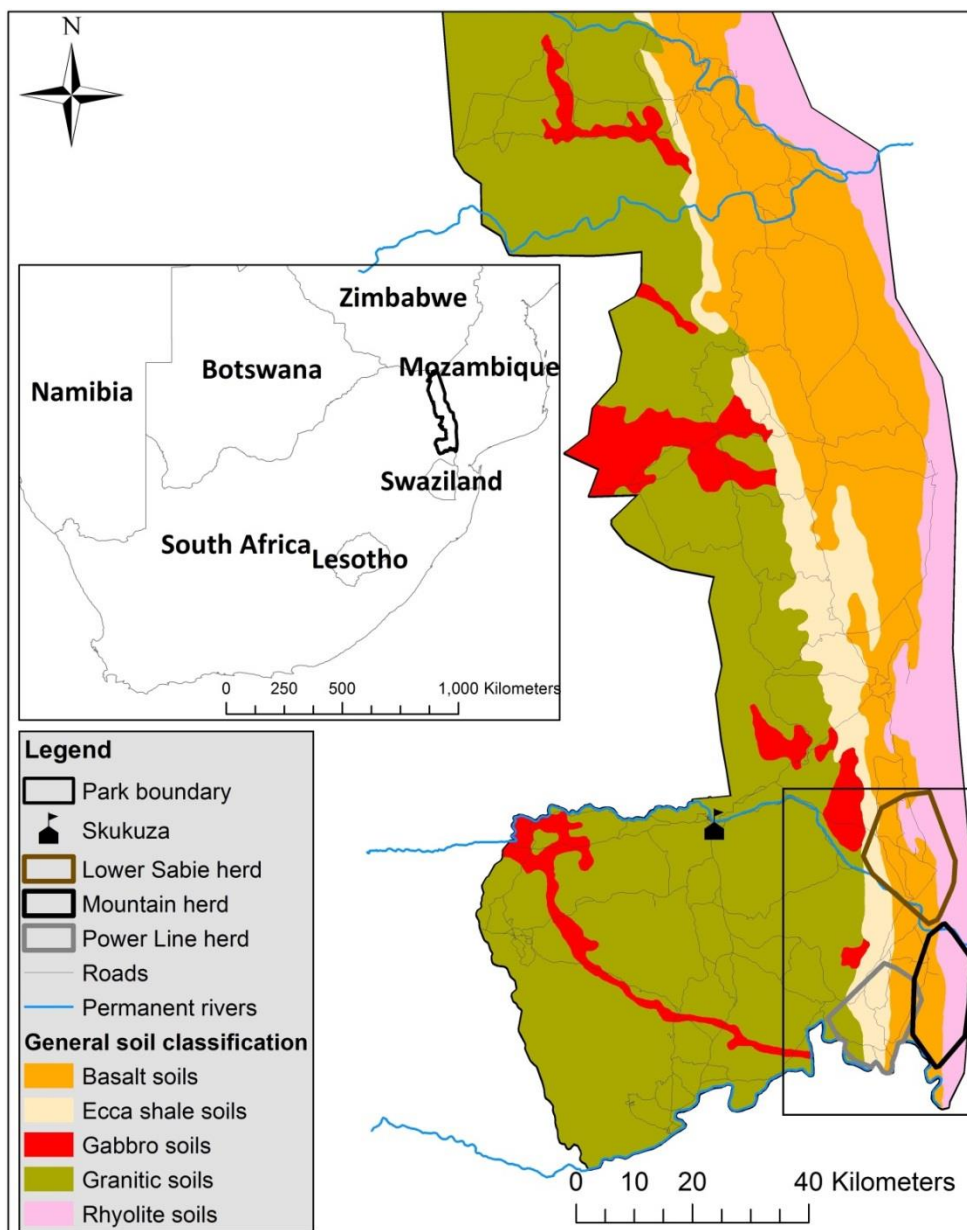
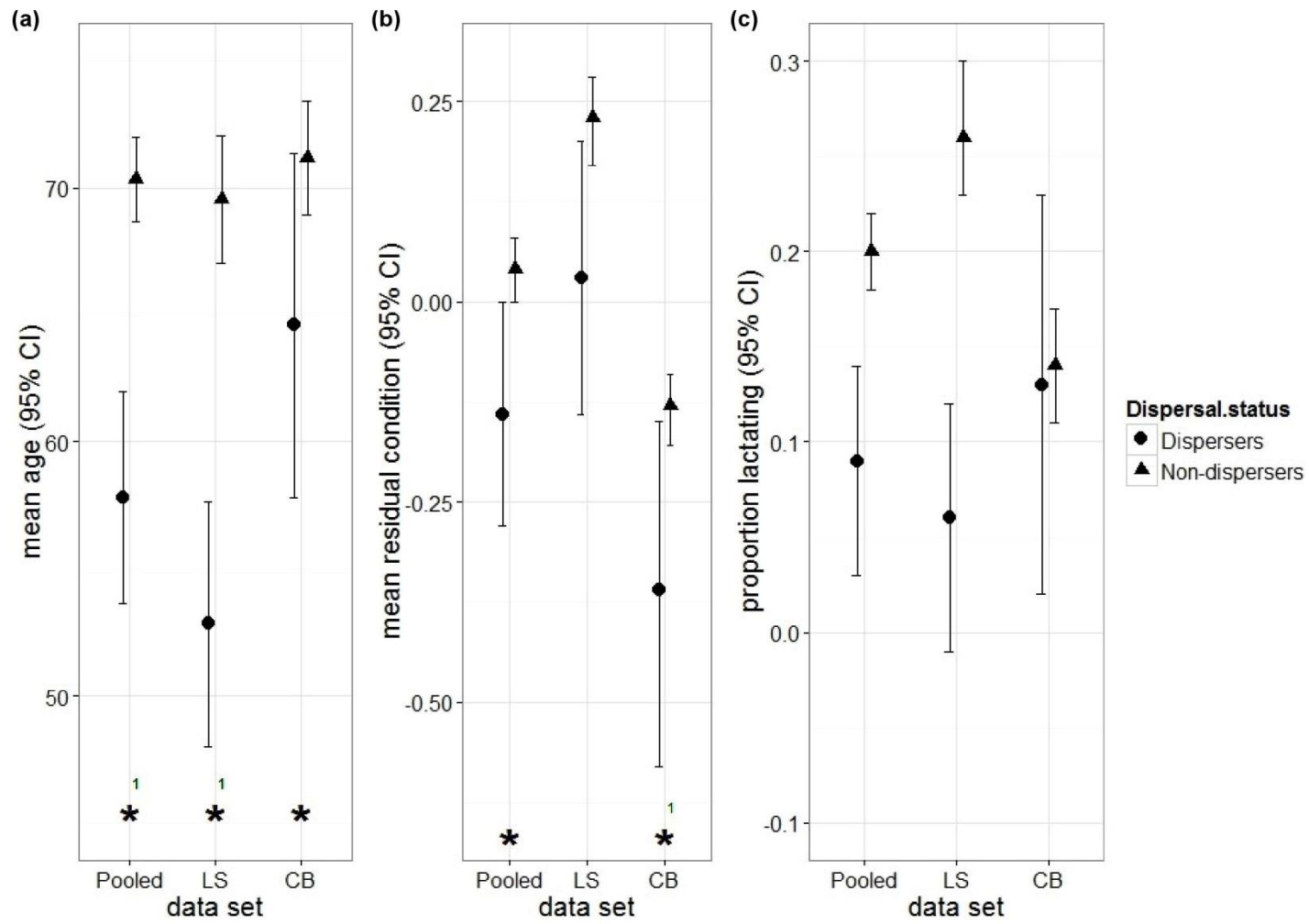


Fig. 1.1 General (black line) and focal study areas (Lower Sabie herd, brown polygon; Mountain herd, black polygon; Power Line herd, gray polygon) for study of dispersal of female African buffalo in Kruger National Park in southern Africa (inset). Initial mass capture of 200 female African buffalo were from the Lower Sabie, Mountain and Power Line herds in June/July and October of 2008, but females dispersed throughout much of the park during the course of the 4-year study.



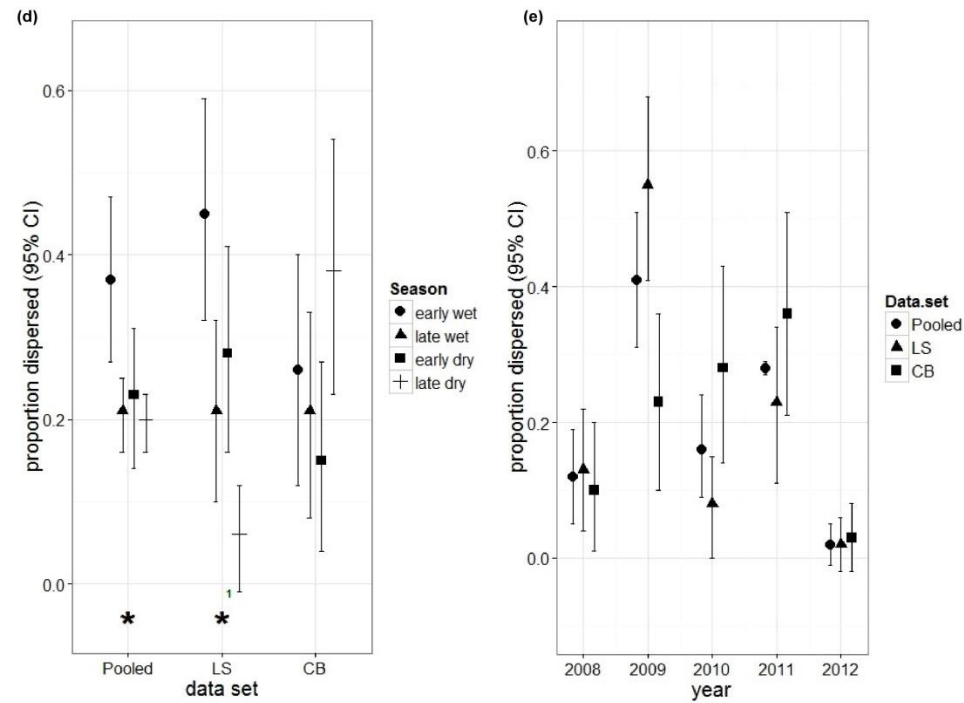


Fig. 1.2 Predictors of female African buffalo dispersal likelihood in the pooled, Lower Sabie and Crocodile Bridge data, Kruger National Park for the period, June 2008 – August 2012: (a) comparison of mean residual condition, (b) comparison of mean age in months, (c) comparison of proportion lactating at capture, (d) proportion dispersed by season and (e) proportion dispersed by year. * indicates whether or not the explanatory variable was included in the final model and ¹ whether the explanatory variable was significant or not.

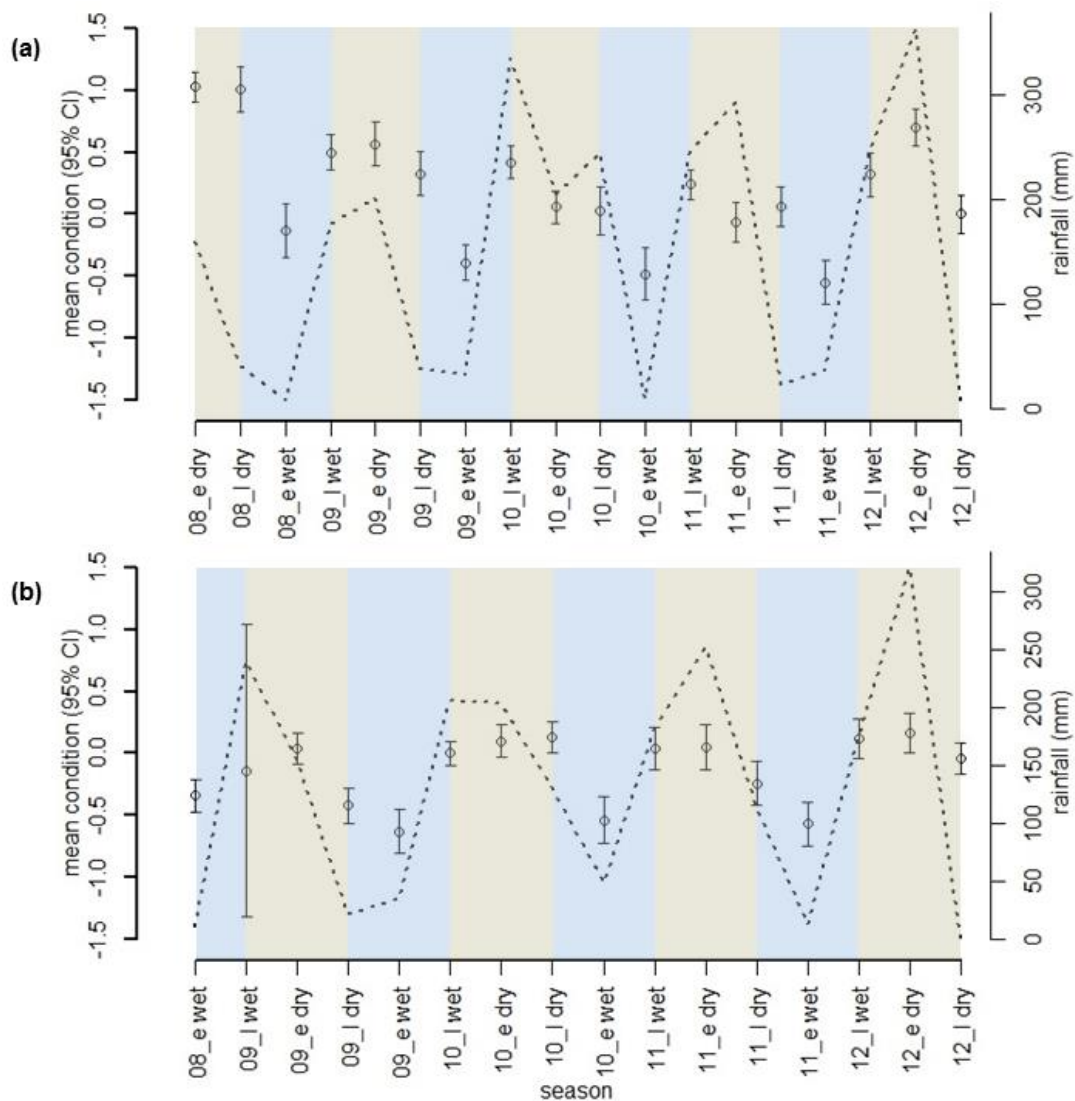


Fig. 1.3 Mean body condition for buffalo in the (a) Lower Sabie herd and (b) Crocodile Bridge herds, showing a single season time lag in variation in mean body condition by season (x-axis) and seasonal rainfall (mm) (dash line) for the period, June 2008 to August 2012.

Supporting Information

Table S1.1 Data available for this study

Measure	Category	Measure Type	Statistical Measure	Biological Significance
Age	Animal trait	Quantitative. Measured in months.	Continuous	Estimated by tooth eruption and wear ^{f, h}
Body condition	Animal trait	Residuals of condition on age due to correlation with age	Continuous	Fat reserves as a measure of body condition ^c
Pregnancy status	Animal trait	Yes/No	Binary	Determined by rectal palpation ^a
Lactation status	Animal trait	Yes/No	Binary	Manual milking of all four teats ^g
Season	Environmental variable	Divided into early wet, late wet, early dry and late dry	Categorical	Quality and abundance of grazing varies by season ^k
Bolus	Experimental/Treatment	Yes/No	Binary	Reduces nematode burden ^d
Strongyle infection	Gastro-intestinal parasites	Quantitative - eggs per gram (logged)	Continuous	Quantifies strongyle infection by FEC ^d
Coccidia infection	Gastro-intestinal parasites	Quantitative - oocysts per gram (logged)	Continuous	Quantifies coccidian species infection in feces by ^b quantifying oocysts ^e

Table S1.1 (continued)

Schistosome status	Gastro-intestinal parasites	Positive/negative	Binary	CAA titer used as a proxy for adult schistosome burden ^j
bTB status	Bacteria	Positive/negative for <i>Mycobacterium bovis</i>	Binary	Use ELISA to diagnose bTB infection ⁱ
Brucellosis status	Bacteria	Positive/negative for <i>Brucella abortus</i>	Binary	Commercial enzyme-link Immunosorbent assay ^e

Sources: ^a Beechler *et al.* 2012; ^b Budischack, Jolles and Ezenwa 2012; ^c Ezenwa, Jolles & O'Brien 2009; ^d Ezenwa *et al.* 2010; ^e Gorsich *et al.* 2015; ^f Grimsdell 1973; ^g Jolles, Cooper & Levin 2005; ^h Jolles 2007; ⁱ Michel *et al.* 2011; ^j Stothard *et al.* 2014; ^k Venter, Scholes & Eckhardt 2003

Table S1.2 Univariate models of fixed effects predicting dispersal likelihood of female African buffalo (Pooled data (1357 observations total; 92 dispersal observations), Lower Sabie data (654 observations total; 53 dispersal observations) and Crocodile Bridge data (705 observations total; 39 dispersal observations). Model terms included in final models: condition (continuous), age (continuous), lactating status (binary), season (categorical) and herd identification (categorical) with the nested effect of (1|Animal_ID/Herd_ID) or random effect of Animal_ID to account for pseudo replication and to acknowledge the different herds.

Data set	Univariates	Effect on likelihood					
		of dispersal	Odds-ratio	Estimate	SE	Z-value	p-value
Pooled	condition	↓	-	-0.41	0.17	-2.42	0.016
	age	↓	-	-0.02	0.00	-3.86	<0.001
	pregnant		0.96	-0.04	0.29	-0.15	0.880
	lactating	↑	0.41	-0.89	0.38	-2.35	0.019
	¹ season_late wet		0.69	-0.37	0.31	-1.21	0.225
	¹ season_early dry	↑	0.48	-0.73	0.29	-2.49	0.013
	¹ season_late dry	↑	0.45	-0.80	0.31	-2.60	0.009
	² year_2009	↑	2.04	0.71	0.36	2.00	0.045
	² year_2010		1.25	0.22	0.41	0.54	0.589
	² year_2011	↑	2.22	0.80	0.38	2.11	0.035
	² year_2012	(↑)	0.26	-1.36	0.78	-1.75	0.081
	³ herd_Lower Sabie	↑	2.38	0.87	0.35	2.50	0.012
	³ herd_Mountain		1.15	0.14	0.48	0.29	0.769
	³ herd_Power Line	↑	2.38	0.87	0.40	2.16	0.031
	strongyles		-	0.08	0.10	0.73	0.463

Table S1.2 (continued)

Lower Sabie	coccidia		-	0.06	0.11	0.58	0.561
	schistosome	(↓)	-	-0.30	0.17	-1.80	0.072
	bovine tuberculosis		0.86	-0.15	0.32	-0.48	0.633
	brucellosis		0.69	-0.37	0.30	-1.24	0.216
	condition	↓	-	-0.62	0.24	-2.57	0.010
	age	↓	-	-0.02	0.01	-3.69	<0.001
	pregnant		0.72	-0.32	0.37	-0.89	0.375
	lactating	↑	0.19	-1.67	0.61	-2.73	0.006
	¹ season_late wet	↑	0.34	-1.07	0.43	-2.48	0.013
	¹ season_early dry	↑	0.32	-1.14	0.38	-2.99	0.003
	¹ season_late dry	↑	0.09	-2.36	0.66	-3.59	<0.001
	² year_2009	↑	3.07	1.12	0.46	2.46	0.014
	² year_2010		0.92	-0.09	0.66	-0.13	0.895
	² year_2011		2.24	0.81	0.52	0.56	0.119
	² year_2012		0.35	-1.06	1.10	-0.97	0.333
	strongyle		-	0.15	0.17	0.91	0.363
Crocodile Bridge	coccidia		-	0.08	0.17	0.47	0.639
	schistosome		-	-0.36	0.26	-1.36	0.173
	bovine tuberculosis		0.99	-0.01	0.44	-0.02	0.984
	brucellosis		0.74	-0.31	0.43	-0.72	0.472
	condition	↓	-	-0.64	0.27	-2.35	0.019
	age		-	-0.01	0.01	-1.34	0.180
	pregnant		1.04	0.04	0.36	0.11	0.912
	lactating		0.94	-0.06	0.50	-0.12	0.908

Table S1.2 (continued)

² season_late wet		1.30	0.27	0.50	0.54	0.593
² season_early dry		0.56	-0.58	0.53	-1.10	0.273
² season_late dry		1.22	0.20	0.43	0.47	0.640
² year_2009		1.16	0.15	0.61	0.24	0.808
² year_2010		1.80	0.59	0.60	0.98	0.327
² year_2011	(↑)	2.79	1.03	0.58	1.76	0.079
² year_2012		0.23	-1.46	1.13	-1.29	0.197
strongyle		-	-0.12	0.18	-0.68	0.498
coccidia		-	-0.01	0.22	-0.05	0.960
schistosome		-	-0.17	0.23	-0.75	0.454
bovine tuberculosis		0.72	-0.33	0.48	-0.70	0.482
brucellosis		0.64	-0.45	0.43	-1.03	0.301

¹ seasonal effects are listed in reference to the early wet season

² year effects are listed in reference to 2008

³ herd effects are listed in reference to the Crocodile Bridge herd

Arrows denote significant variables while arrows in parentheses denote marginally significant variables

Table S1.3 Correlation of fixed effects predicting dispersal likelihood of female African buffalo (Pooled data (1357 observations total; 92 dispersal observations), Lower Sabie data (654 observations total; 53 dispersal observations) and Crocodile Bridge data (705 observations total; 39 dispersal observations). Model terms included in final models: condition (continuous), age (continuous), lactating status (binary), season (categorical), year (categorical) and herd identification (categorical) with the random effect of (Animal_ID) to account for pseudo replication in the pooled and Lower Sabie data and the nested effect of (Animal_ID and Herd_ID) to account for pseudo replication and to acknowledge the different herds.

[illegible]

Table 1.3 (continued)

CB	Age	-0.692	-0.106								
	Lactating	0.152	0.100	-0.212							
	² Seas_lw	-0.294	-0.502	0.293	-0.069						
	² Seas_ed	-0.451	-0.508	0.238	-0.198	0.530					
	² Seas_ld	-0.263	-0.309	0.168	-0.105	0.382	0.372				
	³ Year_09	-0.391	0.283	-0.254	0.050	-0.273	0.023	-0.079			
	³ Year_10	-0.164	0.312	-0.301	0.028	-0.270	-0.147	-0.078	0.617		
	³ Year_11	-0.071	0.363	-0.517	-0.015	-0.375	-0.128	-0.104	0.738	0.610	
	³ Year_12	0.057	0.212	-0.400	-0.004	-0.356	-0.104	-0.218	0.455	0.371	0.504
	¹ Condition	0.296									
	Age	-0.598	-0.031								
	² Seas_lw	-0.162	-0.300	0.092							
	² Seas_ed	-0.118	-0.331	0.004	-	0.543					
	² Seas_ld	-0.060	-0.223	-0.073	-	0.607	0.621				
	³ Year_09	-0.388	0.140	-0.120	-	-0.373	-0.456	-0.495			
	³ Year_10	-0.353	-0.010	-0.274	-	-0.417	-0.344	-0.391	0.756		
	³ Year_11	-0.227	0.064	-0.427	-	-0.421	-0.340	-0.358	0.749	0.817	
	³ Year_12	-0.110	0.010	-0.300	-	-0.314	-0.221	-0.283	0.481	0.535	0.559

Table S1.4 Monthly and annual rainfall (mm) with associated means for the period October 2007 to September 2012 for the Lower Sabie and Crocodile Bridge areas, Kruger National Park.

Lower Sabie							Crocodile Bridge						
Month	07/08	08/09	09/10	10/11	11/12	Mean	Month	07/08	08/09	09/10	10/11	11/12	Mean
October	35.8	9.0	48.3	15.0	40.5	29.7	October	16.8	6.6	24.1	16.0	0.0	12.7
November	156.7	36.0	205.3	123.0	34.5	111.1	November	89.2	137.2	135.8	147.0	22.9	106.4
December	155.8	132.0	81.5	109.0	172.5	130.2	December	89.0	97.0	46.4	120.0	152.4	101.0
January	69.5	161.8	112.5	220.0	254.5	163.7	January	85.0	31.5	121.5	170.0	188.0	119.2
February	43.5	15.5	63.0	57.0	27.0	41.2	February	2.6	85.7	50.2	58.0	53.9	50.1
March	46.9	24.4	29.5	16.0	81.3	39.6	March	31.2	38.1	31.5	24.0	79.0	40.8
April	35.5	3.5	239.3	9.0	8.5	59.2	April	20.9	3.0	127.9	107.0	0.0	51.8
May	5.0	26.7	5.0	12.0	0.0	9.7	May	5.4	11.4	4.1	6.0	0.0	5.4
June	0.2	8.1	0.0	2.0	0.0	2.1	June	8.5	7.9	0.0	0.0	0.0	3.3
July	7.0	9.7	4.0	6.8	0.0	5.5	July	8.4	2.6	18.0	4.3	0.0	6.7
August	2.0	23.3	6.0	0.8	0.0	6.4	August	0.8	32.2	6.0	3.0	0.0	8.4
September	0.0	0.0	0.0	29.2	94.5	24.7	September	1.8	0.0	24.4	6.6	96.3	25.8
Totals	557.9	450.0	794.4	599.8	713.3	623.1	Total	359.6	453.3	590.0	661.9	592.5	531.4

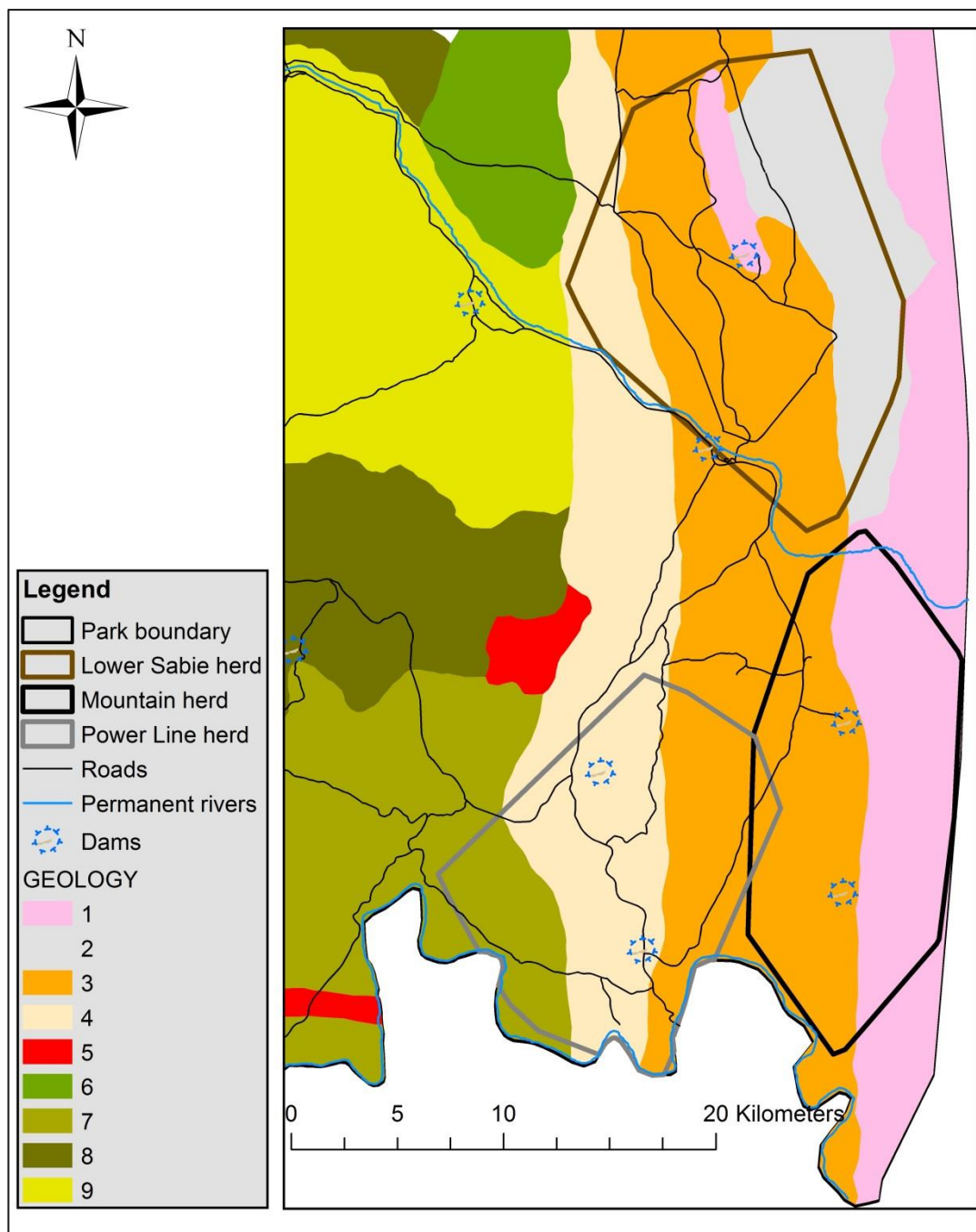


Fig. S1.1 Box area from figure 1 additionally showing, locations of artificial water sources and detailed soil derived geology: 1 rhyolite/dactite soils; 2 rhyolite/basalt soils; 3 basalt soils; 4 ecca shale/mudstone soils; 5 Timbivati gabbro soils and 6-9 various granite/gneiss soils.

2 - Adult dispersal increases disease exposure in female African buffalo

(Syncerus caffer)

Abstract

Dispersal is an important process that reduces competition and inbreeding in wildlife populations. At the individual level, however, animals must balance the potential benefits of dispersal against its costs. Costs may be incurred in the form of risk, such as mortality or potential injury while dispersing, energetic and time costs associated with the energy and time invested in dispersing, and costs associated with lost opportunities, e.g. reduced fecundity due to unfamiliar surroundings and social groups. Disease in particular is another poorly-understood but potentially important factor influencing costs and benefits of dispersal. Dispersal from a crowded habitat may offer an escape from high pathogen and parasite exposure risk, conversely dispersing individuals in this stressful period may have reduced immunity and consequently be more susceptible to infections. In addition, if pathogen exposure profiles differ among social groups, dispersing animals may face new pathogen challenges to which they are immunologically naïve to, when they arrive at a new social group. However, few studies have estimated dispersal costs of large mammals, particularly those with facultative adult dispersal. We investigated individual-level costs and benefits of dispersal in female African buffalo during a 4-year longitudinal study at Kruger National Park (KNP), South Africa. Our objectives were to determine: (1) effects of dispersal on fitness, by comparing survival, and fecundity of dispersing and philopatric (control) buffalo, as well as comparing the difference in pre and post dispersal body condition of dispersers with the change of body condition of philopatric control animals for the same period; (2) disease risks associated with

dispersal, by determining whether burdens of gastro-intestinal parasites and the incidence of bacterial and viral infections changed during dispersal. Our study included 304 adult female buffalo in two herds in the southern KNP, which we followed for four years. The herds occupied contrasting environments, with differing precipitation patterns and geological parent material, leading to very different seasonal resource availability. No significant difference in mortality risk or fecundity was observed between dispersing and philopatric control animals, nor did change in body condition differ. However, we detected disease consequences of dispersal that varied by location. Dispersers from the resource-limited herd suffered more bovine tuberculosis and brucellosis infections after dispersal, both of which are chronic infections with clear, long term effects on survival and fecundity, when compared to controls from the same location. Dispersers from the less resource-limited herds had increases in schistosome burdens. Schistosomes are parasitic worms with relatively minor health effects; relatively long-lived but not as long as the life of the host (i.e., buffalo can reduce their burdens). Previous work has shown that adult buffalo disperse in response to resource limitation due to seasonal forage shortages or density dependent intraspecific competition. Our results suggest that dispersal also incurs costs through increased exposure to infectious diseases, which animals in poor condition can ill afford. Thus, dispersal behavior in African buffalo appears to balance potential benefits of increased access to nutritional resources against risks of disease exposure.

Introduction

Dispersal is an important process for reducing intraspecific competition, finding suitable habitats and inbreeding avoidance (Kokko & López-Sepulcre 2006; Plumb 2009; van Oort *et al.* 2011; Debeffe *et al.* 2014). Dispersal studies have typically focused on natal and sex-biased dispersal (Debeffe *et al.* 2014; Edelman 2014; Moore *et al.* 2014). However, for some large mammal species, adults of both sexes are known to disperse, including bighorn sheep (*Ovis canadensis*) (Gross, Singer & Moses 2000), mountain goats (*Oreamnos americanus*) (Rice 2008) and pronghorn (*Antilocapra americana*) (Jacques, Jenks & Klaver 2009). Such dispersal is important for both conservation and management of wildlife populations as it aids in range expansion and recolonizing of unoccupied habitat (Larter *et al.* 2000; Blundell *et al.* 2002; Ahlering *et al.* 2012), maintenance of gene flow (Shafer *et al.* 2012; Atickem *et al.* 2013; Roffler *et al.* 2014) and demographic rescue (Garant, Forde & Hendry 2007; Carlson *et al.* 2014).

Although dispersal is beneficial to both individuals and the population, the act of dispersal has costs (Ronce 2007; Clobert *et al.* 2012; Travis *et al.* 2012). Dispersal costs are varied and can include fitness costs, such as reduced survival, condition and reproduction. Mortality may be greater for dispersing individuals as they risk moving through and settling in unfamiliar or poor habitats (Yoder *et al.* 2004; Ronce *et al.* 2007), also potentially exposing themselves to increased predation or harvest risk (Stamps *et al.* 2005; Cote & Clobert 2010). Energetic costs associated with dispersal (Bonte *et al.* 2012), like migration (Hein *et al.* 2012; Shepard *et al.* 2013) may also negatively influence condition or growth (Nevoux *et al.* 2013). Nevoux *et al.* (2013)

also found a negative correlation between dispersal distance and fecundity. Evidence that dispersing individuals miss breeding opportunities varies across species (e.g., Monard & Duncan 1996; Soulsbury *et al.* 2008). Infection costs are another potential but poorly understood cost of dispersal: Bonte *et al.* (2012) suggested that the physical act of dispersal may lead to a compromised immune system and thus increased infections. Conversely, particularly for social species, dispersal could enable an individual potentially remove itself from a highly infected habitat and/or from association with highly infected individuals (Altizer, Bartel & Han 2011).

Female African buffalo may disperse as adults (Halley *et al.* 2002; Olff, Ritchie & Prins, 2002; Spaan *et al. in prep*), and thus offer a unique opportunity to examine the costs associated with facultative adult dispersal. African buffalo are large, gregarious water dependent ungulates (Redfern *et al.* 2003), and as patch-selective bulk grazers (Macandza, Owen-Smith and Cross 2004) play an important role in shaping savanna environments. African buffalo are economically valuable due to strong interest by tourists and hunters (Caro & Riggio 2013), but also spread various diseases of concern to the livestock industry (Michel & Bengis 2012) including bovine tuberculosis (Caron, Cross & du Toit 2003; Roug *et al.* 2014), brucellosis (Jolles *et al.* 2008; Alexander *et al.* 2012) and foot-and mouth (Jori *et al.* 2009; Ayebazibwe *et al.* 2010). Therefore, factors influencing African buffalo dispersal likely are important for management, given the potential that facultative adult dispersal is affected by resource conditions that are in turn driven by density dependence, environmental stochasticity, and resources such as water.

We studied adult dispersal in two buffalo herds with contrasting demographic parameters in Kruger National Park (KNP), South Africa. Previous work (Spaan, *Chapter 1*) established that dispersal was influenced by both individual- and population-level characteristics: younger adult buffalo were more likely to disperse. However, at Lower Sabie (LS), buffalo were long-lived (Ezenwa and Jolles 2015), maintained decent body condition and reproduce well (Gorsich *et al.* 2015), whereas at Crocodile Bridge (CB), life expectancy was much shorter (Ezenwa and Jolles 2015), body condition was very low in the dry season, and reproductive rates were low (Gorsich *et al.* 2015). Thus, CB was essentially a sink population that declined from 2008-2012 (Gorsich *et al.* 2015, Table 1).

During the study period, dispersal in the LS herd was unrelated to individual body condition, but was more likely during seasonal resource restriction (Spaan, *Chapter 1*), suggesting that dispersal was a potential response to density dependent food shortage (Plumb *et al.* 2009). In the declining CB herd, animals with low body condition dispersed, suggesting that adult dispersal may be a rescue mechanism (Bonte. & De La Peña 2009) allowing individuals to escape sink populations and seek areas where their prospects for survival and reproduction might be better (Spaan, *Chapter 1*). Thus individuals' decisions to disperse may reflect a complicated gamble: when resources are extremely restricted, individuals most at risk (e.g., in poor condition relative to other herd members) may have the strongest incentive to improve survival and future reproductive potential. However, the potential energetic and other costs to dispersal may result in higher short-term costs for individuals already in poor condition (e.g., further-reduced condition or disease consequences).

In this study, we estimate the impacts of dispersal on adult female African buffalo, examining: (1) effects on fitness, by comparing survival, and fecundity of dispersing and philopatric control buffalo, as well as comparing pre and post dispersal body condition of dispersers with the change in body condition for philopatric control animals for the same period, and (2) disease risks, by estimating whether burdens of gastro-intestinal parasites, strongyles, coccidia and schistosomes, and the incidence of bacterial and viral infections changed during dispersal. Because of the different population trajectories of the LS and CB herds, we predicted 1) that dispersal costs or benefits would differ by herd, 2) that individuals in the declining CB herd would be more likely to incur fitness costs and higher disease risks from dispersal given that poor initial body condition, and 3) that fitness consequences and disease risks for individuals in the stable LS herd were less likely to differ between dispersers and philopatric control animals because of their better initial condition.

Methods

Study area

Our study took place in the Kruger National Park (KNP), South Africa, which lies between 22.5 and 25.5°S, 31.0 and 31.57°E and is ~19 485 km² in extent (Fig. 2.1). The park has one wet season per year with summer rainfall (October-March) ranging north to south from 400 to 700 mm per year. KNP is located at an average altitude of 250 m (range 200-900 m) above sea level with granitic soils in the west

succeeded by Ecce shale, basalt and rhyolites. The variation in moisture between seasons and soil types give rise to large regional variations in food availability (Gertenbach 1983). The main study area spans the landscape types of the Lebombo mountain bushveld, Marula (*Sclerocarya birrea subsp. caffra*)/Knobthorn (*Vachellia nigrescens*) savannah, Delagoa thorn (*Vachellia welwitschii*) thickets, Sabie and Crocodile River thickets and Thornveld (Venter, Scholes & Eckhardt 2003).

The LS and CB herds utilize distinct areas within KNP with different underlying geological features, which give rise to different soils and associated vegetation (Venter, Scholes & Eckhardt 2003). Water distribution (both natural and artificial) within the areas used by the herds also varies (Gaylard, Owen-Smith & Redfern 2003); with access more limited at LS. Buffalo are a water dependent species and herd densities are associated with distance to water (Redfern *et al.* 2003); thus, the spatial distribution of water influences forage availability. Opportunities for dispersal also varied for the study herds, due to their position with respect to the park's boundary fence. The fence restricted movement of LS animals to the east, while the CB animals were restricted to both the south and east (Picket, Cadenasso & Benning 2003).

Definition of dispersal and analysis of spatial data

For the purpose of this study we defined dispersers as “individual buffalo that were recorded outside of their herd of origin's home range and joined with another herd, not return to their herd of origin for at least one season”. For each herd, GPS

locations from the satellite collars were mapped in ArcMap 10.1 (Environmental Systems Research Institute, Inc., Redlands CA) and home ranges estimated for each of the original herds using minimum convex polygon (Worton 1987) in Hawth's Tools (Beyer 2004). This analysis assumed that buffalo with satellite collars reflected the position of the herd. Home ranges were estimated separately for the wet season (October to March) and the dry season (April to September) in each year from September 2009 to August 2012.

Sample collection

Age, condition, pregnancy and lactation status were recorded for all recaptured buffalo, and the experimental individuals received the Panacur bolus. Blood was collected via jugular venipuncture into 10 ml EDTA coated vacutainer tubes, placed on ice and transported to Veterinary Wildlife Services (VWS) laboratory in Skukuza, KNP. Feces were collected rectally and transported back to the lab in a cooler with ice packs. Age was determined by tooth eruption up to 5 years and then judged by tooth wear (Grimsdell 1973; Jolles 2007). Body condition was determined by palpation of fat reserves on the ribs, spine, hips and tail on a scale of 1 (very poor) to 5 (very good) and then averaged (Ezenwa, Jolles & O'Brien 2009). Pregnancy status was determined by rectal palpation (Beechler *et al.* 2012). Lactation was determined by manually milking all four teats (Jolles, Cooper & Levin 2005).

Diagnostics

Methods we employed for macro- and microparasite diagnostics have been described previously (Ezenwa 2003; Budischak, Jolles & Ezenwa 2012; Anderson, Ezenwa & Jolles 2013; Gorsich *et al.* 2015). Fecal egg and oocyst counts were used to assess GI nematode and coccidian infection using a modified McMaster method (Ezenwa 2003). Previous work has shown GI nematode infections in this buffalo population commonly include, *Cooperia fuelleborni*, *Haemonchus placei*, *Haemonchus bedfordi*, and an undescribed *Parabronema* species and that fecal egg counts accurately reflect gastro-intestinal helminth burdens (Budischak *et al.* 2015). A strip ELISA to detect circulating anodic antigen (Bont, Steck & Meyer 1996) was validated for use in African buffalo (Beechler *et al.* *in prep*) and used to determine schistosome infection. TB was diagnosed using a whole-blood gamma interferon assay (BOVIGAM, Prionics), optimized for African buffalo with a sensitivity of 86% and a specificity of 92% (Michel *et al.* 2011). A commercial enzyme-linked immunosorbent assay (IDEXX Brucellosis Serum Ab Test) was used to detect brucellosis (Gorsich *et al.* 2015). Bovine Herpes Virus (BHV), Adenovirus type 3 (AD3) and Parainfluenza Virus type 3 (PI3) serostatus were determined using a commercial ELISA test kit (BioX diagnostics) according to manufacturer's instructions. Bovine Respiratory Syncytial Virus (BRSV) and Bovine Viral Diarrhea Virus (BVDV) serostatus were determined by commercially available competition strip enzyme-linked immunosorbent assay (ELISA) kit for cattle (BioX diagnostics) following manufacture instructions (McNulty 2015).

Dispersal rates

We calculated dispersal risk, which is the number of dispersers/number of buffalo years at risk. Number of buffalo years at risk was calculated as the total time all non-dispersing controls were in the study, as well as the total time all dispersers were in the study prior to dispersal (Spaan, *Chapter 1*).

Fitness costs or benefits – survival

Analyses were conducted for three datasets: pooled data from herds (LS and CB), LS data, and CB data. Survival in dispersing and non-dispersing buffalo was analyzed using a Cox-proportional hazards regression model (CPH) with dispersal as a time dependent variable (Cox 1972). The CPH method allowed us to include buffalo captured later in the study to replace mortalities and buffalo removed before the end of the study, for instance from capture related deaths (Parmar & Machin 1995). We used variables from the best fit CPH model of area of origin, age and age² as described by Ezenwa & Jolles (2015) and Gorsich *et al.* (2015). Area of origin, age and age² were represented as time independent or fixed variables with dispersal added as a permanent event. We then ran all possible models and selected models using Akaike's Information Criteria (AIC, Burnham & Anderson 2002) reporting the top five models (Table S2.2, Supplementary Information). We also examined the importance of each individual predictor by calculating the cumulative AIC weights for each predictor across all models (Table S2.3, Supplementary information)

(Burnham & Anderson 2002). Any further investigation of dispersal as a predictor of survival was limited by the small number of total dispersal mortalities ($n = 12$).

Survival models were fit using the `coxph` function in the survival package of R (Fox & Weisberg 2011). As an alternate measure, we calculated per capita annual risk of mortality for dispersers and controls. This was done by dividing the number of mortalities by the number of buffalo years at risk, for each control group.

Controls

To establish whether dispersers incurred differences in fecundity, condition, or disease, we matched dispersing individuals to control individuals that did not disperse, and then tested for differences for both dispersers and controls before and after the dispersal event for that pair. This approach was necessary because of the potential changes in status over time for all buffalo in the study resulting from seasonal and other variation. All controls were selected by matching individual controls to dispersers by area, bolus status (where necessary) and by age (individuals within 12 months of age or the next closest match). Where multiple qualifying individuals were available to match to a disperser we used a random number generator (<https://www.random.org/>) to randomly select each control. With the CB data, we also matched controls to dispersers by sub-herd.

Fitness costs or benefits – fecundity and body condition

We assessed fitness costs for the three data sets (pooled, LS only, and CB only). We used paired t-tests to compare dispersers' pre vs. post dispersal pregnancy rates and body condition with matched philopatric controls' pregnancy rates and body condition for the same time periods. For the fecundity analysis, we included only individuals of reproductive age (≥ 3.5 years old) (2007). For the body condition analysis, to account for seasonal variation, we used the mean of the two body condition scores that were assessed pre- and post-dispersal.

Infection costs or benefits – gastrointestinal parasite, viral and bacterial infections

Infection costs were also estimated separately for pooled, LS, and CB datasets. We used paired t-tests -to compare individual dispersers' pre- vs. post-dispersal worm burdens and the number of viral and bacterial infections gained or lost with the same metrics for individual philopatric control animals during the same time period. The gastrointestinal parasites included were strongyles, coccidia and schistosomes. The five viral infections included incident events of bovine herpes virus (BHV), adenovirus-3 (AD3) and parainfluenza virus-3 (PI3), bovine respiratory syncytial virus (BRSV) and bovine viral diarrhea virus (BVDV). The two bacterial infections were bovine tuberculosis and brucellosis. All statistical analyses were performed in the program R, v. 3.1.1 (R Core Team 2014).

Ethics statement

All procedures were approved by South African National Parks Board (Reference No. SPARS914) and by Oregon State University and University of Georgia IACUC (Protocol numbers: OSU No. 2833, UGA No. A201010-190-A1).

Results

Dispersal rates

Owing to mortalities and dispersal, not all animals were in the study, or in their herd of origin, for the full study period of four years. Annual dispersal rates for each herd are therefore calculated as the number of dispersers observed in each herd, divided by the number of “buffalo-years-at-risk” of dispersal from that herd. The number of buffalo-years-at-risk of dispersal is calculated by scoring, for each buffalo, the duration from its first capture until it either died or left the herd. These individual observation periods are then added up for all buffalo observed in the herd, to give the total number of buffalo-years-at-risk of dispersing. Dispersal rates thus expressed the annual per-capita “risk” or likelihood of dispersing from a given herd; analogous to incidence rates in epidemiological studies. The annual dispersal rate for the LS herd was significantly higher, at 19.2%, than the annual dispersal rate of 14.5% in the CB area (Spaan, *Chapter 1*).

Fitness costs or benefits – survival

Mortality rates expressed as annual per-capita “risk” or likelihood of mortality for dispersers or controls; analogous to incidence rates in epidemiological studies. Over the course of the study (June 2008 to August 2012) 86 of the 304 monitored buffaloes died. Of those, 12 mortalities were attributed to dispersers, which equated to annual mortality rate of 8.6% for dispersers, while the other 74 mortalities were attributed to non-dispersing controls, which equated to a significantly higher mortality rate of 13.5% for non-dispersing controls. However, survival did not differ between dispersing and philopatric individuals across the pooled or separate datasets, as assessed by univariate tests (Table 2.2) or multivariate models (Table S2.2 and S2.3, Supplementary information).

Fitness costs or benefits – fecundity and body condition

No significant difference was observed in the mean difference in pre vs. post dispersal fecundity rates of dispersers and controls in the pooled ($p = 0.590$), LS ($p = 0.367$), or CB ($p = 0.819$) data (Table 2.3). No significant differences were observed in pre vs. post dispersal body condition of dispersers and controls in the pooled ($p = 0.735$), LS ($p = 0.822$), or CB ($p = 0.323$) data (Table 2.3).

Infection costs or benefits – gastrointestinal parasite, viral and bacterial infections

The mean difference in pre vs. post dispersal strongyle burdens of dispersers and controls likewise did not differ for the pooled ($p = 0.113$), LS ($p = 0.273$), or CB ($p = 0.260$), nor did coccidia burdens for the pooled ($p = 0.551$), LS ($p = 0.165$), or

CB ($p = 0.791$) data (Table 2.4). However, LS suffered higher post dispersal schistosome burdens ($p = 0.046$), but this pattern was weak in the pooled dataset ($p = 0.086$) because it is absent at CB ($p = 0.336$) (Fig 2.3, Table 2.4).

Dispersers at CB suffered more post-dispersal bacterial infections ($p = 0.021$), but this pattern was weak in the pooled dataset ($p = 0.096$) because it is absent at LS ($p = 1.000$) (Fig. 2.3, Table 2.4). No significant differences were observed in change of incidence of viral infections gained/lost between dispersers and controls in the pooled ($p = 0.609$), LS ($p = 0.623$), or CB ($p = 0.303$) data (Table 2.4).

Discussion

With 93 dispersal events and 550 observed buffalo-years, this study is one of the most extensive investigations of adult dispersal in a free-ranging mammal population to date. Despite this, we did not detect any effects of dispersal on survival, fecundity, or body condition (the most commonly assessed metrics of dispersal costs) of the study animals. However, we did observe context dependent costs of dispersal: dispersal was associated with an increased risk of exposure to parasites and pathogens, although that risk differed across herds. For buffalo in the CB herd, dispersal was associated with an increased risk to bovine tuberculosis and brucellosis for buffalo, while dispersers from LS suffered higher infection rate by parasitic schistosomes. Our study thus suggests that the use of more proximate potential outcomes of dispersal, e.g., physiology and disease can be more informative of costs

and benefits of dispersal, than focusing narrowly on fitness effects. Moreover, our findings beg the question whether infectious diseases might play a larger role than previously appreciated in shaping facultative adult dispersal behaviors.

The lack of fitness effects could possibly be explained by the relatively short duration of the study (four years) compared to the lifespan of a buffalo (22 years, (Grimsdell 1973)), making it difficult to detect small differences in lifetime fitness.

There were significant infection costs associated with dispersal. Dispersers from LS suffered higher post-dispersal schistosome burdens, while dispersers from CB suffered higher post-dispersal bacterial infections, a combination of both increased bovine tuberculosis- and brucellosis infection. These patterns can be explained to some degree by infection exposures across the study area. Schistosome positive individuals were more common in the LS herd compared to the CB herds, as well as to some of the herds immediately to the north of the LS herd (Beechler, *in prep*). However, schistosome burdens in LS individuals were significantly lower than for affected individuals in other herds (Beechler, *in prep*). The higher post-dispersal schistosome burdens suggest that dispersers take up low ranking positions in new herds and are forced to feed in high risk areas, during resource restricted periods. Bovine tuberculosis and brucellosis prevalence varied spatially, with bovine tuberculosis prevalence higher in the LS herd compared to the CB herds (Ezenwa & Jolles 2015). Brucellosis prevalence varied by soil type, with higher prevalence on granitic soil profiles compared to basalt soil profiles (Gorsich *et al.* 2015). One of the herds at CB seasonally foraged on granitic soils. The variation in schistosome burden, bovine tuberculosis- and brucellosis prevalence is problematic as dispersers may be

immunologically stressed, naïve to novel pathogens and more susceptible to infection. In a possibly analogous situation, Le Roux *et al.* (2015) found that capture operations disrupted herd structure of African buffalo, which resulted in increased prevalence of bovine tuberculosis, perhaps because stressed animals in new social circumstances are at greater risk of infection.

Costs of dispersal appear to be context dependent. In this study, buffalo leaving the resource stressed herds (CB) bore a higher cost, in terms of infectious diseases, than buffalo from the better performing herd (LS). The LS herd had a higher annual dispersal rate of 19.2%, compared to 14.5% of the CB herds. These patterns suggest a positive feedback loop for healthier populations, in which animals are in better condition to withstand the cost of dispersal and thus may be willing to disperse more readily when they suffer local resource limitations. At the population scale, this suggests healthy populations should be capable of colonizing new areas quite successfully, as would be consistent with the African buffalo's broad geographic range (Sinclair 1977; Mloszewski 1983). Within our study area, this pattern resulted in source-sink dynamics in southern KNP. Many LS individuals dispersed to CB, whilst many of the CB dispersers only dispersed to other herds in the CB area. Thus, persistence of the CB herd may be influenced by the LS herd (Simonis 2012).

Previous work (Spaan, *Chapter 1*) showed that young adult female buffalo tend to disperse when resources become limited due to seasonal forage shortages and/or density dependence/intraspecific competition. Despite this, overall dispersal rates were higher from the seasonally resource limited area. Dispersal rates could reflect the balance of the drive to move away from competition for sparse resources

against the potential disease and social costs of dispersal. These are costs that buffalo in very poor condition can ill afford. Thus, we may predict maximum dispersal rates at intermediate levels of resource limitation. Moreover, dispersal rates may not respond linearly to changes in forage availability resulting from climate change or changes in surface water management on dispersal.

Acknowledgements

This research was supported in part by the National Science Foundation through the NSF Ecology of Infectious Disease Grant awarded to A. Jolles and V. Ezenwa (DEB-1102493/EF-0723928 and EF-0723918). We also acknowledge the essential contributions in animal handling and data collection by field technician Jo Spaan; veterinarians Peter Buss, Brianna Beechler, and Kristie Thompson; and veterinary technicians Jenny Joubert and Khosi Maseko. We would also like to acknowledge Dr. Sam Ferreira for assisting with the registration and support of this project.

References

- Ahlering, M.A., Maldonado, J.E., Fleischer, R.C., Western, D. & Eggert, L.S. (2012) Fine-scale group structure and demography of African savanna elephants recolonizing lands outside protected areas: Demography of elephants outside parks. *Diversity and Distributions*, **18**, 952–961.

- Alexander, K.A., Blackburn, J.K., Vandewalle, M.E., Pesapane, R., Baipoledi, E.K. & Elzer, P.H. (2012) Buffalo, bush meat, and the zoonotic threat of brucellosis in Botswana. *PLoS ONE*, **7**, e32842.
- Altizer, S., Bartel, R. & Han, B.A. (2011) Animal migration and infectious disease risk. *Science*, **331**, 296–302.
- Anderson, K., Ezenwa, V.O. & Jolles, A.E. (2013) Tick infestation patterns in free ranging African buffalo (*Syncerus caffer*): Effects of host innate immunity and niche segregation among tick species. *International Journal for Parasitology: Parasites and Wildlife*, **2**, 1–9.
- Atickem, A., Rueness, E.K., Loe, L.E., Serbezov, D., Bekele, A. & Stenseth, N.C. (2013) Population genetic structure and connectivity in the endangered Ethiopian mountain Nyala (*Tragelaphus buxtoni*): recommending dispersal corridors for future conservation. *Conservation Genetics*, **14**, 427–438.
- Ayebazibwe, C., Mwiine, F.N., Tjørnehøj, K., Balinda, S.N., Muwanika, V.B., Okurut, A.R.A., Belsham, G.J., Normann, P., Siegismund, H.R. & Alexandersen, S. (2010) The role of African buffalos (*Syncerus caffer*) in the maintenance of foot-and-mouth disease in Uganda. *BMC veterinary research*, **6**, 54.
- Beechler, B.R., Broughton, H., Bell, A., Ezenwa, V.O. & Jolles, A.E. (2012) Innate immunity in free-ranging African buffalo (*Syncerus caffer*): Associations with parasite infection and white blood cell counts. *Physiological and Biochemical Zoology*, **85**, 255–264.

Beyer, H.L. (2004) Hawth's analysis tools for ArcGIS.

<http://www.spatialecology.com/htools>.

Blundell, G.M., Ben-David, M., Groves, P., Bowyer, R.T. & Geffen, E. (2002)

Characteristics of sex-biased dispersal and gene flow in coastal river otters: implications for natural recolonization of extirpated populations. *Molecular Ecology*, **11**, 289–303.

Bonte, D. & De La Peña, E. (2009) Evolution of body condition-dependent dispersal in metapopulations. *Journal of Evolutionary Biology*, **22**, 1242–1251.

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

Bont, A., Steck, A.J. & Meyer, U.A. (1996) The acute hepatic porphyrias and their neurologic syndromes. *Schweizerische Medizinische Wochenschrift*, **126**, 6–14.

Budischak, S.A., Jolles, A.E. & Ezenwa, V.O. (2012) Direct and indirect costs of co-infection in the wild: Linking gastrointestinal parasite communities, host hematology, and immune function. *International Journal for Parasitology: Parasites and Wildlife*, **1**, 2–12.

Budischak, S.A., Hoberg, E.P., Abrams, A., Jolles, A.E. & Ezenwa, V.O. (2015) A combined parasitological molecular approach for noninvasive characterization

- of parasitic nematode communities in wild hosts. *Molecular Ecology Resources*, **15**, 1112–1119.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York.
- Carlson, S.M., Cunningham, C.J. & Westley, P.A.H. (2014) Evolutionary rescue in a changing world. *Trends in Ecology & Evolution*, **29**, 521–530.
- Caro, T. & Riggio, J. (2013) The Big 5 and conservation. *Animal Conservation*, **16**, 261–262.
- Caron, A., Cross, P.C. & du Toit, J.T. (2003) Ecological implications of bovine tuberculosis in African buffalo herds. *Ecological Applications*, **13**, 1338–1345.
- Clobert, J., Baguette, M., Benton, T.G. & Bullock, J.M. (eds.) (2012) *Dispersal Ecology and Evolution*. Oxford University Press, Oxford, UK.
- Cote, J. & Clobert, J. (2010) Risky dispersal: avoiding kin competition despite uncertainty. *Ecology*, **91**, 1485–1493.
- Cox, D.R. (1972) Regression models and life-tables. *Journal of the Royal Statistical Society, Series B*, **34**, 187–220.
- Debeffe, L., Focardi, S., Bonenfant, C., Hewison, A.J.M., Morellet, N., Vanpé, C., Heurich, M., Kjellander, P., Linnell, J.D.C., Mysterud, A., Pellerin, M., Sustr, P., Urbano, F. & Cagnacci, F. (2014) A one night stand? Reproductive excursions of female roe deer as a breeding dispersal tactic. *Oecologia*, **176**, 431–443.

- Ezenwa, V.O. (2003) Habitat overlap and gastrointestinal parasitism in sympatric African bovids. *Parasitology*, **126**, 379–388.
- Ezenwa, V. & Jolles, A. (2008) Horns honestly advertise parasite infection in male and female African buffalo. *Animal Behaviour*, **75**, 2013–2021.
- Ezenwa, V.O. & Jolles, A.E. (2015) Opposite effects of anthelmintic treatment on microbial infection at individual versus population scales. *Science*, **347**, 175–177.
- Ezenwa, V.O., Jolles, A.E. & O'Brien, M.P. (2009) A reliable body condition scoring technique for estimating condition in African buffalo. *African Journal of Ecology*, **47**, 476–481.
- Fox, J. & Weisberg, S. (2011) Cox proportional-hazards regression for survival data in R. Appendix to An R and S-PLUS companion to applied regression. Available at:
<http://socserv.mcmaster.ca/jfox/Books/Companion/appendix/Appendix-Cox-Regression.pdf>.
- Funston, P.J., Skinner, J.D. & Dott, H.M. (1994) Seasonal variation in movement patterns, home range and habitat selection of buffaloes in a semi-arid habitat. *African Journal of Ecology*, **32**, 100–114.
- Garant, D., Forde, S.E. & Hendry, A.P. (2007) The multifarious effects of dispersal and gene flow on contemporary adaptation. *Functional Ecology*, **21**, 434–443.
- Gaylard, A., Owen-Smith, N. & Redfern, J. (2003) Surface water availability: Implications for heterogeneity and ecosystem processes. *The Kruger*

- Experience* (eds J.T. Du Toit, K.H. Rodgers & H.C. Biggs), pp. 171–188. Island Press, Washington DC.
- Gertenbach, W.P.D. (1983) Landscapes of the Kruger National Park. *Koedoe*, **26**, 9–121.
- Gillis, E.A. & Krebs, C.J. (2000) Survival of dispersing versus philopatric juvenile snowshoe hares: do dispersers die? *Oikos*, **90**, 343–346.
- Gorsich, E.E., Bengis, R.G., Ezenwa, V.O. & Jolles, A.E. (2015) Evaluation of the sensitivity and specificity of an enzyme-linked immunosorbent assay for diagnosing brucellosis in African buffalo (*Syncerus caffer*). *Journal of Wildlife Diseases*, **51**, 9–18.
- Gorsich, E.E., Ezenwa, V.O., Cross, P.C., Bengis, R.G. & Jolles, A.E. (2015) Context-dependent survival, fecundity and predicted population-level consequences of brucellosis in African buffalo. *Journal of Animal Ecology*, **84**, 999–1009.
- Grimsdell, J.J.R. (1973) Age determination of the African buffalo, *Syncerus caffer* Sparrman. *African Journal of Ecology*, **11**, 31–53.
- Gross, J.E., Singer, F.J. & Moses, M.E. (2000) Effects of disease, dispersal, and area on bighorn sheep restoration. *Restoration Ecology*, **8**, 25–37.
- Gustine, D.D., Parker, K.L., Lay, R.J., Gillingham, M.P. & Heard, D.C. (2006) Interpreting resource selection at different scales for woodland caribou in winter. *Journal of Wildlife Management*, **70**, 1601–1614.

- Halley, D.J., Vandewalle, M.E.J., Mari, M. & Taolo, C. (2002) Herd-switching and long-distance dispersal in female African buffalo *Syncerus caffer*. *African Journal of Ecology*, **40**, 97–99.
- Hein, A.M., Hou, C. & Gillooly, J.F. (2012) Energetic and biomechanical constraints on animal migration distance: Constraints on animal migration distance. *Ecology Letters*, **15**, 104–110.
- Jacques, C.N., Jenks, J.A. & Klaver, R.W. (2009) Seasonal movements and home-range use by female pronghorns in sagebrush-steppe communities of western South Dakota. *Journal of Mammalogy*, **90**, 433–441.
- Jolles, A.E., Cooper, D.V. & Levin, S.A. (2005) Hidden effects of chronic tuberculosis in African buffalo. *Ecology*, **86**, 2358–2364.
- Jolles, A.E. (2007) Population biology of African buffalo (*Syncerus caffer*) at Hluhluwe-iMfolozi Park, South Africa. *Africa Journal of Ecology*, **45**, 398–406.
- Jolles, A.E., Ezenwa, V.O., Etienne, R.S., Turner, W.C. & Olf, H. (2008) Interactions between macroparasites and microparasites drive infection patterns in free-ranging African buffalo. *Ecology*, **89**, 2239–2250.
- Jori, F., Vosloo, W., Du Plessis, B., Bengis, R., Brahmabhatt, D., Gummow, B. & Thomson, G.R. (2009) A qualitative risk assessment of factors contributing to foot and mouth disease outbreaks in cattle along the western boundary of the Kruger National Park. *Revue scientifique et technique*, **28**, 917.

- Larter, N.C., Sinclair, A.R.E., Ellsworth, T., Nishi, J. & Gates, C.C. (2000) Dynamics of reintroduction in an indigenous large ungulate: the wood bison of northern Canada. *Animal Conservation*, **3**, 299–309.
- Le Roux, N., Cooper, D., van Helden, P.D., Hoal, E. G. & Jolles, A.E. (2015) Disease control in wildlife: Evaluating a test and cull programme for bovine tuberculosis in African buffalo. *Transboundary and Emerging Disease*.
- Macandza, V.A., Owen-Smith, N. & Cross, P.C. (2004) Forage selection by African buffalo in the late dry season in two landscapes. *South African Journal of Wildlife Research*, **34**, 113–121.
- McNulty, C. (2015) *African buffalo as reservoir hosts for infectious respiratory pathogens in Kruger National Park, South Africa*. MSc. thesis, University of Wisconsin-Madison, Madison.
- Michel, A.L., Cooper, D., Jooste, J., de Klerk, L.M. & Jolles, A.E. (2011) Approaches towards optimizing the gamma interferon assay for diagnosing *Mycobacterium bovis* infection in African buffalo. *Preventative Veterinary Medicine*, **98**, 142-151.
- Michel, A.L. & Bengis, R.G. (2012) The African buffalo: A villain for inter-species spread of infectious diseases in southern Africa. *Onderstepoort Journal of Veterinary Research*, **79**, 26–30.
- Mloszewski, M.J. (1983) *The Behaviour and Ecology of the African Buffalo*. Cambridge University Press, Cambridge.
- Monard, A.-M. & Duncan, P. (1996) Consequences of natal dispersal in female horses. *Animal behaviour*, **52**, 565–579.

- Parmar, M.K.B. & Machin, D. (1995) *Survival analysis: A practical approach*. John Wiley & Sons, Chichester, UK.
- Picket, S.T.A., Cadenasso, M.L. & Benning, T.L. (2003) Biotic and abiotic variability as key determinants of savanna heterogeneity at multiple spatiotemporal scales. *The Kruger Experience* (eds J.T. du Toit, K.H. Rodgers & H.C. Biggs), pp. 22–40. Island Press, Washington DC.
- Plumb, G.E., White, P.J., Coughenour, M.B. & Wallen, R.L. (2009) Carrying capacity, migration, and dispersal in Yellowstone bison. *Biological Conservation*, **142**, 2377–2387.
- R Development Core Team (2014) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org/>
- Redfern, J.V., Grant, R., Biggs, H. & Getz, W.M. (2003) Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology*, **84**, 2092–2107.
- Rice, C.G. (2008) Seasonal altitudinal movements of mountain goats. *Journal of Wildlife Management*, **72**, 1706–1716.
- Rodrigues, A.M.M. & Johnstone, R.A. (2014) Evolution of positive and negative density-dependent dispersal. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20141226.
- Roffler, G.H., Talbot, S.L., Luikart, G., Sage, G.K., Pilgrim, K.L., Adams, L.G. & Schwartz, M.K. (2014) Lack of sex-biased dispersal promotes fine-scale genetic structure in alpine ungulates. *Conservation Genetics*, **15**, 837–851.

- Ronce, O. (2007) How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annual Review of Ecology, Evolution, and Systematics*, **38**, 231–253.
- Roug, A., Clifford, D., Mazet, J., Kazwala, R., John, J., Coppolillo, P. & Smith, W. (2014) Spatial predictors of bovine tuberculosis infection and *Brucella* spp. exposure in pastoralist and agropastoralist livestock herds in the Ruaha ecosystem of Tanzania. *Tropical Animal Health and Production*, **46**, 837–843.
- Ryan, S.J. & Jordaan, W. (2005) Activity patterns of African Buffalo (*Syncerus caffer*) in the Lower Sabie region, Kruger National Park, South Africa. *Koedoe*, **48**, 117–124.
- Shafer, A.B., Northrup, J.M., White, K.S., Boyce, M.S., Côté, S.D. & Coltman, D.W. (2012) Habitat selection predicts genetic relatedness in an alpine ungulate. *Ecology*, **93**, 1317–1329.
- Shaw, A.K., Jalasvuori, M. & Kokko, H. (2014) Population-level consequences of risky dispersal. *Oikos*, **123**, 1003–1013.
- Shepard, E.L.C., Wilson, R.P., Rees, W.G., Grundy, E., Lambertucci, S.A. & Vosper, S.B. (2013) Energy landscapes shape animal movement ecology. *The American Naturalist*, **182**, 298–312.
- Simonis, J.L. (2012) Demographic stochasticity reduces the synchronizing effect of dispersal in predator-prey metapopulations. *Ecology*, **93**, 1517–1524.
- Sinclair, A.R.E. (1977) *The African buffalo, a Study of Resource Limitation of Populations*. Chicago University Press, Chicago.

- Smit, I.P. (2013) Systems approach towards surface water distribution in Kruger National Park, South Africa. *Pachyderm*, **53**, 91–96.
- Smit, I.P.J., Grant, C.C. & Devereux, B.J. (2007) Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biological Conservation*, **136**, 85–99.
- Spaan, R.S., Epps, C.W., Ezenwa, V.O. and Jolles, A.E. (2015) Why did the buffalo cross the park? Intrinsic and extrinsic drivers of dispersal. *In prep.*
- Stamps, J.A., Krishnan, V.V. & Reid, M.L. (2005) Search costs and habitat selection by dispersers. *Ecology*, **86**, 510–518.
- Tittler, R., Fahrig, L. & Villard, M.-A. (2006) Evidence of large-scale source-sink dynamics and long-distance dispersal among wood thrush populations. *Ecology*, **87**, 3029–3036.
- Travis, J.M.J., Mustin, K., Bartoń, K.A., Benton, T.G., Clobert, J., Delgado, M.M., Dytham, C., Hovestadt, T., Palmer, S.C.F., Van Dyck, H. & Bonte, D. (2012) Modelling dispersal: an eco-evolutionary framework incorporating emigration, movement, settlement behaviour and the multiple costs involved. *Methods in Ecology and Evolution*, **3**, 628–641.
- van Hooft, W.F., Groen, A.F. & Prins, H.H.T. (2003) Genetic structure of African buffalo herds based on variation at the mitochondrial D-loop and autosomal microsatellite loci: Evidence for male-biased gene flow. *Conservation Genetics*, **4**, 467–477.

- van Oort, H., McLellan, B.N. & Serrouya, R. (2011) Fragmentation, dispersal and metapopulation function in remnant populations of endangered mountain caribou. *Animal Conservation*, **14**, 215–224.
- Venter, F.J., Scholes, R.J. & Eckhardt, H.C. (2003) The abiotic template and its associated vegetation pattern. *The Kruger Experience* (eds J.T. Du Toit, K.H. Rodgers & H.C. Biggs), pp. 83–129. Island Press, Washington DC.
- Worton, B.J. (1987) A review of models of home range for animal movement. *Ecological Modelling*, **38**, 277–298.
- Yoder, J.M., Marschall, E.A. & Swanson, D.A. (2004) The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. *Behavioral Ecology*, **15**, 469–476.

Table 2.1 Contrasting demographic parameters (survival, body condition, fecundity, and population growth rate) of African buffalo for the Lower Sabie and Crocodile Bridge herds, Kruger National Park for the period June 2008 to August 2012

Demographic parameters	Lower Sabie	Crocodile Bridge
¹ survival	↑	↓
² body condition	↑	↓
² fecundity	↑	↓
² population growth (λ)	1.13 (95% CI: 1.13-1.16)	0.85 (95% CI: 0.85-0.90)

¹ Ezenwa & Jolles (2015)

² Gorsich *et al.* (2015)

Table 2.2 Univariate models determining whether dispersal is a significant predictor of survival of female African buffalo for the period June 2008 to August 2012 in the pooled, Lower Sabie and Crocodile Bridge areas, Kruger National Park

Data set	Predictor	Odds-ratio	Estimate	LB	UB	p-value
				95% CI	95% CI	
Pooled	dispersal	1.04	-0.04	0.51	1.82	0.900
Lower Sabie	dispersal	1.57	0.45	0.56	4.36	0.390
Crocodile Bridge	dispersal	1.11	0.10	0.46	2.70	0.820

Table 2.3 Output from paired t-tests comparing the change in pre and post dispersal pregnancy rates between dispersers and controls, and the change in for the pooled, Lower Sabie and Crocodile Bridge data for the period June 2008 to August 2012.

Area	Fitness measure	Disperser		Control		n	LB	UB	p-value
		Mean	SD	Mean	SD		95% CI	95% CI	
Pooled	pregnancy rate	0.23	0.51	0.17	0.54	50	-0.25	0.14	0.590
Lower Sabie	pregnancy rate	0.23	0.49	0.09	0.58	25	-0.44	0.17	0.367
Crocodile Bridge	pregnancy rate	0.23	0.54	0.26	0.50	25	-0.24	0.30	0.819
Pooled	body condition	-0.21	0.60	-0.25	0.50	44	-0.27	0.20	0.735
Lower Sabie	body condition	-0.44	0.69	-0.40	0.51	22	-0.37	0.05	0.822
Crocodile Bridge	body condition	0.03	0.39	-0.10	0.47	22	-0.38	0.13	0.323

Table 2.4 Output from paired t-tests comparing either the change in worm burden or the number of viral and bacterial infections gained in the dispersal period between dispersing and controls individuals for the pooled, Lower Sabie and Crocodile Bridge data for the period June 2008 to August 2012. Viral infections included incidence data for bovine herpes virus, adenovirus type 3, parainfluenza virus type 3, and serostatus for bovine respiratory syncytial virus and bovine viral diarrhea virus. Bacterial infections included the chronic infections bovine tuberculosis and brucellosis.

Area	Infections	Effect	Dispersers		Controls		n	LB	UB	p-value
			Mean	SD	Mean	SD		95% CI	95% CI	
Pooled	Strongyles		-0.08	1.32	0.22	1.28	79	-0.66	0.07	0.113
Lower Sabie	Strongyles		-0.02	1.31	0.23	1.16	45	-0.69	0.20	0.273
Crocodile Bridge	Strongyles		-0.15	1.34	0.21	1.44	34	-1.00	0.28	0.260
Pooled	Coccidia		-0.16	1.25	-0.03	1.51	79	-0.55	0.30	0.551
Lower Sabie	Coccidia		-0.36	1.21	-0.20	1.70	45	-0.78	0.45	0.165
Crocodile Bridge	Coccidia		0.12	1.28	0.19	1.21	34	-0.67	0.51	0.791
Pooled	Schistosome	(↑)	0.11	0.84	-0.13	0.52	59	-0.03	0.50	0.086
Lower Sabie	Schistosome	↑	0.28	0.64	0.02	0.21	26	0.01	0.51	0.046
Crocodile Bridge	Schistosome		-0.03	0.95	-0.24	0.66	33	-0.24	0.67	0.336
Pooled	Viruses +/-		0.00	1.01	0.11	0.95	46	-0.53	0.32	0.609
Lower Sabie	Viruses +/-		-0.05	0.90	-0.18	0.85	22	-0.43	0.70	0.623
Crocodile Bridge	Viruses +/-		0.04	1.12	0.38	0.97	24	-0.99	0.32	0.303
Pooled	Bacteria +/-	(↑)	0.16	0.02	0.06	0.01	49	-0.02	0.22	0.096
Lower Sabie	Bacteria +/-		0.08	0.02	0.08	0.02	26	-0.16	0.16	1.000
Crocodile Bridge	Bacteria +/-	↑	0.26	0.06	0.04	0.01	23	0.04	0.40	0.021

Arrows denote significant variables while arrows in parentheses denote marginally significant variables

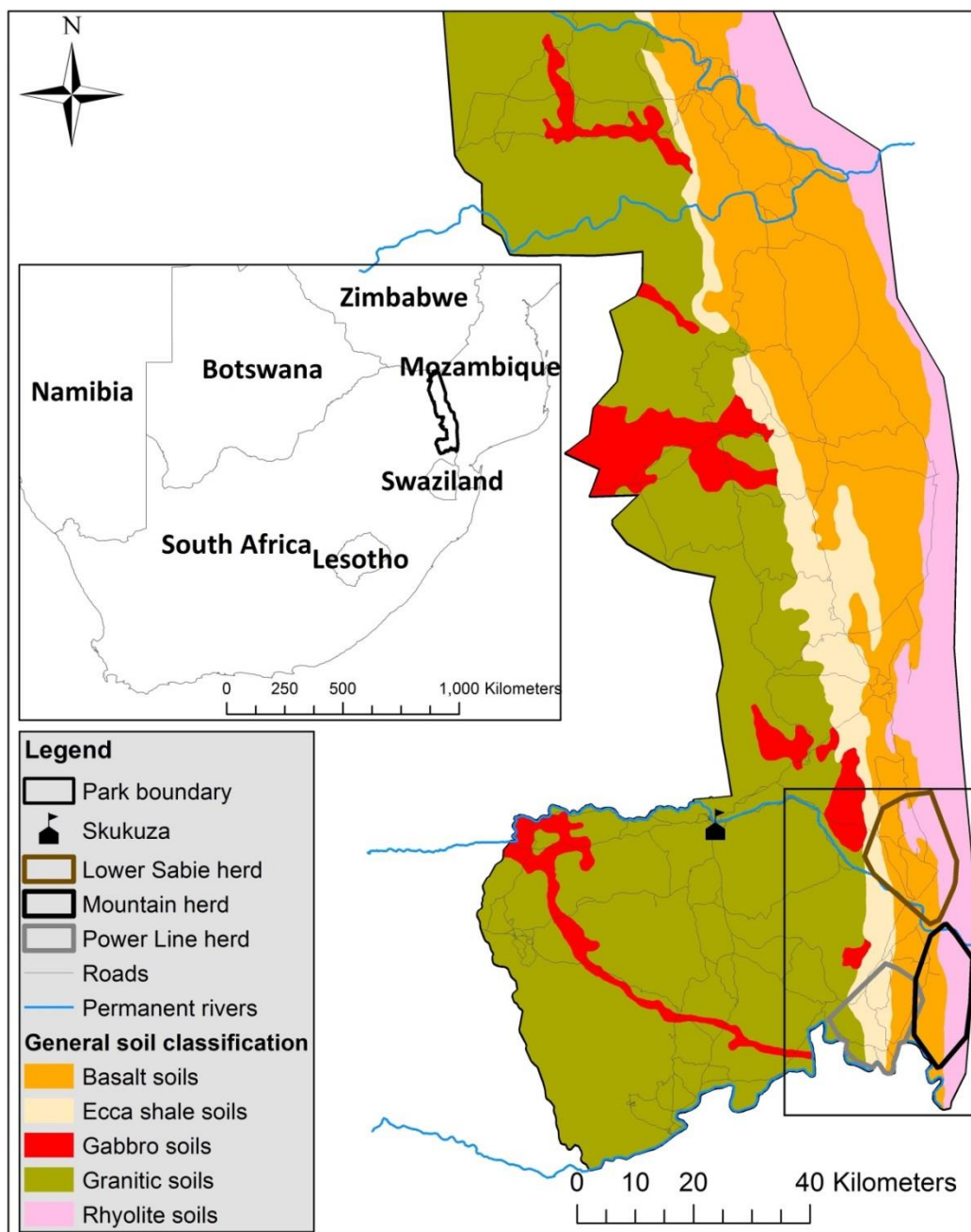
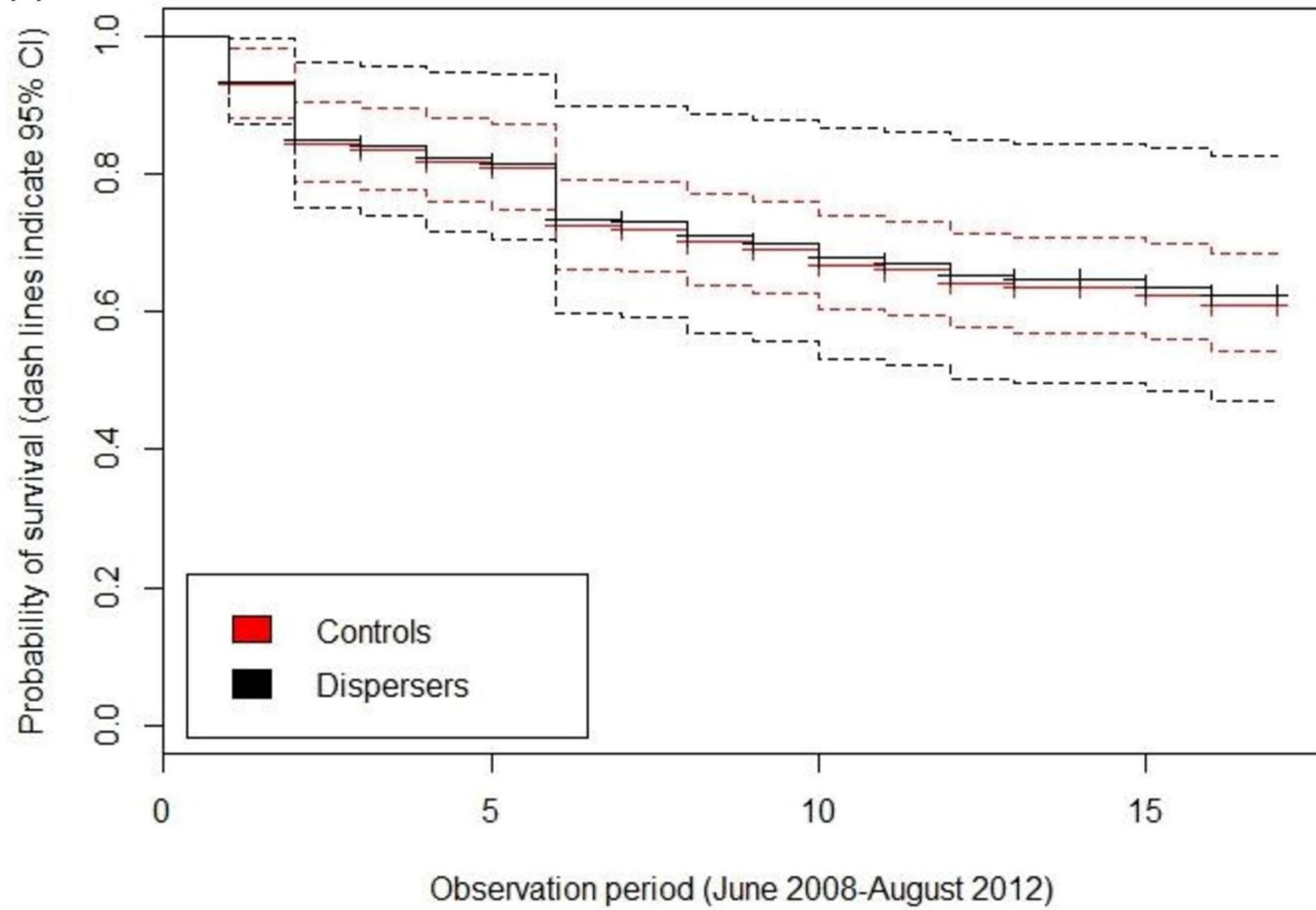


Fig. 2.1 General (black line) and focal study areas (Lower Sabie herd, brown polygon; and Crocodile Bridge herds made up of Mountain herd, black polygon; Power Line herd, gray polygon) for study of dispersal of female African buffalo in Kruger National Park in southern Africa (inset). Initial mass capture of 200 female African buffalo were from the Lower Sabie, Mountain and Power Line herds in June/July and October of 2008, but females dispersed throughout much of the park during the course of the 4-year study.

(a)



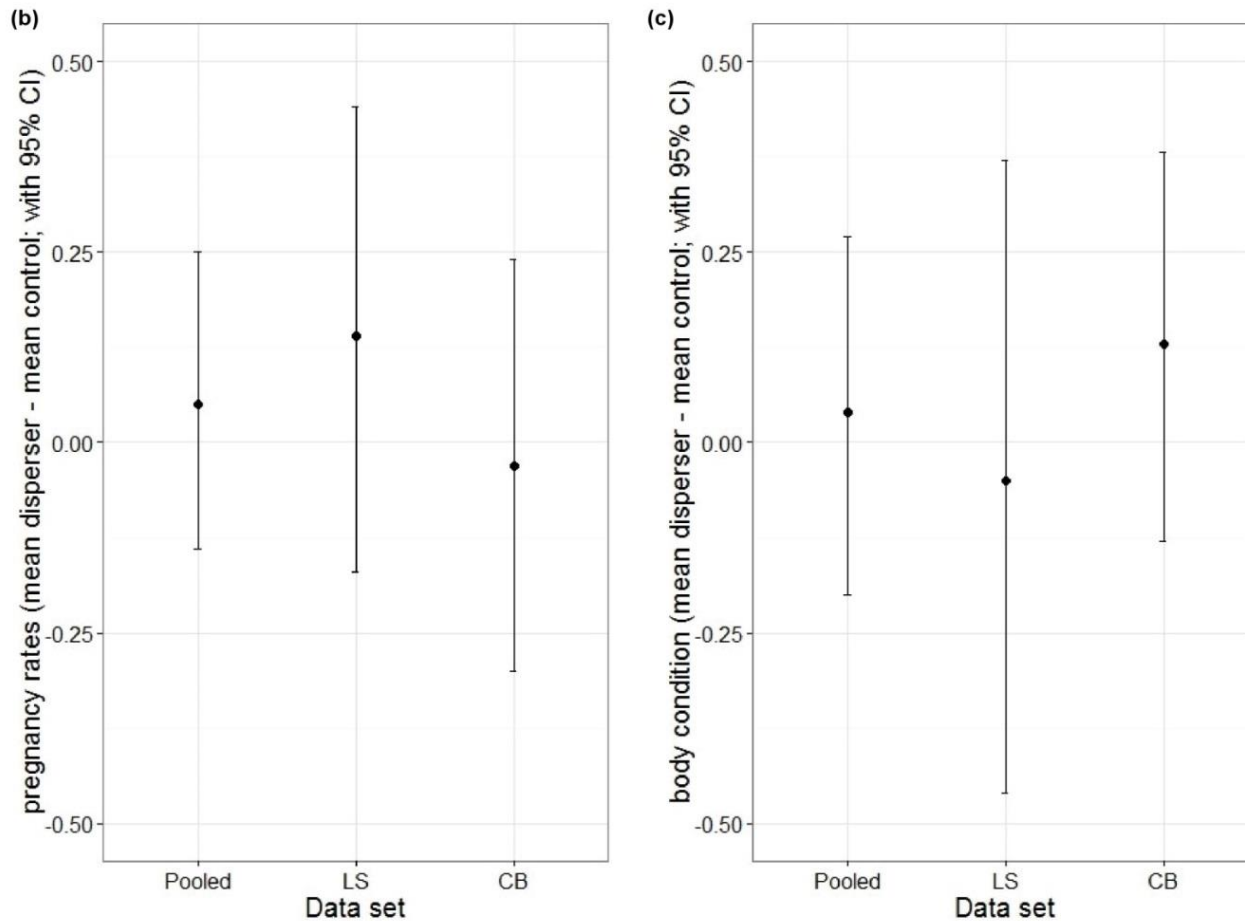
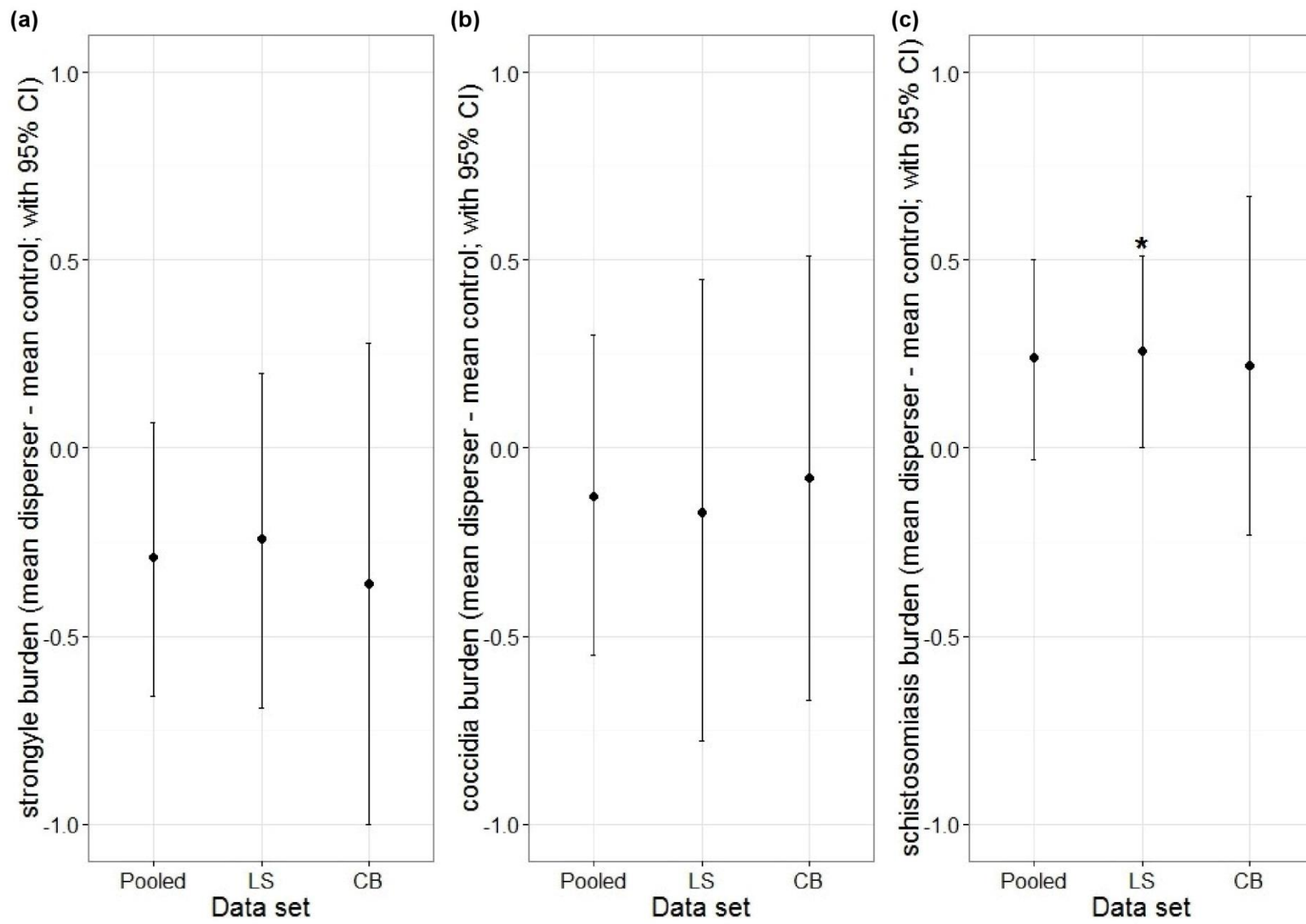


Fig 2.2 Fitness measures of African buffalo in Kruger National Park, for the period, June 2008 – August 2012, showing: (a) output from Cox proportional-hazards regression model comparing survival of dispersing (black) and philopatric controls (red) for the pooled data, and output from paired t-tests comparing the mean difference in pre vs. post dispersal (b) pregnancy rates, and (c) body condition of dispersers and controls in the pooled, Lower Sabie (LS) and Crocodile Bridge (CB) data. Positive differences indicate higher disperser values.



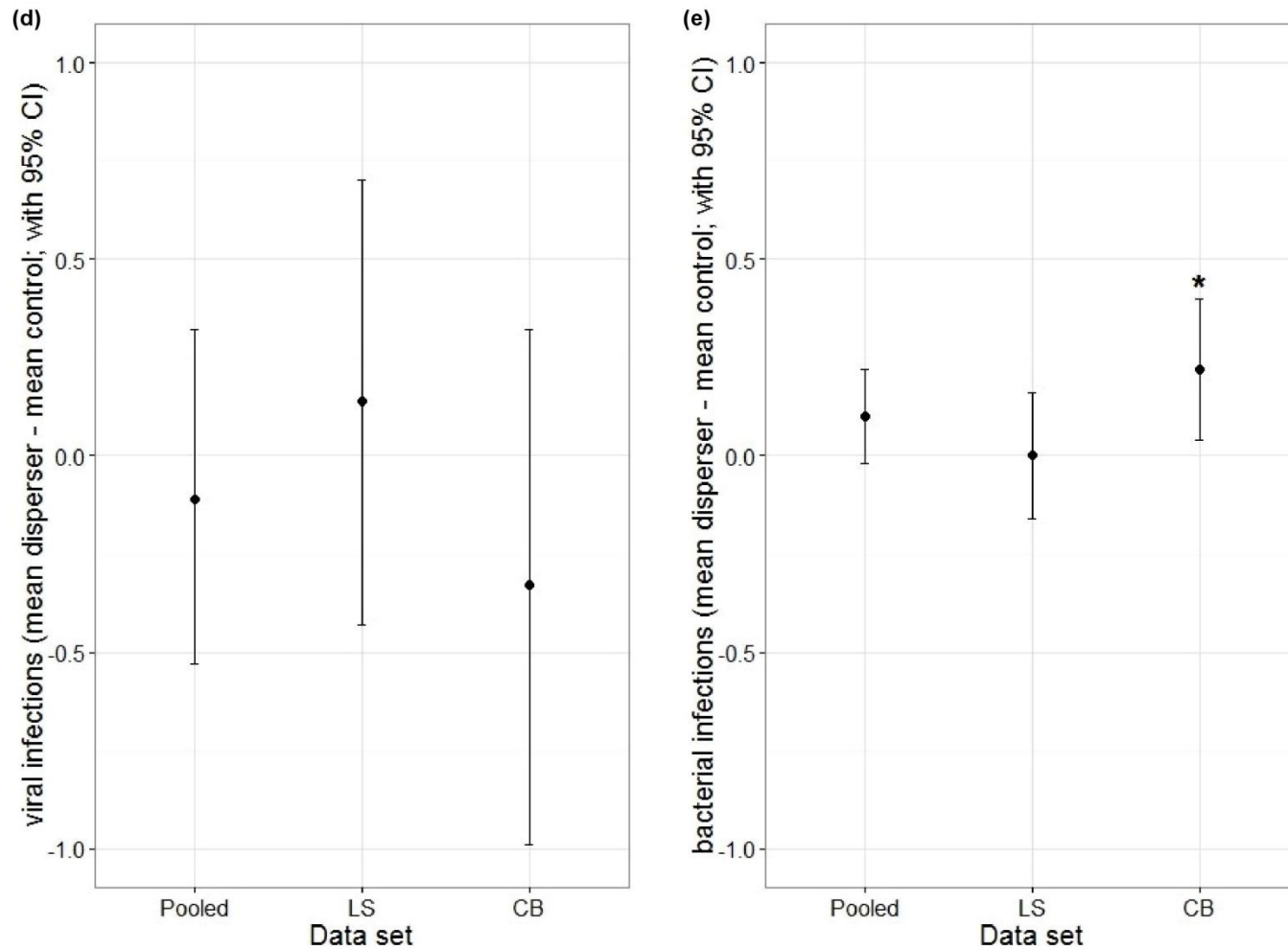


Fig 2.3 Infection measures of African buffalo in Kruger National Park, for the period, June 2008 – August 2012, showing output from paired t-tests comparing the mean difference in pre vs. post dispersal: (a) strongyle burdens (b) coccidia burdens, (c) schistosome burdens, (d) viral infections, and (e) bacterial infections, of dispersers and controls in the pooled, Lower Sabie (LS) and Crocodile Bridge (CB) data. Positive differences indicate higher disperser values. * indicates significant difference.

Supporting Information

Table S2.1 Data available for this study

Measure	Category	Measure Type	Statistical Measure	Biological Significance
Age	Animal trait	Quantitative. Measured in months.	Continuous	Estimated by tooth eruption and wear ^{g, i}
Body condition	Animal trait	Quantitative. Measured on a scale of (1 v. good – 5 v. poor)	Continuous	Fat reserves as a measure of body condition ^d
Pregnancy status	Animal trait	Yes/No	Binary	Determined by rectal palpation ^a
Lactation status	Animal trait	Yes/No	Binary	Manual milking of all four teats ^h
Season	Environmental variable	Divided into early wet, late wet, early dry and late dry	Categorical	Quality and abundance of grazing varies by season ^l
Bolus	Experimental/Treatment	Yes/No	Binary	Reduces nematode burden ^e
Strongyle infection	Gastro-intestinal parasites	Quantitative - eggs per gram (logged)	Continuous	Quantifies strongyle infection by FEC ^e
Coccidia infection	Gastro-intestinal parasites	Quantitative - oocysts per gram (logged)	Continuous	Quantifies coccidian species infection in feces by quantifying oocysts ^e

Table S2.1 (continued)

Schistosome infection	Gastro-intestinal parasites	Quantitative -	Binary	CAA titer used as a proxy for adult schistosome burden ^k
bTB status	Bacteria	Positive/negative for <i>Mycobacterium bovis</i>	Binary	Use ELISA to diagnose bTB infection ^j
Brucellosis status	Bacteria	Positive/negative for <i>Brucella abortus</i>	Binary	Commercial enzyme-link Immunosorbent assay ^f
Bovine Herpes Virus status	Viruses	Positive/negative	Binary	Use ELISA to diagnose BHV ^b
Adenovirus status	Viruses	Positive/negative	Binary	Use ELISA to diagnose AD3 ^b
Parainfluenza status	Viruses	Positive/negative	Binary	Use ELISA to diagnose PI3 ^b
Bovine Respiratory Syncytial Virus status	Viruses	Positive/negative	Binary	Use ELISA to diagnose BRSV ^b
Bovine Viral Diarrhea status	Viruses	Positive/negative	Binary	Use ELISA to diagnose BVFV ^b

Sources: ^a Beechler *et al.* 2012; ^b McNulty 2015; ^c Budischack, Jolles and Ezenwa 2012; ^d Ezenwa, Jolles & O'Brien 2009;

^e Ezenwa *et al.* 2010; ^f Gorsich *et al.* 2015; ^g Grimsdell 1973; ^h Jolles, Cooper & Levin 2005; ⁱ Jolles 2007; ^j Michel *et al.* 2011;

^k Stothard *et al.* 2014; ^l Venter, Scholes & Eckhardt 2003

Table S2.2 Model selection tables from Cox proportional hazards models predicting survival of female African buffalo for the period June 2008 to August 2012 in the pooled, Lower Sabie and Crocodile Bridge data sets in Kruger National Park showing 5 top models based on Akaike's Information Criterion (AIC). Model terms included in final models included herd dispersal (binary), herd (binary), age (continuous) and quadratic age term (continuous).

Data set	Model	AIC	Δ AIC	AICWt
Pooled	herd+age+age ²	862.07	0.00	0.58
	disperser+herd+age+age ²	863.81	1.74	0.24
	herd+age	866.45	4.39	0.06
	herd	867.47	5.40	0.04
	disperser+herd+age	868.18	6.11	0.03
Lower Sabie	age	229.62	0.00	0.22
	age+age ²	229.73	0.11	0.21
	disperser	230.31	0.69	0.16
	age ²	230.54	0.92	0.14
	disperser+age	231.12	1.50	0.10
Crocodile Bridge	age+age ²	551.50	0.00	0.46
	disperser+age+age ²	553.50	2.00	0.17
	age	553.88	2.38	0.14
	age ²	555.04	3.54	0.08
	disperser	555.42	3.93	0.07

Table S2.3 Cumulative AIC weights for each predictor variable from every possible Cox proportional hazard model across the set of predictor variables considered. Maximum cumulative weight for each predictor variable is 1; explanatory variables varied by data set but included dispersal, area of origin, age and the quadratic term for age.

Data set	Response variable	dispersal	herd	age	age ²
Pooled	survival	0.30	1.00	0.91	0.85
Lower Sabie	survival	0.43	na	0.63	0.52
Crocodile Bridge	survival	0.32	na	0.82	0.74