The decline of the globally threatened Rudd's Lark in one of its last remaining core sites, the Wakkerstroom grasslands

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Abstract

The Rudd's Lark *Heteromirafra ruddi* is a globally threatened species with a fragmented population occurring in one of the world's most poorly-protected biomes, the grasslands. This, together with its endemism to the Highveld of South Africa and climate envelope modelling which predicts a dramatic reduction in its available habitat, places the species firmly in the cross-hairs of extinction risk. This thesis aims to gain a better understanding of Rudd's Lark population trends, habitat preference and threats in one of its most important remaining core sites in the grasslands around Wakkerstroom, Mpumalanga Province, which are under private ownership and used predominantly for grazing.

My objectives were, first, to determine whether the species has declined in the Wakkerstroom area since a survey conducted in 2002 by David Maphisa. Second, to determine what habitat variables predict Rudd's Lark incidence, whether there has been a change in its available habitat and in farm management practices, and whether the species has changed in its habitat selection since the previous survey. Finally, I aimed to investigate whether other grassland birds (particularly other threatened grassland endemics) also respond to fine-scale habitat variation and share habitat preference with the Rudd's Lark.

I found both absolute lower numbers of Rudd's Larks (5 transects with Rudd's Lark present down from 9 in 2002; 9 individuals down from 32), and a lower probability of encounter (significantly lower in the case of individuals). Seven transects had been lost to crop production, two of which formerly contained Rudd's Larks. Forb and dead vegetation cover had significantly increased at a coarse scale, but vegetation variables did not explain any significant variation in Rudd's Lark incidence at either a fine or a coarse scale within 2016. However, Rudd's Larks appear to be occupying subtly different habitat now compared to 12 years ago: lark territories surveyed in 2016 had less bare ground and more but shorter grass cover than in 2002. Most farmers reported warmer conditions in recent years and that burning generally took place between August and October, matching the analysis of remotely-sensed fire data from the past ten years and implying that destructive late-season fires are not common. Correspondingly, I found that burning regimes did not predict Rudd's Lark incidence. Among other threatened grassland species, Yellow-breasted Pipits showed a clear preference for taller grass and higher altitudes, unlike Rudd's Larks which showed no detectable preferences.

In summary, direct loss of grassland habitat through conversion to crops appears to be a pressing threat to Rudd's Larks, although the species has also declined within the remaining area of grassland habitat. The specific drivers of this decline remain unclear given that the observed changes in grassland structure since 2002 do not correspond with Rudd's Lark habitat selection. Taken together, these findings are very concerning given that the Wakkerstroom area is considered to be one of the last remaining core sites for the species, and call its IUCN threat status of globally Vulnerable into question. A priority for future research will be to understand what limits Rudd's Larks to its current pockets of occupancy within its remaining apparently suitable grassland habitat, and whether increasing grassland fragmentation will accelerate its decline.

Key words: fire, grassland, habitat selection, *Heteromirafra ruddi*, IUCN status, rangelands, Rudd's Lark, threatened species, transects

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Introduction

South African Grasslands

In his seminal work on the veld types of South Africa, Acocks (1953) suggested that much of the country's grasslands did not reflect the climate of the region but were the result of human-induced fire and clearing for agriculture (Bond et al. 2003). He suggested that these factors created an environment in which natural forest cover – still patchily present in the landscape – is inhibited (Acocks 1953). However, there is growing evidence that the grasslands of South Africa are, instead, ancient and non-anthropogenic in origin (Bond et al. 2003). Evidence for this includes dated pollen cores (Meadows & Linder 1993) and charcoal deposits (Scott 2002) which suggest that fire has been influencing the landscape for far longer than human activity. Even more pertinent is the presence of endemic species in these areas (Bond 2016), since endemism is often indicative of a long-standing relationship between the relevant species and their environment. If the fires that regulate the grasslands of South Africa were anthropogenic in origin – that is, relatively recent – then low levels of both faunal and floral endemism would be expected (Bond et al. 2003). Instead, the biome contains several endemic forbs and shrubs (Cowling & Hilton-Taylor 1994), fish (Skelton et al. 1995), and mammals (Lombard 1995), many of which are threatened (Neke & Du Plessis 2004).

These grasslands are also a key habitat for avian assemblages. In 1998 Birdlife International (and partners, including Birdlife South Africa) identified the grasslands of southern Africa as one of 76 endemic bird areas of the world that should be assigned the highest conservation priority (Stattersfield et al. 1998). Ten endemic bird species reside here, six of which are threatened (Collar et al. 1994). A further four (non-endemic) threatened species have major strongholds in this region (Collar et al. 1994). Since then, Birdlife South Africa has identified an Important Bird and Biodiversity Area (IBA) region centered on the towns of Wakkerstroom, Volksrust and Memel in the eastern Highveld (Marnewick et al. 2015). Although IBAs are not themselves protected areas, they represent focal points for the conservation efforts of BirdLife South Africa. Within the grassland IBA, three protected areas have been declared, strengthening the conservation status of the area by "providing protection against mining and assisting landowners to manage the grassland on their farms for particular species or communities of birds" (BirdLife South Africa 2015).

The grassland biome has long been considered one of southern Africa's most threatened vegetation types (Macdonald et al. 1993). The highland grasslands of Mpumalanga, in particular, are poorly conserved (Matthews et al. 1993). These areas have historically been subjected to extensive agricultural transformation, including intense grazing and frequent burning (Jansen et al. 1999), as well as afforestation (Allan et al. 1997). The pressures on grassland avian assemblages resulting from such a combination of factors has already been documented: Brennan & Kuvlesky (2005) predicted that the widespread and ongoing decline of grassland birds across the USA is poised to become one of the major wildlife crises of the 21st century. Furthermore, the bird species suite of South Africa's grassland biome was recently identified along with those of the Fynbos as potentially the most vulnerable to climate change (Huntley & Barnard 2012). This study estimated that just less than one third of South Africa's grassland has already been lost, primarily through agricultural transformation (Huntley & Barnard 2012).

Fire and grazing

Grassland is indisputably South Africa's most agriculturally productive biome (Neke & Du Plessis 2004). Much of the highland grasslands are used for livestock production (Maphisa et al. 2009). To this end, fire is used to control ticks (van Niekerk et al. 2006) and remove unpalatable vegetation in order to improve grass regeneration and grazing (Mentis & Biglake 1981). However, Tainton (1999) found that farmers in these areas often burn irrespective of unpalatable litter build-up. A study of sour grassveld, the dominant grass-type in the Wakkerstroom area, showed that intense burning (in combination with grazing) has contributed to habitat fragmentation and changes in vegetation type and species composition (Edwards 1981). There is also evidence that grasslands in South Africa have been overstocked since the 1930s (Downing 1978), and intense grazing has been cited as one of the major factors that has changed the composition of the highland grasslands of Mpumalanga (Jansen et al. 1999).

Conservation in Agricultural Landscapes

There is an increasing realization among ecologists and conservationists that populations of wild species can and must be preserved within landscapes where agriculture is the dominant land use (Tscharntke et al. 2005). Human land-use does not always equate to habitat destruction (Tsharntke et al. 2005); non-intensive management of grasslands, in particular, has been found to be important for conservation (Bignal & McCracken 1996). Indeed, several studies have revealed that certain bird species prefer agricultural land, such as the Chough (*Pyrrhocorax pyrrhocorax*) (Bignal & McCracken 1996) and Blue Crane (*Anthropoides paradiseus*) (van Velden et al. 2016), even when suitable natural habitat is available. McIntyre & Barrett (1992) described the grasslands of New South Wales, Australia, as a constantly shifting mosaic of habitats that for most biotic species provided a continuum of varying suitability, rather than a fragmented landscape. Certainly in South Africa, some threatened bird species (such as Botha's Lark *Spizocorys fringillaris*) in high elevation grasslands have been described as preferring habitat that has experienced a certain degree of heavy grazing (Maphisa et al. 2009, Taylor et al. 2015). In the absence of natural herbivores in agricultural landscapes, this ecological role would necessarily be played by livestock such as sheep or cattle.

However, the relationship between vegetation structure and avian assemblages is often complex (e.g. Jansen et al. 1999, Benton et al. 2002, Coppedge et al. 2008, Kleijn et al. 2010). Conversion to agriculture may not destroy the habitat of a bird species outright, but healthy populations cannot be maintained if the habitat is not of sufficient quality (Morrison 1986). It is therefore essential that the right management intensity is maintained or developed (Bignal & McCracken 1996). A study of farmland birds in the United Kingdom between 1970 and 1990 found that more than 80% of species (n=26) had declined in both range and abundance due to changes in agricultural practices (Benton et al. 2002). This was linked to the decrease in arthropod numbers as a result of farming intensification. In the specific case of high elevation grasslands, Jansen et al. (1999) found that the Red-winged Francolin (*Scleroptila levaillantii*) is highly vulnerable to heavy grazing and frequent burning in Mpumalanga Province, South Africa, while Donald et al. (2010) reported a rapid decline in the population of the Liben Lark (*Heteromirafra archeri*) in Ethiopia on account of overgrazing by pastoralists.

If conservation within agricultural systems is to be achieved, farmers must necessarily be included as active stakeholders, as conservation projects are by necessity mediated through them (Ahnström et al. 2009). This includes an understanding of the various factors that affect their decision-making. Farmers play an interesting role at the interface between humans and nature; research suggests that a large percentage of farmers consider themselves “close to the land” and employ their local knowledge and understanding within a position of intergenerational stewardship (Liffman et al. 2000, Bieling & Plieninger 2003). Simultaneously, farmers can be viewed as the perpetrators of habitat destruction and environmental pollution driven by utilitarianism (Ahnström et al. 2009, Sullivan et al. 1996).

As with any ecological consideration, understanding the specific environmental and socio-economic context is vitally important. Farmers in the high elevation grasslands of South Africa are primarily concerned with livestock, specifically sheep and cattle (Maphisa et al. 2009). Local observations also suggest that a significant increase in crop production in the area is currently underway, though perhaps not to the degree of dramatic intensification and industrialization experienced in western Europe. In the UK, for example, the resulting decline in range and abundance of birds in the agricultural landscape prompted Krebs et al. (1999) to herald a “second Silent Spring”. Nonetheless, the avian assemblage of South Africa’s high altitude grassland is certainly at risk (Collar et al. 1994, Allan et al. 1997, Jansen et al. 1999, Maphisa et al. 2009, Huntley & Barnard 2012). Factors such as burning and grazing do play a role in determining the habitat suitability for birds in the region, most notably a number of threatened species such as Rudd's Lark *Heteromirafra ruddi* and Botha's Lark *Spizocorys fringillaris* (Hockey et al. 1988, Allan et al. 1997, Maphisa et al. 2009). While crop production could become a major threat, the cumulative effect of fire and grazing regimes could also be causing the grassland to become incrementally less suitable. How best to facilitate the transformation of agricultural production from a biodiversity inhibitor into a contributor to ecosystem integrity is a major challenge in this region, as well as world-wide (Scherr & McNeely 2008).

Rudd's Lark (*Heteromirafra ruddi*)

Rudd's Lark is a grassland bird endemic to the highlands of eastern South Africa (Hockey et al. 1988). The species was first described from a sample collected in Wakkerstroom in 1904 (Grant 1908). Until recently, Rudd's Lark was considered one of three members of the genus *Heteromirafra*, but Archer's Lark (*H. archeri*) and the Liben Lark (*H. sidamoensis*) of Ethiopia have been found to be conspecific and should now be considered a single species with the name *H. archeri* (Spottiswoode et al. 2013). These two species (*H. archeri* and *H. ruddi*) are both highly threatened grassland endemics and are among the species most at risk of becoming continental Africa's first avian extinction in recorded history (Spottiswoode et al. 2009).

The distribution of Rudd's Lark is highly localized and patchy (Hockey et al. 1988, Maphisa et al. 2009), with the species historically occupying isolated sites in the Free State (FS), KwaZulu-Natal (KZN), Mpumalanga (MP) and Eastern Cape (EC) provinces of South Africa (Hockey et al. 1988). This distribution and the naturally cryptic nature of the species (Hockey et al. 1988) mean that Rudd's Lark has defied a confident or comprehensive assessment of its status. As such, its threat level has been subject to change over the past few decades, and continues to be the result of crude estimations (Taylor et al. 2015). In the South African Red Data Book of Birds published 17 years ago (Barnes 2000), Rudd's Lark was listed as critically endangered on account of habitat loss and fragmentation, and projected to potentially decline by up to 80% over 15–20 years. However, these threats were subsequently deemed less severe than initially thought, and the species' status was downgraded to Vulnerable in 2006 (Birdlife International 2016b). In the most recent edition of the South African Red Data Book, the species has been listed as regionally Endangered and globally Vulnerable (Taylor et al. 2015) which is a puzzling mismatch given the species is endemic to South Africa. The issue arose because the Eskom Red Data Book was compiled independently by Birdlife South Africa and did not directly feed into the IUCN Red List (James Westrip, *in litt.*). As a result BirdLife International is awaiting comments and feedback on their forum for some species – such as Rudd's Lark – before updating the IUCN Red List accordingly (http://www.birdlife.org/globally-threatened-bird-forums/category/threatened-african-birds/).

The Eskom Red Data Book of Birds lists Rudd's Lark as regionally endangered based on the following criteria:

A2. An observed, estimated, inferred or suspected population size reduction of ≥ 50% over the last 10 years or three generations, whichever is the longer, where the reduction or its causes may not have ceased OR may not be understood OR may not be reversible, based on (c) under A1:

c. A decline in area of occupancy, extent of occurrence and/or quality of habitat.

A3. A population size reduction of ≥50%, projected or suspected to be met within the next 10 years or three generations, whichever is the longer (up to a maximum of 100 years), based on (c) under A1:

c. A decline in area of occupancy, extent of occurrence and/or quality of habitat.

A4. An observed, estimated, inferred, projected or suspected population size reduction of ≥50% over any 10 year or three generation period, whichever is longer (up to a maximum of 100 years in the future), where the time period must include both the past and the future, and where the reduction or its causes may not have ceased OR may not be understood OR may not be reversible, based on (c) under A1:

c. A decline in area of occupancy, extent of occurrence and/or quality of habitat.

B2. Area of occupancy estimated to be less than 500 km^2, and estimates indicating:

a. Severely fragmented or known to exist at no more than five locations.

b. Continuing decline, observed, inferred or projected, in the following:

(i) extent of occurrence

(ii) area of occupancy

(iii) area, extent and/or quality of habitat

(iv) number of locations or subpopulations

(v) number of mature individuals.

C1. Population size estimated to number fewer than 2500 mature individuals

Even within its core range, of which Wakkerstroom forms a part, the species is generally scarce (Dean & Allan 1997, Taylor et al. 2015). Population estimates for the entire Rudd's Lark population are varied: Siegfried (1992) estimated between 1500 and 500 individuals; Barnes (2000) set the lower limit at 2500.

A comparison between the two South African Bird Atlas Projects (SABAP1: 1987–1991 vs. SABAP2: 2007–present) suggests a range retraction of 50% (Birdlife International 2016a) and its absence from former strongholds such as Matatiele (KZN) and Ncora Dam (EC) has been noted (Birdlife International 2016a, N. Theron *in litt*. 2016). As it stands, it would appear that Wakkerstroom in Mpumalanga is one of the last remaining core sites for Rudd's Lark, along with the Stormberg in the Eastern Cape and Memel in the Free State (Maphisa et al. 2009, N. Theron *in litt* 2016, Taylor et al. 2015). Thus, the species is subject to the classic "double jeopardy" of low abundance and narrow distribution that equate to a high risk of extinction (Gaston 1998).

Birdlife South Africa maintains an active interest in Rudd's Lark and continues to conduct field searches in previously known locations with the aim of developing a niche model for the species (N. Theron & R. Colyn *in litt.* 2016). However, the paper published by Maphisa et al. (2009) is the most recent scientific study of *H. ruddi* available, and inspired this thesis. Hockey et al. (1988) reported the presence of Rudd's Lark in some heavily grazed areas such as Matietiele, but the fine-scale study by Maphisa et al. (2009) in the Wakkerstroom area suggests that the species prefers lightly grazed grassland. Both studies concluded that Rudd's Lark does not occur in ungrazed areas of dense grass. Maphisa et al. (2009) found that Rudd's Lark was encountered disproportionately in habitat that had been burned during winter, as opposed to unburnt habitat, and that nesting started earlier and lasted longer on sites burned earlier in the year. Late burning was linked to a possible shortening of the breeding season and subsequently greater susceptibility to nest predation (Maphisa et al. 2009). They also noted that the species appears to prefer altitudes above 1800 m. This equates to a narrow altitudinal band as the grassland in this region only extends to an elevation of 2250 m (Muchai 2002), above which the grass gives way to rocky slopes and peaks. Rudd's Lark was reported to select gradients of less than 10°; it avoided valley bottoms and moderate to steep slopes. In terms of diet, Rudd's Lark was found to rely heavily on grasshoppers (Maphisa et al. 2009). This is notable as van Wingerden et al. (1992) reported grasshoppers to be very sensitive to grassland management, though in that specific case the primary determinant was the high level of fertilization, a factor largely not applicable to the rangelands in which Rudd's Lark occurs.

Climate Change

The effect of climate change on individual species has been the subject of much debate within both the scientific and policy-making communities. This relates to the inference of a causal link between climate change and an effect on the biological system (which in turn affects the target species), as well as the relative importance of climate change as a contributing factor to this effect (Parmesan & Yohe 2003).

Biologists point to the importance of persistent and accumulative effects of climate change, while economists would discount factors that are not strongly influential in the present (Parmesan & Yohe 2003). As an added difficulty, background trends caused by climate change that could prove important in the long term are potentially confounded by the more urgent and powerful effects of habitat loss (Parmesan & Yohe 2003, Kleijn et al. 2010). Jarzyna et al. (2015) found that regions with a high level of fragmentation had a weaker association between climate change and changes in the avian community. The quality of grassland habitats is also poorly understood, making the vulnerability of grassland birds to climate change difficult to predict (Jarzyna et al. 2016).

Research has shown that a shifting climate can be linked to changes in farm management that in turn affect avian assemblages. For example, Kleijn et al. (2010) found that Dutch farmers mowed their grasslands at the same temperature cue – and associated stage of vegetation growth – in 1982 and 2005, despite a significant temporal difference in when this growth took place due to increased temperature. The Black-tailed Godwit *Limosa limosa* did not shift its breeding ecology to accommodate this change, however, resulting in a poorer survival rate of godwit chicks (Kleijn et al. 2010). A study of grasslands in the north-eastern United States reported that the probability of avian extinction increased with rising temperatures where grass cover was low (Jarzyna et al. 2016). Thus, farm management strategies that did not preserve grass cover in such areas could adversely affect bird survival rates. This dovetails with research by Donald et al. (2010) that linked aridification to heightened pastoral pressure on the Liben plain of Ethiopia, which resulted in increased bare ground cover that adversely affected the population of the Liben Lark *H. sidamoensis*.

Such climate change effects may be exacerbated by population fragmentation and vary with altitude in the grassland biome. Decades of research on the Greater Prairie Chicken *Tympanuchus cupido* have shown that the fragmentation of grasslands can have a profoundly negative effect (Samson 1980). This effect is magnified by climate change: smaller grassland patches support smaller populations, which are more vulnerable to environmental stochasticity such as increasing temperatures (Ribic et al. 2009, Jarzyna et al. 2016). As for altitude, Crick (2003) suggests that range shifts in bird species are likely to occur as a result of climate warming in montane regions. Jarzyna et al. (2015) found that high elevation regions in the State of New York experienced greater changes in the composition of avian communities, while Flousek et al. (2015) reported that the population trends of birds in the Giant Mountains of the Czech Republic also reflected adverse effects of climate. Regarding birds in high elevation grasslands, the Water Pipit *Anthus spinoletta* of southern Europe and Asia has been identified as highly at risk from potential future climate change (Melendez & Laiolo 2014). On the African continent, Huntley et al. (2006)

predicted that birds endemic to the montane grasslands of East Africa would become more restricted in their ranges as a result of the climate change-induced expansion of arid zones. Finally, in the case of Rudd's Lark, Huntley & Barnard (2012) have reported that this high-elevation grassland specialist will potentially be the species most negatively impacted by climate change (in a survey of 94 grassland and fynbos species in southern African). In their study, two of three established general circulation models predicted both Rudd's and Botha's Lark to lose all suitable climatic habitat by 2085 (Huntley & Barnard 2012). Correspondingly, a model of potential distribution constructed by Maphisa et al. (2009), altitude ranked above NDVI, peak growth period and slope as the most important factor for predicting Rudd's Lark habitat selection. This study also found that both Rudd's and Botha's Lark are concentrated within a narrow altitudinal band (Maphisa et al. 2009). Taken together, these factors suggest that Rudd's Lark is at significant risk of losing optimal habitat due to climate change. This is particularly concerning for a high-altitude, patchily-occurring species that has little room to manoeuvre in terms of expanding its range into higher elevations, since grassland habitat at higher elevations does not exist.

Botha's Lark *Spizocorys fringillaris*

The threat of habitat fragmentation and conversion of land for agriculture faced by Rudd's Lark is shared by Botha's Lark. This species is also endemic to the upland grasslands of South Africa, occurring predominantly at the eastern edge of the Vaal River catchment, and is listed by the IUCN as globally Endangered. The population of Botha's Lark is suspected to be less than 2500 individuals, as a result of local extinctions and range contraction, though data is lacking and confidence in this estimate is low (Taylor et al. 2015). Though similar in distribution to Rudd's Lark, broadly speaking, Botha's Lark is thought to prefer different fire and grazing regimes (Maphisa et al. 2009): it selects heavily grazed and trampled grassland that has been recently burnt or not burnt at all (Maphisa et al. 2009). These two species are therefore likely to require their own nuanced and specific conservation strategies.

Rationale & Objectives

My research evaluated the potential decline of Rudd's Lark in one of its last remaining core sites, the Wakkerstroom grasslands of south-eastern Mpumalanga. It also aimed to build on the current knowledge of the species' habitat preference. The research on Rudd's Lark in the Wakkerstroom area conducted by David Maphisa between 2002 and 2004 provided an excellent opportunity to investigate these aspects by providing baseline data collected 14 years ago (Maphisa 2004). Of particular interest were his transect-based surveys conducted between 20 November 2002 and 10 January 2003 (hereafter "2002" for brevity). My primary objective was to determine whether the population of Rudd's Lark had declined since the 2002 survey, by comparing the presence/absence and detection rate of individuals along replicated transects in 2016. My second objective was to ask, if Rudd’s Lark has declined, what environmental factors might explain this decline? To address it I collected environmental and ground cover data using the same method as the 2002 study, and used these data to determine whether any changes had occurred since 2002 in land cover and in the habitat selection of Rudd’s Lark, as well as test for predictors of Rudd’s Lark incidence within the 2016 survey. I also conducted interviews with local farmers to better understand how farmers manage the grassland in the area and whether their self-reported management practices have changed over time. Finally, I compared Rudd’s Lark habitat preference with that of other endemic grassland specialists, in order to determine how conservation action targeted at Rudd’s Lark might affect the rest of this species suite. In so doing, I aimed to gain a better understanding of the status of the Rudd’s Lark population in the Wakkerstroom area by combining findings from these various lines of inquiry.

Methods

Study site

My study took place within 30 km of the town of Wakkerstroom in the provinces of Mpumalanga and KwaZulu Natal, South Africa. The Wakkerstroom grasslands are considered to be a critical "patch" in the localized and isolated distribution of Rudd's Lark (Hockey et al. 1988, Maphisa et al. 2009).

Vegetation cover at the study site is categorized as "sandy Highveld grassveld" (Low & Rebelo 1996), a combination of the previously separate "turf highland sourveld" and "north-eastern sandy Highveld" described by Acocks (1953). The area experiences mild to warm summers and cold and dry winters, with summer rainfall ranging between 700 mm and 1200 mm (Muchai 2002). Topographically it is characterized by "high altitude plateaus and undulating plains" (Little et al. 2015). Land-use is predominantly large-scale livestock farming, particularly of beef cattle (Muchai 2002), though sheep and an increasing amount of crop production are also present (David Maphisa *in litt* 2016).

Before fieldwork began, I selected a core range within the original study site to prioritize data collection in the field. The resulting core area included >90% of the transects where the species was recorded during that survey. It was approximately 380 km^2 in size (compared with the original Wakkerstroom site of approximately 1200 km^2), and included 44 of original transects surveyed in 2002. The transects were located predominantly to the north west of Wakkerstroom (see Figure 1).

All relevant landowners were contacted to arrange permission to walk on the farms while searching for Rudd's Lark. No landowner denied me access outright; however, I failed to make an arrangement with the owners of the hunting reserve as I was unable to conduct unaccompanied transect walks due to the presence of dangerous game.

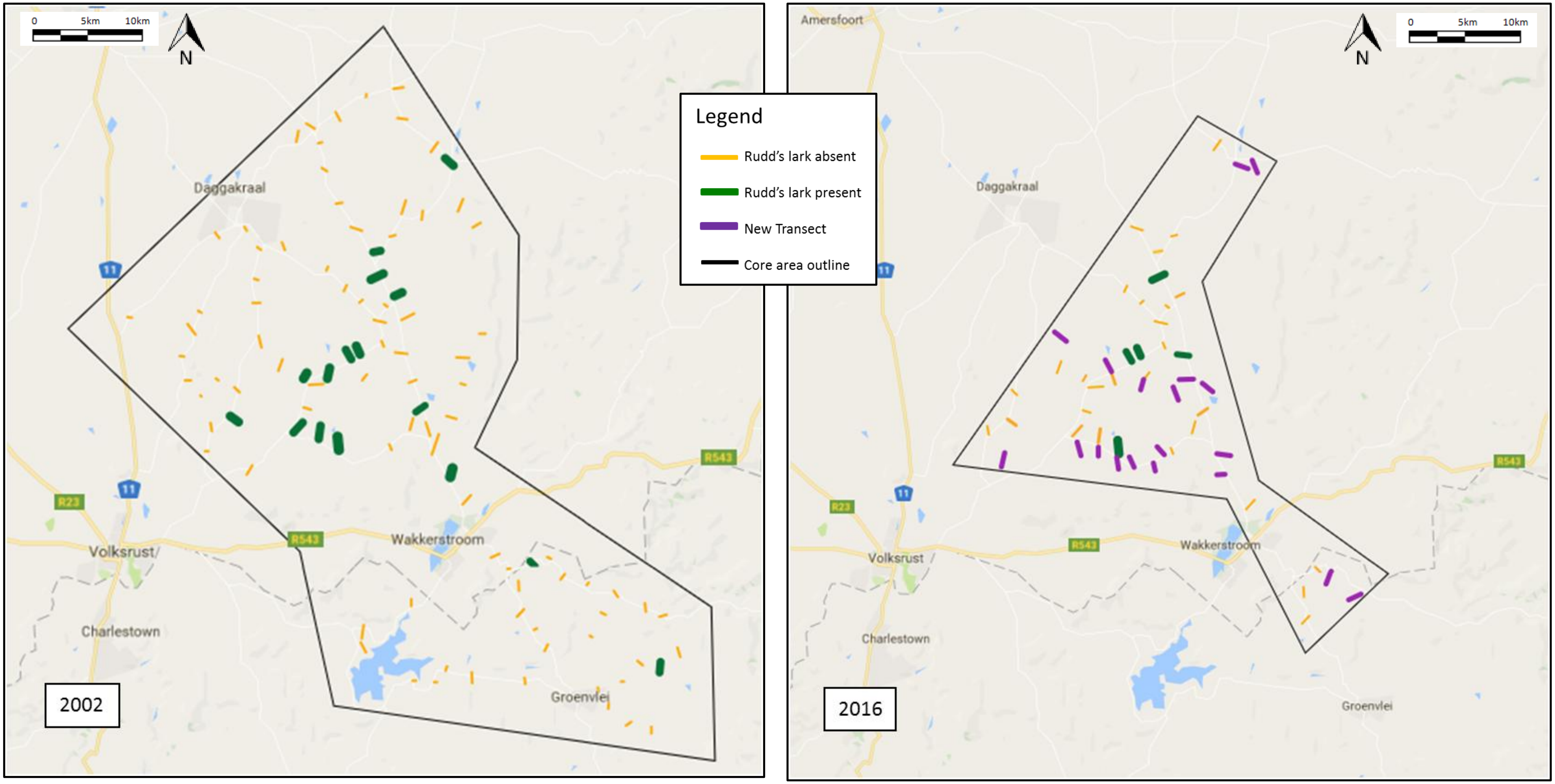

Figure 1: Two maps of the Wakkerstroom region showing the survey area and transects covered by David Maphisa in 2002 (n=103) (left) and the reduced "core" area that I covered in 2016 (right). A total of 19 new transects were added to 33 that were repeated, for a final transect tally of 52 in 2016.

Transect selection

Original transects replicated from the 2002 study

The 44 transects from the 2002 study were further reduced to 33 because seven had since been ploughed and converted to agriculture, two transects are now within a hunting reserve where I was not permitted to walk, one transect in the core area was substantially covered with thicket, and one transect was defined by inaccurate GPS coordinates. Of the final 33 transects that were originally conducted in 2002, minor GPS inaccuracies were accounted for as follows: where transects appeared to cross over public roads, the replicated transect would start on one side of the road and proceed away from the road, extending beyond the end of the transect (according to the GPS) by the distance "lost" on the other side of the road. Transect length (calculated from the 2002 GPS co-ordinates) was preserved, even where transects were not found to be rounded to the nearest hundred meters.

New transects surveyed in 2016

In order to improve the sampling within the study area, I identified a further 19 transects within the core range, bringing the total number of transects to 52. These new transects were selected based on superficially suitable Rudd's Lark habitat. In the 2002 study, transects were generally positioned at 2 km intervals along public roads and extended at 90 degrees into the grassland, although the angle was adjusted where necessary to avoid unsuitable habitat such as water bodies. Transects were allocated only on one side of the road at each interval, even where both sides had suitable habitat. In 2016, both sides of the road were considered and the interval for transects on the same side of the road was reduced to 1.5 km. Spottiswoode et al. (2009) used a minimum distance of 1 km between transects when surveying the congeneric Liben Lark *H. archeri*, where the maximum distance a displaying male was identified at was 444 m. For Rudd's Lark, the maximum distance at which an individual bird was identified during the 2002 survey was estimated to be 400 m (at least by call), and 380 m during my survey in 2016, suggesting that 1.5 km is more than a sufficient distance between transects to avoid any risk of recording the same bird twice. As was the case in the study in 2002, the map by Warwick Tarboton in *Wakkerstroom bird & nature guide* was used to navigate the public roads around Wakkerstroom (Tarboton & Tarboton 2004). New transects extended 1000 m into the grassland, unless landscape features such as water bodies or ploughed fields prevented it. In such cases, transects were either angled to avoid such features, or ended at the nearest 100 m interval before the obstacle.

Transects

Transects on foot were conducted between 20 November 2016 and 17 December 2016. This time period corresponded with the first survey conducted from 20 November 2002 to 10 January 2003, which was originally motivated by the peak in territorial activity of Rudd's Lark (Maphisa et al. 2009). Transects were walked between 06:00 and 10:00, following the 2002 study and chosen because males have been found to sing or display most during this period (Maphisa et al. 2009). I used a GPS (Garmin eTrex 30x) to locate the start and end points of each original transect, and re-recorded these positions. The weather and start time were recorded at each transect start, and the end time and transect length were recorded at each transect end, before walking back to the starting point. I was accompanied on every transect walk by a locally-based bird guide, either David Nkosi or Norman Ncube, both of whom have over ten years of experience in the field and are very familiar with Rudd's Lark. Transects took an average of 18 minutes to complete from start to finish, including stops to identify and record birds.

Birds

During each transect, we recorded every bird species identified by sight or sound (including flying overhead), with the exception of species that were audible from very long distances, such as Bokmakierie *Telophorus zeylonus*, cuckoos and doves. The range of detection was estimated to be in the region of 200 m on either side of the transect line. However, large threatened birds such as cranes, korhaans and bustards were recorded regardless of distance, with a note made if they were judged to be more than 200 m away from the transect. For non-target species (i.e. not Rudd's or Botha's Lark), only the species name was recorded, except in the case of Yellow-breasted Pipits where number of calling males was also noted, as this was a threatened species encountered regularly on transects. We stopped only to ascertain and record the identity of a call or a seen bird.

When Rudd's or Botha's Lark were identified, we determined to the best of our ability the location of where the individual was first detected. If necessary, we left the transect to determine the bird's location and record the GPS co-ordinates where the bird was first detected, or directly underneath in the case of displaying males. We recorded any other individuals within the same area as part of these records (for example, a female on the ground responding to a male, or fledgling near a nest site). We would then return to where the transect had been left, and continue on. In a few cases, we detected more birds after having left the transect when trying to locate an initially detected bird. In such cases, we noted a rough location and returned to it after the transect walk had been completed. That is, we did not immediately follow up on birds identified off-transect.

On the return walk, any new bird species encountered was recorded. Rudd’s Larks detected off-transect were revisited in an attempt to more accurately mark their position using GPS for subsequent vegetation surveys. The final records for Rudd’s Lark reflected birds in the following categories: birds detected (by sight or sound) on transects; birds considered to be partners of the birds detected initially (these birds were detected when responding to their partners, usually by way of an alarm call); fledglings; “extra” adult birds detected in the territories of other birds; and “ghost” birds where a call was detected too distantly to determine a location.

In an attempt to determine how many additional Rudd’s Larks may have been associated with each male detected during transect walks, we made an additional 20 minute visit to transects where three or more male Rudd’s Larks were found, to determine whether birds were in pairs or had fledglings. Due to time constraints, transects on which only a single bird was detected were not revisited.

Vegetation

Vegetation was sampled on the return walk of each transect at 100 m intervals, starting at the end point and finishing 100 m away from the start point (i.e. a 1 km transect comprised 10 sampling points). Where transect length was not rounded to the nearest hundred meters, vegetation sampling did not start at the end but rather rounded to the nearest 100 m interval that was still within the transect (e.g. a transect of 933 m would have the first vegetation sampling point at 900 m). For comparability, I used exactly the same sampling approach as was employed in 2002 (Maphisa 2004). That is, at each site a 0.3 m x 0.3 m quadrat was thrown randomly c. 5 m away from the transect on each side, giving two vegetation samples per sampling point. The quadrat was a metal frame with rods dividing the internal space into nine squares (each 10 x 10 cm). The dominant ground cover in each square was recorded (categories: grass, forb, bare ground, stone and dead vegetation). The predominant grass height at the four corners of each thrown quadrat was also measured to the nearest cm using a ruler. At each sampling point (that is, a single measure for the two quadrats) the following factors were recorded: grazing, fire, slope and altitude. Grazing was determined based on the presence and extent of cropped tussocks (categories: lightly grazed, heavily grazed, ungrazed). Fire was recorded as having occurred within the previous year if burnt stumps were evident, or, in a few cases, where old grass was absent (categories: burned, unburned). Slope was recorded by estimating by eye whether a slope was flat, less than 30° or greater than 30° (categories: plateau, gently sloping, steeply sloping, valley bottom). Altitude was recorded using GPS.

The locations of Rudd’s and Botha’s Larks recorded along transects were revisited on the return walk for the purpose of recording the factors above. For Rudd’s Lark territories, ten quadrats were thrown at random within c. 20 m of where the bird had been recorded, and vegetation sampling conducted for each, for consistency with the 2002 survey. One measure of grazing, fire, slope and altitude was recorded at each site. For Botha’s Lark, two quadrats were thrown within c. 20 m of where the bird was recorded, unless the bird(s) was seen only in flight. One measure of grazing, fire, slope and altitude was recorded at each of these sites.

Generally, the landscape where vegetation was recorded was sufficiently homogenous that the fine-scale vegetation parameters above seemed sufficient to capture natural variation. The high-altitude grasslands of Wakkerstroom have no trees, large termite mounds or extensive cattle trails, in contrast to *Heteromirafra* habitat in Ethiopia (Spottiswoode et al. 2009). However, I recorded when sampling points had notably rocky ground cover, featured a visibly heavy presence of a shrub in the *Vernonia* genus (species likely *natalensis*), or showed evidence of having been ploughed at some point historically.

Transect replication

My study (17 November 2016 to 17 December 2016) loosely replicated the timing of David Maphisa’s transect-based survey between 20 November 2002 and 11 January 2003. Additionally, I repeated a subset of the transects within my study area in order to assess detectability of Rudd’s Lark. Owing to time constraints I prioritized which transects to repeat as follows, based on vegetation traits and my field assistant’s experience: 0 (poor quality, n = 15), 1 (medium quality, n = 17) or 2 (high quality, n = 20). I was then able to begin repeating transects based on these scores, starting with the high quality ones. Any transects where Rudd’s Lark had been found either in the 2002 survey or my own in 2016 automatically qualified for a repeat, regardless of their apparent “quality”. I repeated 28 transects, of which 9 were medium quality and 19 were high quality.

On each replicated transect, we once again recorded all bird species encountered (following the same protocol as before) as well as the same method for recording Rudd’s and Botha’s Larks where they were encountered. No vegetation surveys were conducted during these replicate surveys, for consistency with the 2002 survey and because the time elapsed since the initial survey (range: 3–20 days, mean: 12 days) was too short for significant vegetation changes to have occurred.

Farmer interviews

In order to gain a better understanding of the land use in the Wakkerstroom area, I conducted interviews with some of the local landowners (with signed consent). Land within the study area was divided into three management groups: commercial farms (9), hunting reserves (1) and communal farms (1). I was able to conduct seven interviews: six with commercial farmers, and one with one of the primary stakeholders on the communal farm. These farmers accounted for the ownership or management of all the land where Rudd’s Lark was found during the 2016 survey, except for one landowner who could not be reached for an interview.

All interviews were conducted formally and face-to-face at the respective landowners’ homes. A total of 17 questions were consistently asked to each participant (see Appendix B for the full questionnaire). Six interviews were conducted directly by me in English or Afrikaans, and one in isiZulu via my guide David Nkosi. The content of the interview included agricultural details of the farm, participant awareness of Rudd’s Lark, perception of changes in climate and the fire regimes employed by management. Ethics clearance was obtained from the university of Cape Town’s Faculty of Science Research Ethics Committee (Ethics number: FSREC 060 – 2016) and each participant signed a permission form that allowed the anonymous use of the information they provided. Due to the small number of interviews conducted, results are summarized without statistical analysis.

Data analysis

General

For the subset of 33 transects surveyed in both 2002 and 2016, my “first round” of the 2016 survey (i.e. not including repeats) was considered to be comparable to the transects surveyed in 2002. For the questions relating to vegetation change and the habitat preference of Rudd’s Lark, I analyzed the data at both a coarse and a fine scale. The coarse scale used mean scores along each transect for the different vegetation covers and average grass height, combined with a presence/absence rating for Rudd’s Lark. This was intended to give an impression of where Rudd’s Lark was present and where it was absent at a scale that could be applied to a broad level of management. However, I felt that this scale could potentially mask the actual habitat selection by Rudd’s Lark in cases where transects crossed fences or included a highly varied landscape (e.g. a Rudd’s Lark might be found on a small section of plateau, but the mode of the slope estimate at the coarse scale might reflect the steep slope of the adjacent escarpment). This discrepancy would then be accounted for at the fine scale, where vegetation samples were preserved at the 100 m scale and compared with exact point locations where Rudd’s Lark was recorded. Hereafter, "fine scale" refers to these 100 m sampling points, while "coarse scale" refers to the mean or mode along transects (depending on whether the variables were numerical or categorical).

Data were analyzed in R (R Core Team 2016) using various linear regression models. When considering the best-fitting models in each of the analyses, the Akaike Information Criterion (AIC) score for each model was compared, with the lowest-scoring model considered to be the best fitting (Maphisa et al. 2016). Where multiple models provided similar explanatory power (that is, models were within two AIC of each other), a model averaging function was applied using the packages "MuMIn" and "AICcmodavg" (Burnham & Anderson 2002) in R. This determined which individual variables had the greatest importance based on the variables that occurred mostly frequently in the set of best models (Grueber et al 2011). Slopes and confidence intervals are reported for each predictor variable. Models did not converge when transect length was included as an "offset" (a term used to weight the random effect when it is variable, in this case transects of unequal length). Models also did not converge when Julian day (days since November 1) was included as a fixed effect. I thus excluded these factors from the model sets. I tested both factors as fixed effects against the response variable of Rudd's Lark presence/absence at the coarse scale, and in both cases the effect was not significant (Length: $\beta = 0.003$; 95% CI: –0.002, 0.010; Julian day: $\beta = -0.039$; 95% CI: –0.243, 0.152).

Population comparison between 2002 and 2016

I used a generalized linear model (GLM) to compare the probability of encountering Rudd's Lark on transects in 2002 and in 2016. The model's binary response variable was the presence or absence of Rudd's Lark recorded on transects for each survey, while the fixed effect was the survey ID (that is, 2002 versus 2016). The summary of the model indicated the degree of difference; I then used the package "least square means" (Lenth 2016) in R to generate the least square mean and upper and lower confidence for the 2002 and 2016 which were then back-transformed and plotted onto a graph (Figure 1).

Spatial auto-correlation

When observations of the same type (such as transects where Rudd's Lark are present) are recorded in geographic space, there is a possibility that these objects are spatially auto-correlated (Valcu & Kempenaers 2010). That is, they may be of the same type simply because of their proximity to one another (positive spatial auto-correlation). For example, certain vegetation variables may be correlated with Rudd's Lark incidence simply because the larks are spatially close to one another, and so should not be regarded as statistically independent. Alternatively, Rudd's Larks may choose territories that are significantly removed from the territories of other individuals, leading to negative spatial auto-correlation.

I therefore tested for spatial auto-correlation between transects based on the presence and absence of Rudd's Lark using Moran's I (Fortin & Dale 2005) in R using the packages "ape" (Paradis et al. 2004).

At the coarse scale I assessed the geographic correlation between the midpoints of the 52 transects. The result was a Moran's I value of 0.008 and p=0.256, indicating that spatial auto-correlation was not present between the transects based on the presence/absence of Rudd's Lark. At the fine scale I conducted the test using the geographic coordinates for each individual vegetation sampling point, as well as for the recorded Rudd's Lark "territories". The result was a Moran's I value of 0.062 and p<0.001. However, models that were structured to account for spatial autocorrelation using the R package "spaMM" (Rousset & Ferdy 2014) failed to converge, and so a standard GLMM structure was used. This meant that spatial variation was still accounted to some extent by using Transect ID as a random effect. Considering that Moran's I ranges from -1 to 1 and can be interpreted as analogous to Pearson's correlation coefficient (Valcu & Kempenaers 2010), a Moran's I value of 0.062 explains less than 1% of the variation in spatial distribution of transects. This low effect size suggests that excluding the effect of spatial autocorrelation in this case would not exclude the source of much variation, despite the statistical significance of Moran's I.

Principal Components Analysis of habitat variables

Before building model sets I first tested for collinearity between the five ground cover variables (grass, bare ground, forbs, stones, and dead vegetation), which summed to 1. At the transect level, grass cover was found to be strongly negatively correlated with all four of the other variables (bare = -0.64; forbs = -0.68; dead vegetation = -0.65; stones = -0.50) which were correlated positively with each other to varying degrees. Performing the same test at the fine scale showed a similar pattern but with weaker correlations, with grass still negatively correlated with bare ground, forbs, dead vegetation and stones (-0.52; -0.45; -0.54; -0.19 respectively), which again were all weakly positively inter-correlated.

Therefore, I used a Principal Components Analysis (PCA) to reduce the number of five proportional and intercorrelated ground cover variables to a smaller number of uncorrelated ground cover axes, and included the first two principal components in the models. This was done separately for the coarse- and fine-scale data. Because "average grass height" was considered *a priori* to be an important factor in my analysis, as well as recorded in centimeters rather than proportionally, it was included as a separate covariate. Loadings scores above a threshold value of 0.4 (or below –0.4) were considered relevant to interpretation (Stevens 1992).

Rudd’s Lark habitat selection in 2016

At the coarse (i.e. transect) scale, the raw data are presented showing a comparison of transects with and without Rudd’s Lark present with respect to their ground cover variables, average grass height, and altitude. To assess which habitat variables best accounted for the presence of Rudd’s Lark, I used a generalized linear mixed effects model (GLMM) with binomial error structure and logit link function. The data were from both the first round of 52 transects and the 28 revisits; thus Transect ID was included as the random effect variable in order to account for this repetition. All numeric variables were scaled. Scaling accounts for the different scales of measurement present in the data (for example, proportional ground cover values ranged from 0 to 1, while altitude ranged from 1700 to 2000) by subtracting the mean and multiplying by the standard deviation for each value (Becker et al. 1988). This also allowed for model averaging and the interpretation of mean slopes as effect sizes. I tested a series of models including biologically realistic combinations of the fixed effects PC1, PC2 (uncorrelated combinations of ground cover covariates), average grass height (continuous), altitude (continuous), fire (categorical) and grazing (ordinal). Grazing type was re-named in the data so that alphabetical order reflected grazing intensity and could be analyzed as such in R. Measures of topographical slope were too subjective to use in the models, but are included in the presentation of the raw data.

At the fine (i.e. 100 m sampling point) scale, the raw data are presented showing a comparison of the “random” samples (every 100 m along transects) and marked Rudd’s Lark territories in terms of ground cover variables, average grass height, altitude, fire, grazing and slope. I resampled two out of the ten samples taken at each territory for comparison with the control samples taken along transects. The same GLMM structure was used as at the coarse scale, but using 374 fine-scale vegetation points sampled in the 2016 survey. Models thereafter included some combination of the fixed effects PC1, PC2 (ground cover variables), average grass height, altitude, fire, grazing and slope as fixed effects, while Transect ID remained the random effect.

Vegetation change between 2002 and 2016

A comparison of the vegetation structure between 2002 and 2016 was also conducted, following the procedure used in Maphisa et al. (2016). The data from the 33 transect surveys common to both years was used, with the following ground cover variables: average grass height (mean per transect), evidence of fire within the last year (modal value per transect) and level of grazing (modal value per transect). Since previous studies had suggested that grass cover and grass height are important to Rudd’s Lark (Maphisa et al. 2009, 2016), these were selected as response variables, along with forb and bare ground cover since histograms of the raw data suggested these variables had changed to a noticeable degree between the two surveys. I first tested for a difference between the two study periods by using "year" as the fixed effect and "Transect ID" as the random effect in a GLMM structure. In order to assess what else might explain a change in the above-mentioned vegetation variables, I constructed model sets that also included "Fire" and "Grazing" as additional fixed effects. For the response variables (grass, forbs, bare ground), the models assumed a binomial distribution (with a logit link function) which necessitated the inclusion of a "weights" term as the response variables were recorded as a proportion (number of squares covered by the variable out of nine, and averaged across all the grid samples per transect). This allowed the response variables in each case to be treated as a binomial denominator. For average grass height I used a linear mixed effects model, as the distribution of the response variable was not binary (or adjustable using a weight term in the same way as the proportion variables).

Change in Rudd's Lark habitat selection

To test whether the habitat selection of Rudd's Lark had changed between the 2002 and 2016 survey, I used a GLM structure to compare the vegetation data from the 81 territories recorded in 2002 and the 17 recorded in 2016. Survey ID (2002 vs 2016) was used as a binary response variable while altitude, average grass height and the first two Principal Components extracted from a PCA of this data set were included as fixed effects. The model family was specified as binomial with a logit link. All variables were scaled prior to analysis.

Rudd's Lark habitat preference versus other grassland specialists

I combined the Botha's Lark habitat data collected in the field from point locations where this species was recorded (n=5) with data from Rudd's Lark territories (n=17) and analyzed this using a GLM to assess whether there were any consistent habitat differences between point locations where each species was recorded. The response variable was species ID in binary form (Rudd's Lark=1, Botha's Lark=0), in order to test whether any fixed effects accounted for differences in habitat selection. Fixed effects included the first two Principal Components from the dedicated PCA, average grass height, altitude, fire and grazing. Stone cover was entirely absent at both Rudd's Lark and Botha's Lark sites, and thus excluded from the analysis. Model family was specified as binomial with a log link function.

Using the presence/absence data of other bird species on the 52 transects surveyed (and 28 revisits) in 2016, I also assessed the absolute habitat preference at the coarse scale of Botha's Lark as well as each of three other threatened grassland specialists: Yellow-breasted Pipit *Anthus chloris*, Black-winged Lapwing *Vanellus melanopterus* and Southern Bald Ibis *Geronticus calvus.* The response variable for each model was presence or absence of the focal species, while covariates included in each GLMM set were average grass height, altitude, PC1 and PC2 from the transect data PCA, fire and grazing (fixed effects) as well as Transect ID (random effect). I also tested for spatial auto-correlation in each case.

Species diversity

Having collected presence/absence data of all bird species on the 52 transects (as well as 28 revisits) surveyed in 2016, I constructed a GLMM model set to test whether any environmental covariates could explain the variance in bird diversity across the transects. Species richness (number of species seen on each transect) was used as the response variable, while Transect ID was included as a fixed effect. PC1 and PC2 from the PCA conducted on the coarse scale vegetation data were used as fixed effects, as well as average grass height, altitude, fire and grazing. Because of the count nature of the response variable, the family specified was poisson with a log link function. I also generated a species accumulation curve using the package "vegan" (Oksanen et al. 2017) in R to test how well my survey accounted for total bird species diversity in the area.

Landscape data on fire incidence and land use

Using the Google Earth Engine (GEE) I processed fire history data for the 14 years since the previous study of Rudd's Lark in Wakkerstroom (Google Earth Engine Team, 2015), using data from the Fire Information for Resource Management System (FIRMS). FIRMS delivers active fire data at a spatial resolution of 1 km x 1 km and a temporal resolution of 1–2 days.

For the annual timing of fires, two four-month periods were selected that corresponded with "negative" (November to February) and "positive or neutral" (July to October) effects on Rudd's Lark, categorized following conclusions of the previous survey (Maphisa et al. 2009). The positive or neutral period corresponded to the timing of planned burns reported by local farmers in interviews. These data were extracted from the GEE and clipped to my core area (380 km^2) in ArcMap 10.2 (ESRI 2013), where the average number of fires per 1 km^2 was generated.

For land cover, the 72 Class GTI South African National Land Cover Dataset was used to assess changes in land cover between two point samples in 1990 and 2013 (the only years where these data were available at a suitably fine scale; GEOTERRIMAGE 2015). This was clipped to my core study area in ArcMap 10.2 and quantified in terms of total land cover of each land cover type. Of the 72 classes, I selected "grassland", "rain-fed crops", "high intensity irrigated crops", "orchards", "plantations" and "urban" as the classes of interest for the analysis. I used these data to test the hypothesis that there has been an increase in crop production and a decrease in available grassland in the core area occupied by the

Rudd’s Lark, as defined in section *Study Area*. Appendix A shows the breakdown of the six cover variable classes I chose in terms of their parent groups and descriptions (Table A8).

Results

Distribution

In total, 39 Rudd’s Larks were recorded between 20 November and 17 December 2016, comprising 17 birds with territories (i.e. singing males), 8 birds associated with territorial birds (“partners”), 6 fledglings, 2 “extra” males that had invaded another male’s territory, and 6 cases where birds were heard but not seen (“ghost birds”).

In the initial survey of the 52 transects walked in 2016, Rudd’s Lark was present on only five transects, with a total of nine singing or displaying male individuals overall. The second survey of 28 transects (which included all transects where Rudd’s Lark was found in the first round) also yielded five transects where Rudd’s Lark was present. This included two transects where Rudd’s Lark had not been detected in the first round (thus increasing the number of transects where Rudd’s Lark was present to seven), and two transects where Rudd’s Lark had been detected in the first round but not the second. The number of individuals detected increased from 9 to 18 (i.e. 9 additional birds were detected in the second survey). If the maximum number of larks found on transects over the course of both rounds is considered, three transects contained a single male, one transect had three males, two transects had four males and one transect had six.

Of the 33 transects common to both surveys, Rudd’s Lark was found on 9 transects in 2002, but on 5 in 2016. On these 33 transects, 32 singing or displaying Rudd’s Larks were recorded in 2002, while only 9 such individuals were recorded in 2016. Figure 2 shows the probability of Rudd’s Lark being present on transects in 2002 compared to 2016, while Figure 3 shows the probability of encountering an individual Rudd’s Lark in 2002 compared to 2016. Even if the second round conducted in 2016 were included for these 33 transects (thus introducing a bias towards greater search effort in 2016), the number of transects where Rudd’s Lark was present did not increase, while the number of larks increased only slightly from 9 to 13. Encounters with Rudd’s lark were too few to generate a meaningful detection function or estimate territory density using distance sampling (Maphisa et al. 2009).

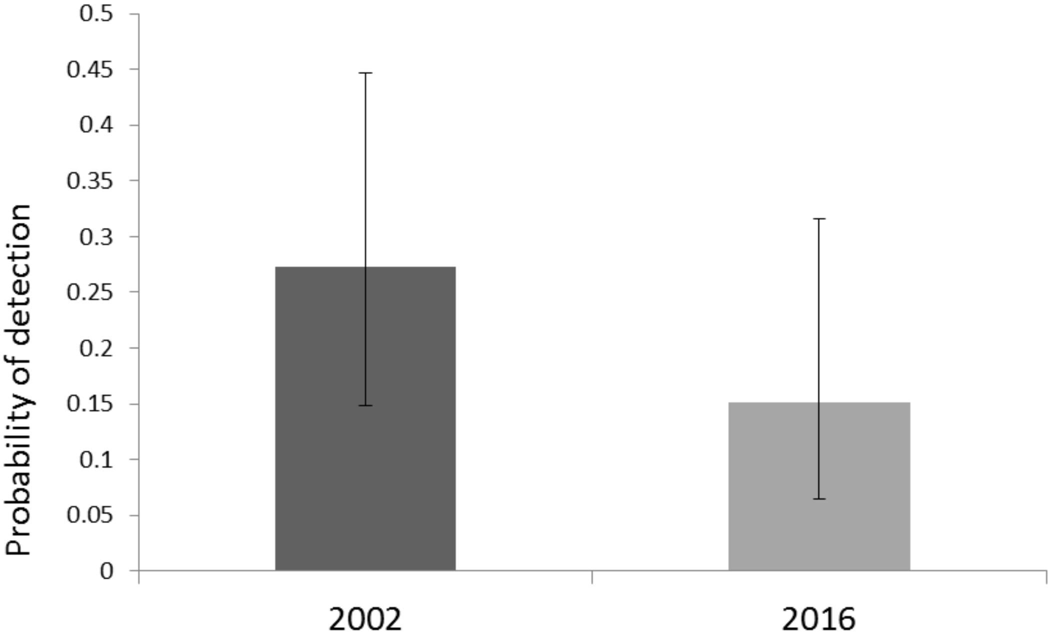

Figure 2: The probability of Rudd's lark being present on transects (n=33) between 2002 and 2016, with presence or absence on transects as the response variable. Difference was not significant (GLM; p = 0.234).

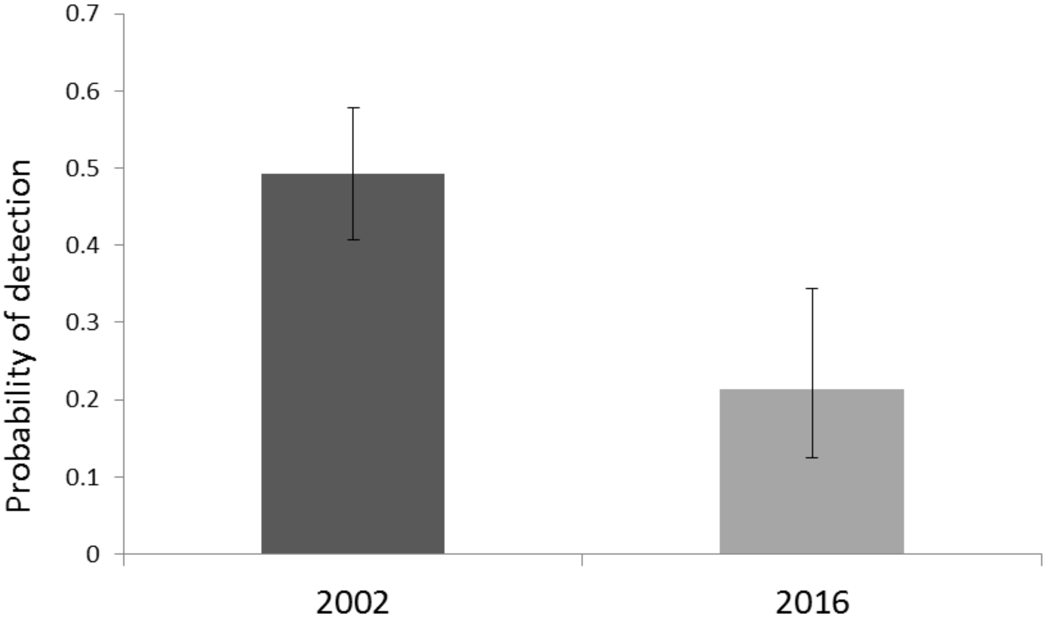

Figure 3: The probability of an individual Rudd's lark being present on transects (n=33) based on count data between 2002 and 2016, with number of individual larks on transects as the response variable. Difference was significant (GLM; p = 0.001).

Rudd’s Lark habitat selection

Coarse scale predictors of Rudd’s Lark incidence

The raw data show little difference for ground cover variables between transects with Rudd’s Lark present and transects with Rudd’s Lark absent (Figure 4a). However, they show a trend towards Rudd’s Lark being present on transects with higher elevation and shorter average grass height (mean altitude = 1874 m; mean grass height = 4.37 cm) than those where it was absent (mean altitude = 1832 m; mean grass height = 5.55 cm) (Figure 4b and 4c). Statistical analyses follow below.

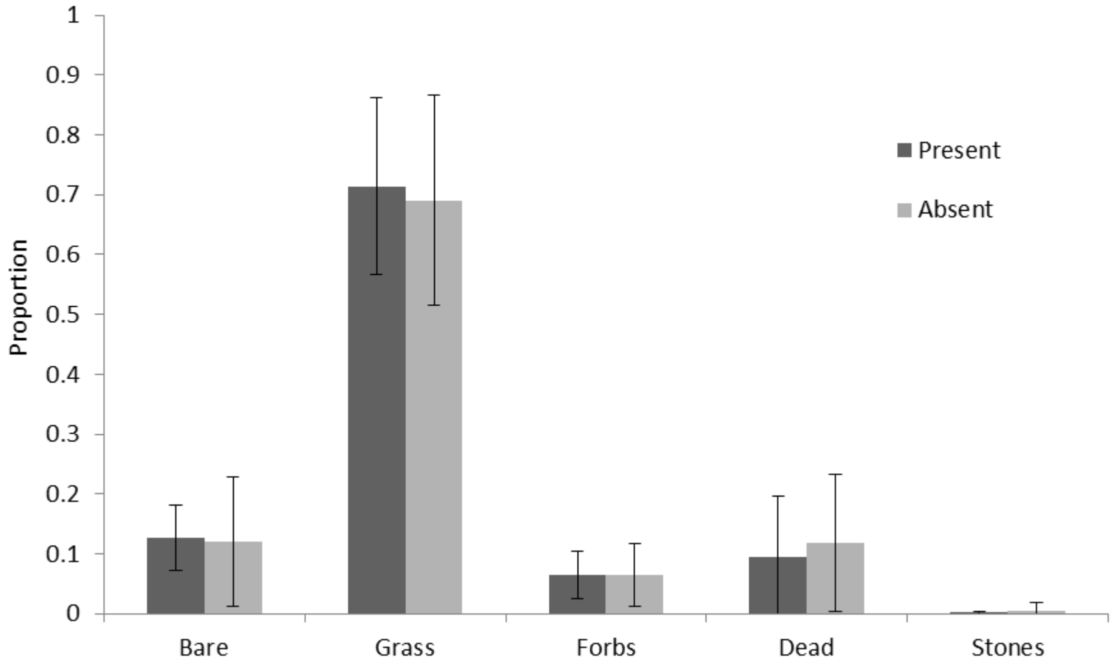

Figure 4a: The proportions of ground cover variables for transects with Rudd’s lark present (n=7) compared to transects with Rudd’s lark absent (n=26) in 2016.

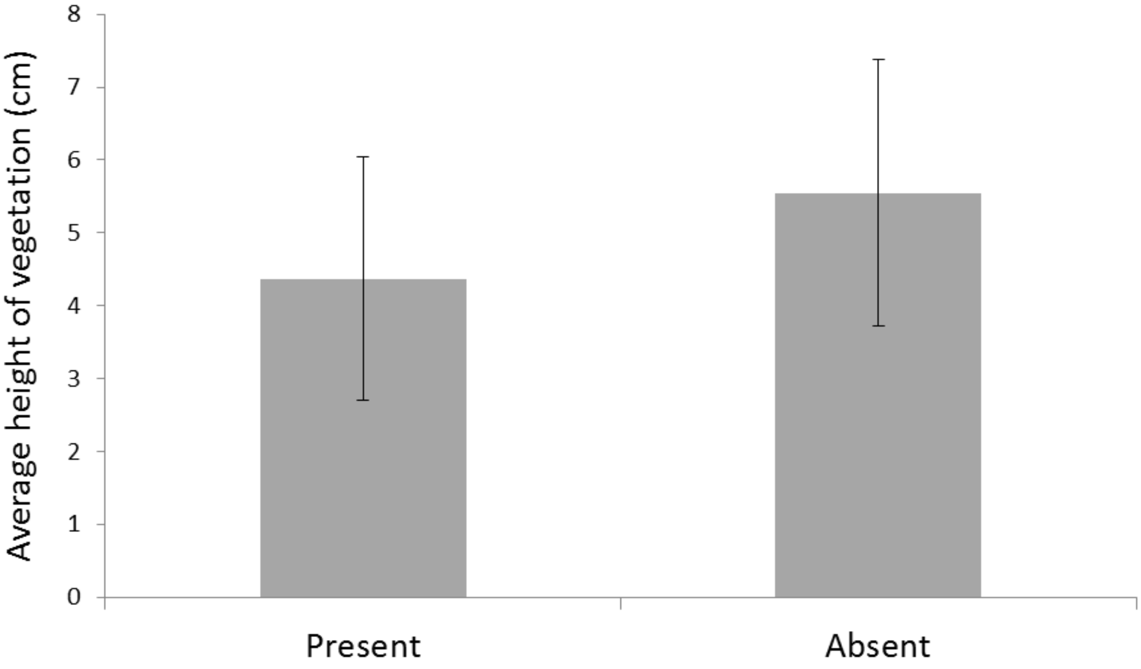

Figure 4b: The average grass height for transects with Rudd's lark present (n=7) compared to transects with Rudd's lark absent (n=26) in 2016.

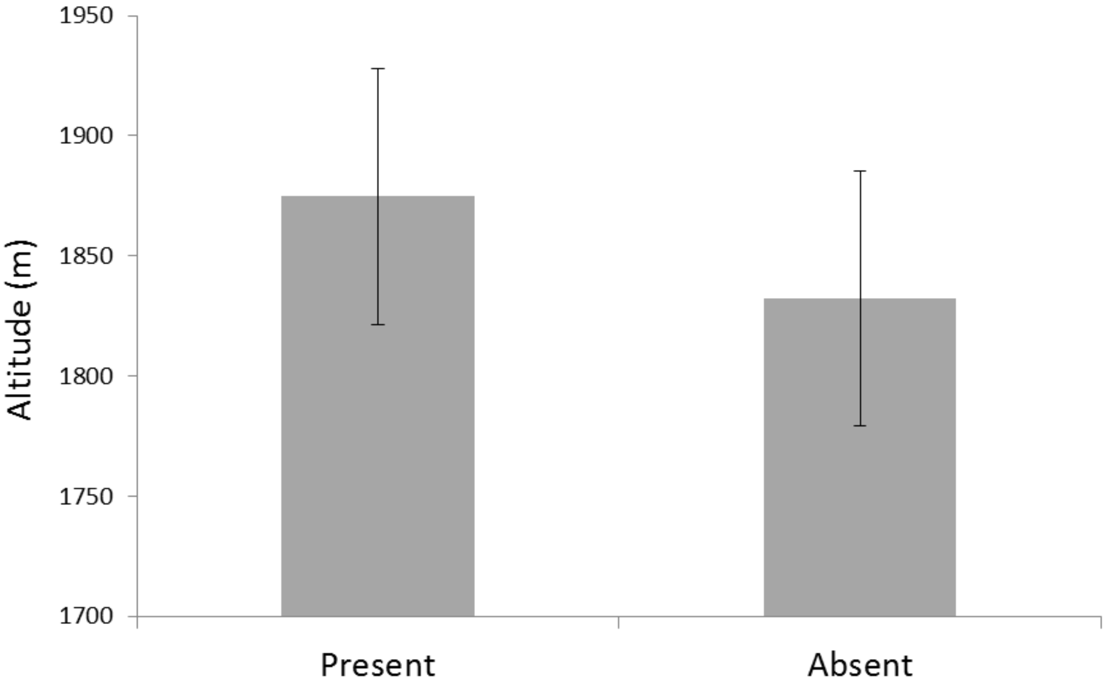

Figure 4c: The altitude of transects with Rudd's lark present (n=7) compared to transects with Rudd's lark absent (n=26) in 2016.

For the PCA of the transect-scale data, the first two Principal Components (PC1 and PC2) explained 72% of the variation in the ground cover data. Appendix A shows a plot of how the transects cluster in two-dimensional space and the alignment of the habitat variables according to the influence of the first two Principal Components (Figure A1); the same data are also replotted including a key for the presence/absence of Rudd's Lark in this depiction of the environment (Figure A2).

PC1 showed positive loadings for grass cover and negative loadings for bare ground and forb cover, while PC2 loaded positively for dead vegetation cover and negatively for stone cover. In other words, PC1 reflected a high proportion of grass cover and an absence or low abundance of forbs and bare ground, whereas PC2 reflected dead vegetation, primarily dead grass; stone cover was rare overall.

Having determined the most important principal components and the absence of spatial auto-correlation (Moran's I = 0.008; p = 0.256), I constructed a model set for predicting the occurrence of Rudd's Lark according to PC1, PC2, average grass height and altitude. No model provided better explanatory power than the null. That is, the presence of Rudd's Larks on transects was not explained by any covariates with more power than random variation in the environment. A model with altitude as the only fixed effect showed that no significant difference existed between transects with and without Rudd's Lark (β = 0.365; 95% CI: -9.402, 10.572). Similarly, when average grass height was the only fixed effect, no significant difference was found (β = -1.315; 95% CI: -29.493, 7.663). The Appendix shows a table of the first five models that performed best after the null models (Table A1).

Fine scale predictors of Rudd's Lark incidence

The fine scale raw data indicate a similar relationship between Rudd's Lark presence and absence at the 100 m scale (that is, 17 Rudd's Lark territories compared to 356 random samples) as at the coarse scale reported above: Figure 5 shows ground cover variables, and Figure 6a–e show average grass height, altitude, fire, grazing and slope respectively. For fire, random points were fairly evenly divided into burned (47%) and unburned (53%), as were Rudd's Lark territories (52% burned, 48% unburned). For grazing, a much higher proportion of samples were lightly grazed (79%) than heavily grazed (9%) or ungrazed (12%), as were Rudd's Lark territories (88% lightly grazed, 12% heavily grazed), although no Rudd's Larks were present at ungrazed sites. Finally, a low proportion of random samples were recorded as valley bottom (5%), steep slope (16%) and plateau (15%), with most samples in the gentle slope category (64%). Rudd's Lark territories, by contrast, were either recorded on plateaus (47%) or gentle slopes (53%); none were recorded on valley bottoms or steep slopes.

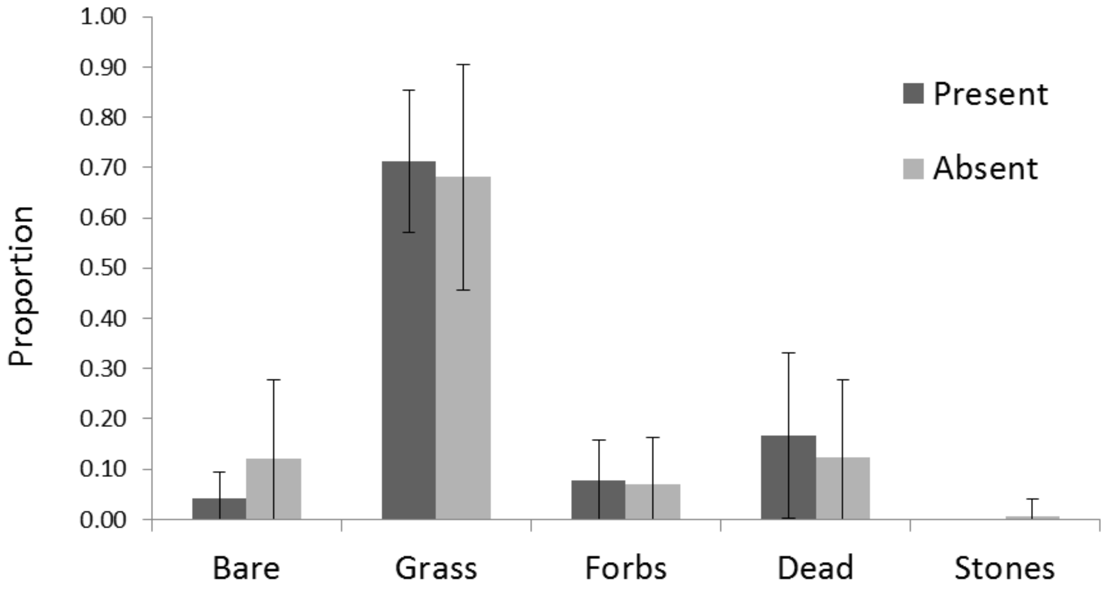

Figure 5: The proportions of ground cover variables for Rudd's lark territories (n=17) compared to random sampling points (Rudd's lark absent, n=356) in 2016.

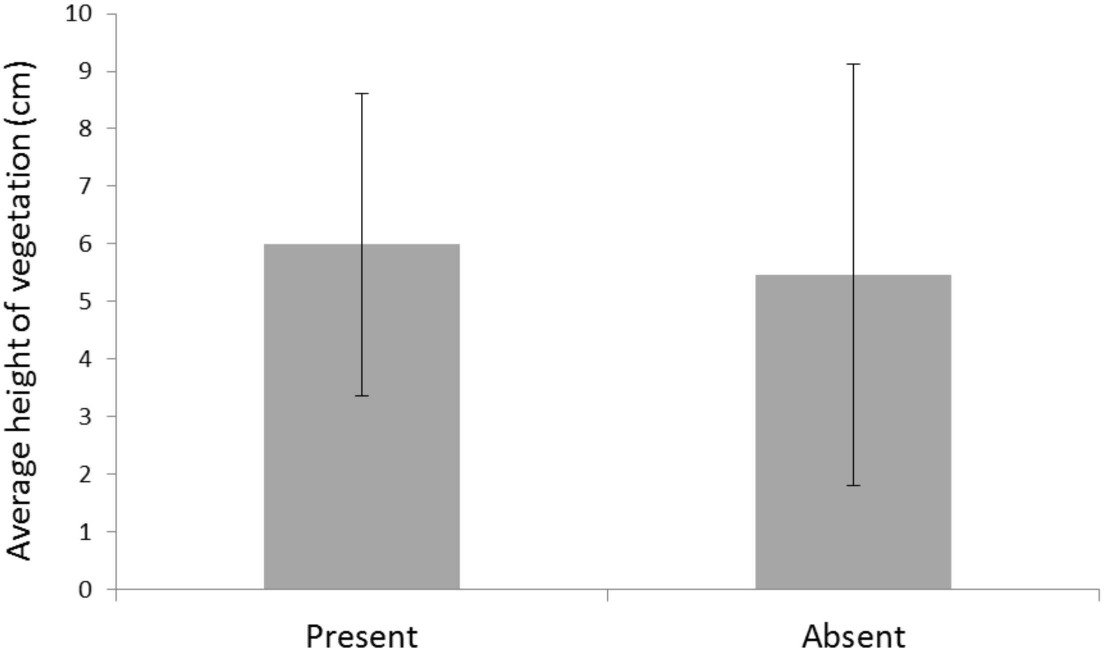

Figure 6a: The average grass height for Rudd's lark territories (n=17) compared to random sampling points (Rudd's lark absent, n=356) in 2016.

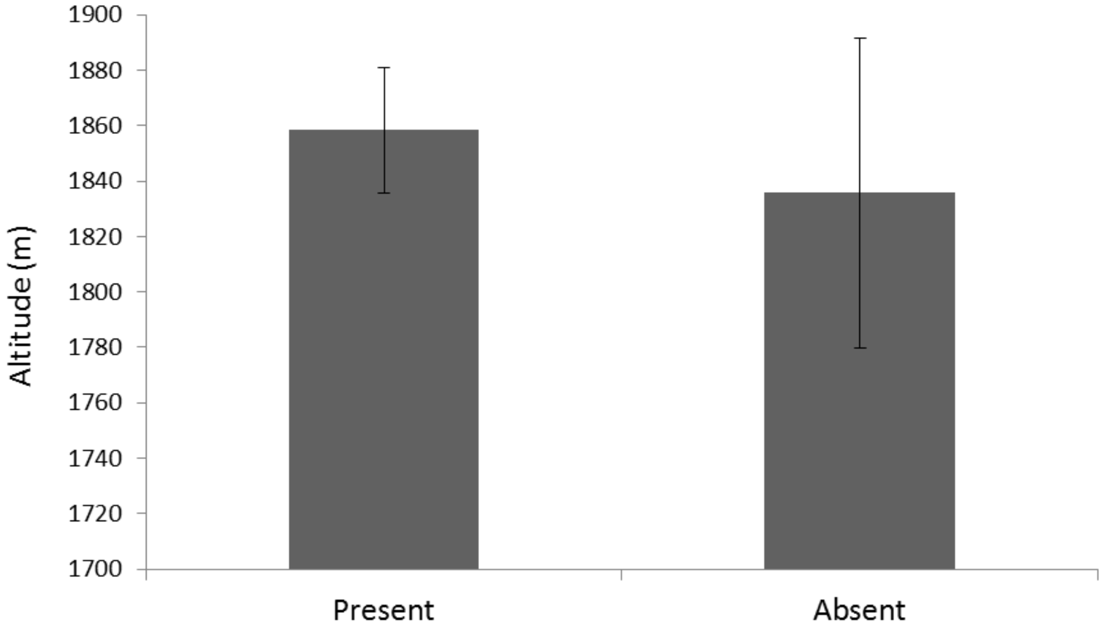

Figure 6b: The altitude of Rudd's lark territories (n=17) compared to random sampling points (Rudd's lark absent, n=356) in 2016.

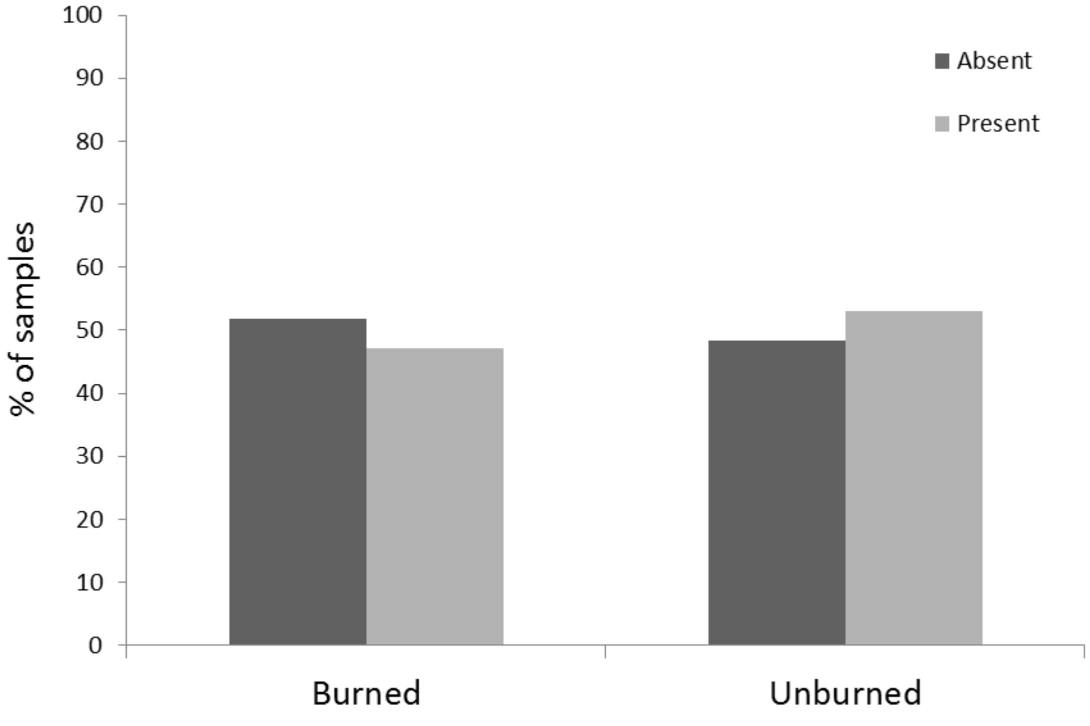

Figure 6c: The distribution of burn-type for Rudd's lark territories (n=17) compared to random sampling points (Rudd's lark absent, n=356) in 2016.

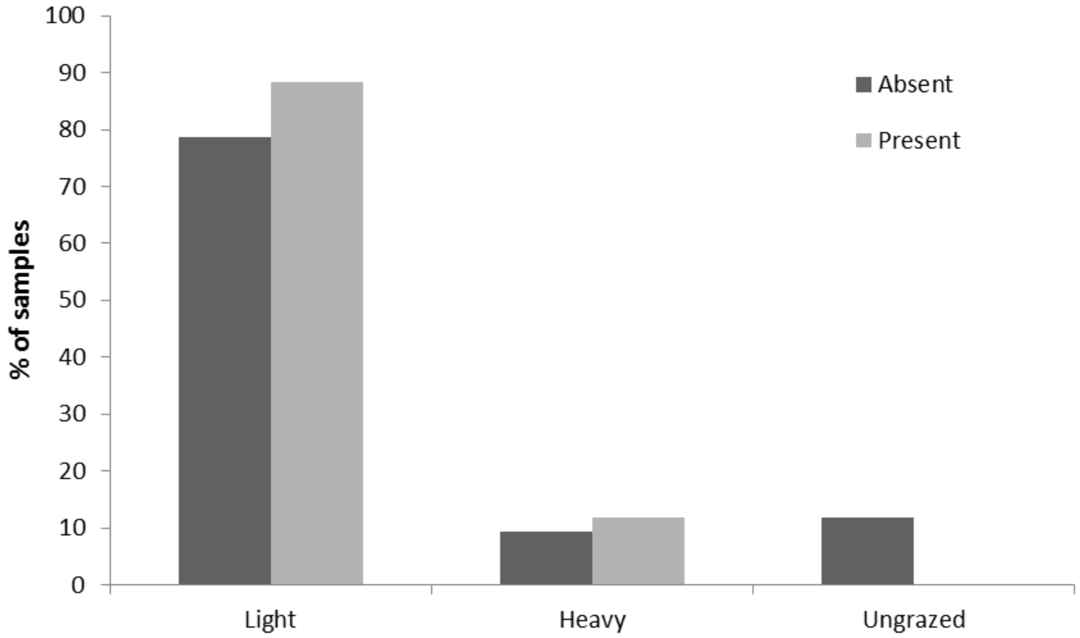

Figure 6d: The distribution of grazing-type for Rudd’s lark territories (n=17) compared to random sampling points (Rudd’s lark absent, n=356) in 2016.

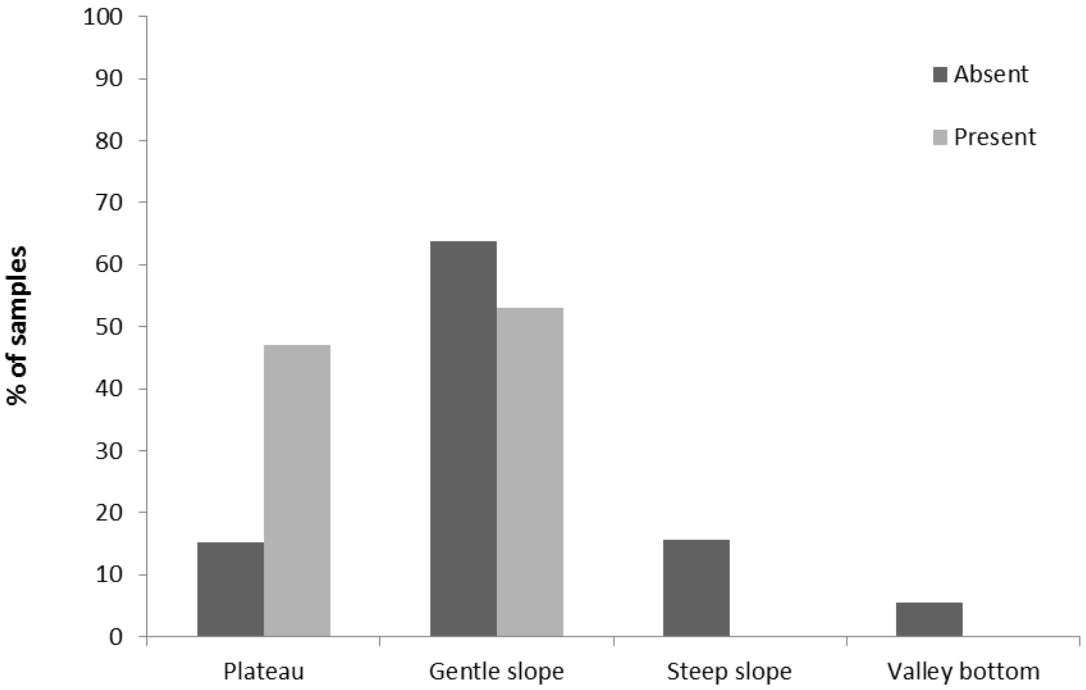

Figure 6e: The distribution of slope-type for Rudd’s lark territories (n=17) compared to random sampling points (Rudd’s lark absent, n=356) in 2016.

The first two Principal Components for the fine-scale vegetation data explained 62% of the variation. PC1 showed strong negative loadings for grass cover, and positive loadings for forb cover, while PC2 showed a negative loading for bare ground and positive loadings for dead vegetation cover. These Principal Components, along with average grass height, altitude, fire, grazing and slope were included in the model set. However, as with the coarse scale analysis, no model with covariates improved on the null. The Appendix shows a table of the first five models that performed best after the null models (Table A2).

Vegetation change

Grass cover

There was a trend towards a slight decrease in grass cover between the two surveys, but the change was not significant (β = -0.009; 95% CI: -0.118, 0.099). Two models performed well, one with Fire (across years) as the only fixed effect and the other with Year and Fire, suggesting that these two factors best explained the variation in grass cover across transects (Table 1). Based on the model averaging function, Fire was the most important explanatory variable for change in variation in grass cover, and grass cover was significantly greater on unburned transects than burned transects across years (β = 0.157; 95% CI: 0.011, 0.303).

Table 1. Environmental predictors of grass cover based on the averaging of two models that improved equally on the null model. Asterisks indicate predictors that were significant in their effect (* = significant; ** = very significant; *** = extremely significant).

Grass cover					
Variable	Estimate (β)	Std. Error	Low. conf. int.	Upp. Conf. int.	Importance
Fire*	0.157	0.09465	0.011	0.303	1.00
Year	-0.009	0.07580	-0.118	0.099	0.57

Average grass height

Average grass height was not significantly different between the two surveys (β = -0.012; 95% CI: -1.177, 1.091). The best-performing model also included Fire and Grazing (across years) as fixed effects, although the model with these two variables combined with "Year" also performed well, suggesting that a combination of all three factors explain the variation in average grass height across transects. The model averaging function ranked Fire and Grazing as the two most important variables (Table 2). Average grass height was significantly taller on unburned than burned sites across the years (β = 0.523; 95% CI: 0.272, 2.517). No level of grazing was significantly different from the others with respect to predicting grass height, though unsurprisingly both heavily grazed transects and lightly grazed transects had shorter grass than ungrazed transects (β = -1.102; 95% CI: -3.201, 0.997) and (β = -2.270; 95% CI: -5.583, 0.143), respectively across years.

Table 2. Environmental predictors of average grass height based on the averaging of two models that improved equally on the null model. Asterisks indicate predictors that were significant in their effect (* = significant; ** = very significant; *** = extremely significant).

Average grass height					
Variable	Estimate (β)	Std. Error	Low. conf. int.	Upp. Conf. int.	Importance
Fire*	0.523	0.561	0.272	2.517	1.00
Grazing	Light: -1.102	Light: 1.049	Light: -3.201	Light: 0.997	1.00
	Heavy: -2.720	Heavy: 1.431	Heavy: -5.583	Heavy: 0.143	
Year	-0.012	0.567	-1.177	1.091	0.29

Forbs

Forb cover increased significantly between the two surveys (β = 0.420; 95% CI: -3.237, -2.729). Similarly to grass cover, variation in forb cover was best explained by a model with Year as the only fixed factor. The model with Year and Grazing (across years) also performed well, though based on model averaging Year was the most important (Table 3). Forb cover was not significantly different between grazing types.

Table 3. Environmental predictors of forb cover based on the averaging of two models that improved equally on the null model. Asterisks indicate predictors that were significant in their effect (* = significant; ** = very significant; *** = extremely significant).

Forb cover					
Variable	Estimate (β)	Std. Error	Low. conf. int.	Upp. Conf. int.	Importance
Year***	0.420	0.113	-3.237	-2.729	1.00
Grazing	Light: 0.155	Light: 0.262	Light: -0.137	Light: 0.969	0.37
	Heavy: 0.260	Heavy: 0.409	Heavy: -0.056	Heavy: 1.453	

Dead vegetation

Dead vegetation cover increased significantly between 2002 and 2016 (β = 0.368; 95% CI: 0.174, 0.563). Two models competed well, one with Year as the only fixed effect and one with Year and Grazing offering reasonable explanatory power for the variation in the cover of dead vegetation. Year was the most important variable according to the model averaging function (Table 4). Dead vegetation cover was lower on burned than on unburned transects across years, though not significantly. Dead vegetation cover was greater on lightly grazed transects and less on heavily grazed transects when compared with ungrazed transects across years, though not significantly.

Table 4. Environmental predictors of dead vegetation cover based on the averaging of three models that improved equally on the null model. Asterisks indicate predictors that were significant in their effect (* = significant; ** = very significant; *** = extremely significant).

Dead vegetation cover					
Variable	Estimate (β)	Std. Error	Low. conf. int.	Upp. Conf. int.	Importance
Year***	0.374	0.102	0.174	0.563	1.00
Grazing	Light: 0.184 Heavy: -0.024	Light: 0.256 Heavy: 0.242	Light: -0.164 Heavy: -0.713	Light: 0.868 Heavy: 0.621	0.52

In summary, no significant change was found in either grass cover or average grass height between 2002 and 2016. By contrast, both forb cover and dead vegetation increased significantly between the two study periods. Within the model sets considering grass cover and average grass height, both variables were found to be significantly greater on unburned transects than burned transects. Appendix A shows a summary of all models that bettered the null in each model set (Table A3).

Change in Rudd's Lark habitat selection between 2002 and 2016

The analysis of Rudd's Lark territories in 2002 (n=17) vs 2016 (n=81) produced a "best" model that included PC1, PC2 and average grass height as fixed effects. All three covariates proved to be significant predictors of the change in Rudd's Lark habitat selection. PC1 loaded negatively for grass and positively for bare ground, while PC2 loaded positively for bare ground and negatively for dead vegetation. Together they accounted for 61% of the variation in ground cover across all Rudd's Lark territories. PC1 was significantly different between the two surveys (β = -1.688; 95% CI: -3.021, -0.738), as was PC2 (β = -4.081; 95% CI: -6.687, -2.389). Because the estimates were negative, the positive or negative signs associated with the ground cover loadings must be inverted. That is, Rudd's Lark occupied sites with less bare ground cover and more grass and dead vegetation cover in 2016 than in 2002, according to the first two principal components. Furthermore, the effect of average grass height decreased significantly (β = -1.140; 95% CI: -2.252, -0.264), indicating greater use of shorter grass in 2016 than in 2002. Appendix A shows a summary of all models that performed better than the null (Table A4).

Species diversity

In total, 96 species were recorded, including grassland specialists such as Yellow-breasted Pipit *Anthus chloris* (found on 35% of transects; the 14th most frequently encountered species out of 96), Blue Korhaan *Eupodotis caerulescens* (12%, 36th), Southern Bald Ibis *Geronticus calvus* (12%, 36th) and Botha's Lark *Spizocorys fringillaris* (8%, 47th). Rudd's Lark was encountered on 10% of transects and was the 40th most frequently encountered species. A full list of species can be found in Appendix A (Table A7). The species accumulation curve shows that my sampling effort in describing the region's entire bird community was reasonably good based on the first survey of the 52 transects (Appendix A: Figure A3); the curve approaches the asymptote suggesting that further species accumulation would have been slow (Ugland et al. 2003).

Four models provided better explanatory power for species richness variation than the null model, and were similar in explanatory power to one another. These comprised various combinations of PC1 and PC2 (from the transect vegetation PCA), average grass height and altitude. Model averaging showed that PC2 (positive loading for dead vegetation, negative loading for stones) and average grass height had by far the highest relative importance values, at 1.00 and 0.8 respectively (Table 5). However, only PC2 was significant (β = 0.070; 95% CI: 0.012, 0.128). In summary, bird diversity increased significantly with an increase in dead vegetation cover and a decrease in stone cover. Appendix A shows the eleven best models that improved on the null model (Table A5).

Table 5. Environmental predictors of bird diversity based on the averaging of four models that improved equally on the null model. Asterisks indicate predictors that were significant in their effect (* = significant; ** = very significant; *** = extremely significant).

Bird Diversity					
Variable	Estimate (β)	Std. Error	Low. conf. int.	Upp. Conf. int.	Importance
PC2*	0.070	0.029	0.012	0.128	1.00
Average grass height	0.061	0.032	-0.003	0.125	0.80
Altitude	0.049	0.034	-0.018	0.115	0.44
PC1	0.020	0.022	-0.025	0.064	0.14

Habitat selection: Rudd’s Lark vs other grassland specialists

Botha’s Lark

Botha’s Lark was found on four transects out of the 52 surveyed in 2016, with 12 individuals counted. At the coarse scale, no spatial auto-correlation was found for transects where Botha’s Lark was present (Moran’s I = -0.045, p = 0.433). However, no model in this set provided more explanatory power than the null model.

Black-winged Lapwing and Southern Bald Ibis

No spatial auto-correlation was found between transects with Black-winged Lapwing (n = 6, Moran’s I = 0.041, p = 0.073) and Southern Bald Ibis (n = 6, Moran’s I = -0.011, p = 0.803) were found. No model in either of these sets provided more explanatory power than the respective null models.

Yellow-breasted Pipit

Yellow-breasted Pipit was found on 21 transects out of the 52 surveyed in 2016, with 59 individuals counted. No spatial auto-correlation was found between transects containing Yellow-breasted Pipit (Moran’s I = -0.049, p = 0.057). Two models improved on the null by a similar degree; models included a combination of altitude, average grass height and PC2 (positive loading for dead vegetation, negative loading for stones) (Table 6). Model averaging indicated that altitude and average grass height were the most important explanatory factors. Yellow-breasted Pipits selected transects at significantly higher altitude than the mean (β = 1.787; 95% CI: 0.511, 3.062), and with taller average grass height (β = 0.668; 95% CI: -0.027, 1.364). Appendix A shows the two best models that improved on the null model for Yellow-breasted Pipit, as well as the five best models for Botha’s Lark, Black-winged Lapwing and Southern Bald Ibis, though none improved on the null (Table A6).

Table 6. Environmental predictors of Yellow-breasted Pipit presence along transects based on the averaging of two models that improved equally on the null model. Asterisks indicate predictors that were significant in their effect (* = significant; ** = very significant; *** = extremely significant).

Yellow-breasted Pipit *Anthus chloris*					
Variable	Estimate (β)	Std. Error	Low. conf. int.	Low. Conf. int.	Importance
Average grass height	0.668	0.346	-0.027	1.364	1.00
Altitude*	1.787	0.634	0.511	3.062	1.00
PC2	0.383	0.313	-0.248	1.013	0.39

Landscape data on fire incidence and land use

Fires occurred at an average frequency of 0.361 per km^2 between July and October ("well-timed fires" for Rudd's Lark) over the past 14 years. The minimum was 0.136 (2015) and the maximum was 0.831 (2002). The average frequencies per year for these months are presented in Figure 7a. Fires in the 2016 core area occurred at an average frequency of 0.051 per km^2 between November and February ("poorly-timed fires" for Rudd's Lark) over the past 14 years. The minimum was 0 (2006/2007, 2012/2013 and 2016/2017) and the maximum was 0.314 (2013/2014). The average frequencies per year for these months are presented in Figure 7b.

Grassland increased in the core area by 6.61% between the 1990 and 2013 surveys (from 75.71% to 80.72% of the total area), while rain-fed crops decreased by 29.67% (from 16.67% to 11.72% of the total area; Figure 8a). High-intensity irrigated crops, plantations and urban cover all increased between the two surveys (by 127.23%, 25.14% and 1135% respectively), though these cover types occur at much smaller proportions of the total area than grassland and rain-fed crops (Figure 8b). Note that for display purposes Figure 8a and 8b are plotted on different scales. Orchards were absent in 1990, but represented 0.03% of the total area in 2013.

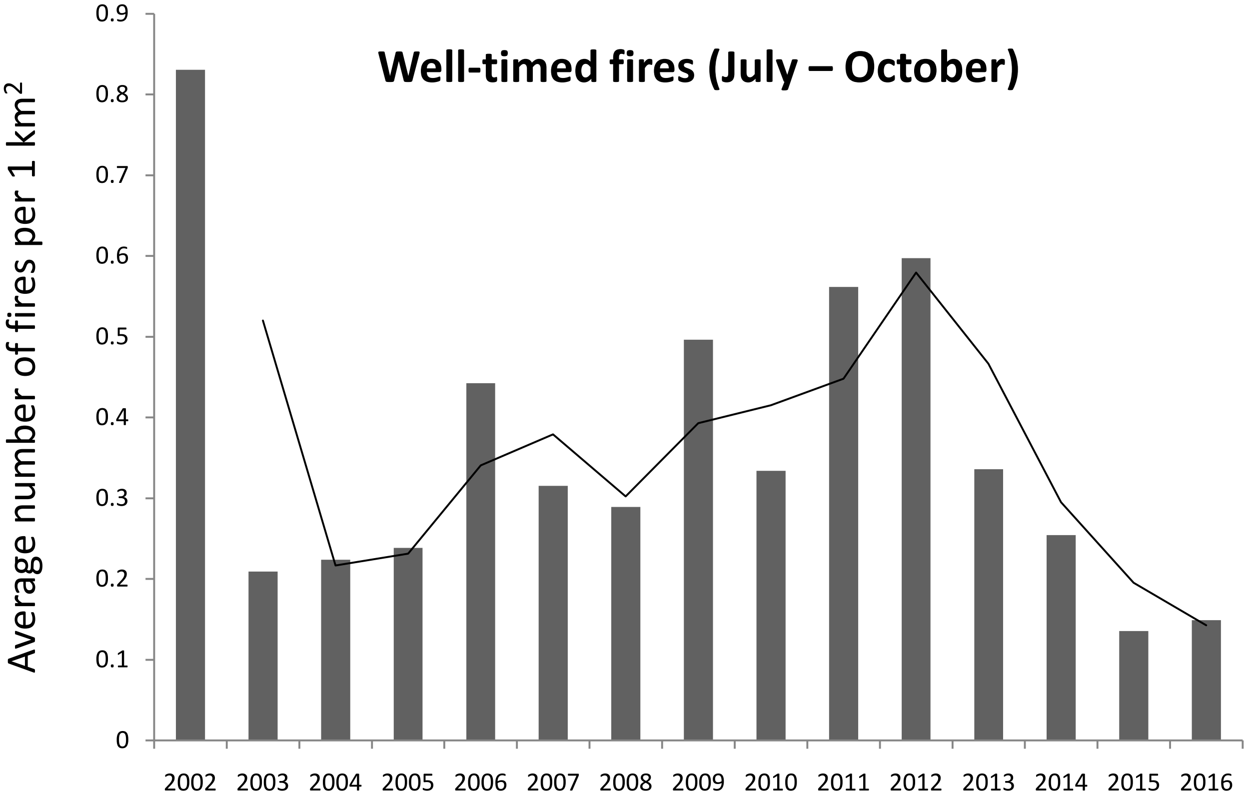

Figure 7a: The trend in average fires per km^2 for well-timed fires with regards to Rudd's lark ecology, from 2002 to 2016.

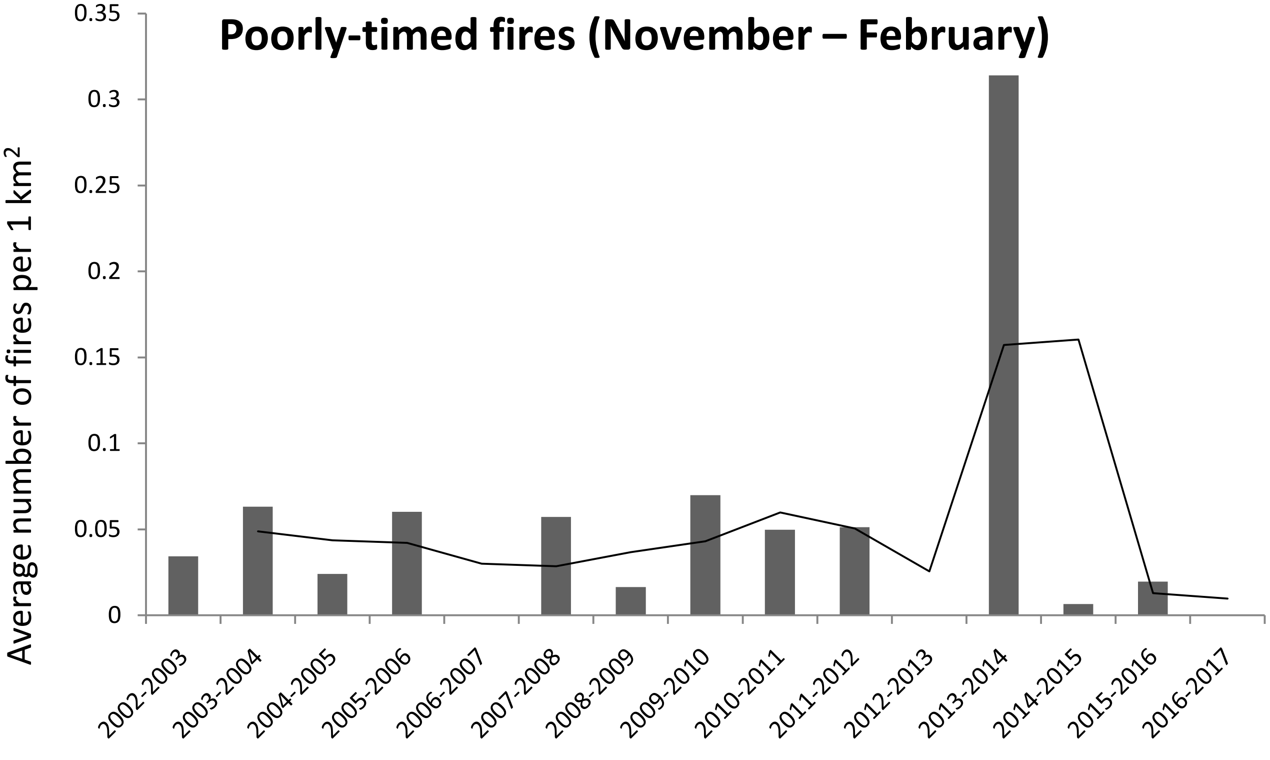

Figure 7b: The trend in average fires per km^2 for poorly-timed fires with regards to Rudd's lark ecology, from 2002 to 2016.

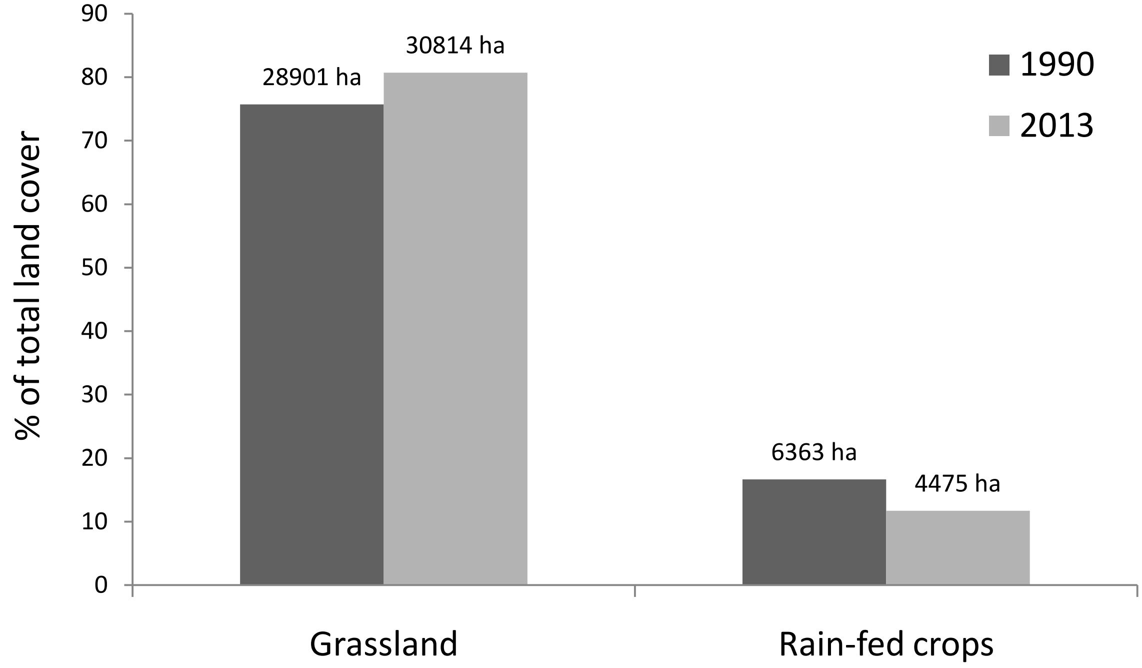

Figure 8a: Changes in the percentage cover of grassland and rain-fed crops between 1990 and 2013 (absolute amount of land cover shown in hectares above each column)

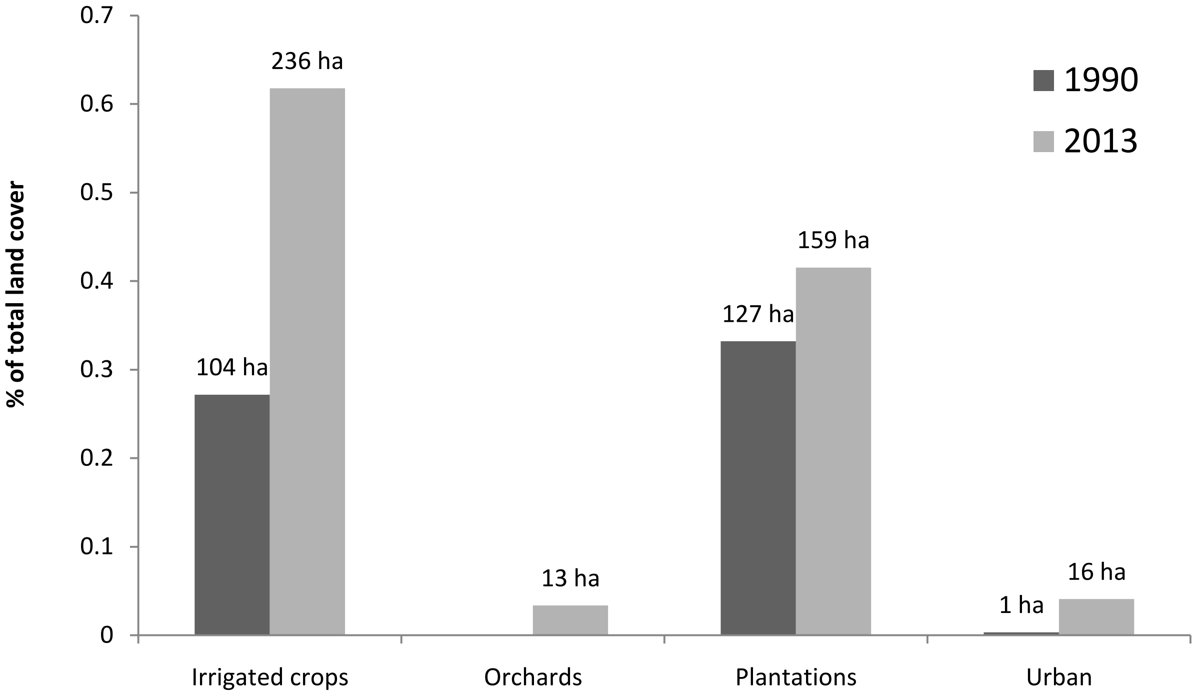

Figure 8b: Changes in the percentage cover of grassland and rain-fed crops between 1990 and 2013 (absolute amount of land cover shown in hectares above each column)

Farmer Interviews

Farm history

All farmers interviewed were either landowners or land managers of the land in question. Experience ranged from several years to more than four decades. Farms varied in size from 1000 hectares to 6 500 hectares. Land-use was for cattle (66%), sheep (23%) and crops (11%) (n=5; not all farmers disclosed land cover percentages). Four farmers reported no changes in management in the last ten years, while three said that they had significantly increased the land cover used for crops. However, all three of the latter farmers reported that they had re-planted historically ploughed fields that been hitherto lying fallow, rather than converted untouched grassland to crops.

Climate change

Five out of seven farmers reported a significant increase in temperature, including noticeably warmer winters and less frequent snowfall. This was likely based on qualitative impressions rather than recorded measurements. Opinion of rainfall trends was varied, with one farmer suggesting an increase, three a decrease and three suggesting no great change had occurred in the last decade. At least two farmers based their rainfall estimates on rain measurements taken on their farms. One farmer suggested a change from drizzle-type rain to thunderstorms. However, the 2014/2015 season was cited as the worst drought in living memory. Two farmers reported the construction of many new dams to safeguard against dry periods.

Conservation and Rudd's Lark

Responses relating to conservation in the area were mixed. Four out of seven farmers reported that they had been contacted by conservation organizations, and three of these were actively involved in programs (such as the Crane Custodianship Program). Farmers were generally aware of key large bird species on their farm such as Secretarybirds *Sagittarius serpentarius* and Blue Cranes *Anthropoides paradiseus* or Grey-Crowned Cranes *Balearica regulorum* (five out of seven), while Botha's Lark and Yellow-breasted Pipits were each listed by a single farmer respectively. Four farmers were aware of Rudd's Lark, though only two had seen it on their farms, and both said that they needed a guide to identify it. None were aware of a population decline in the Rudd's Lark population, although three farmers expressed interest in the conservation of the species. One farmer benefited financially from birders visiting his land, while another had an open-door policy for bird guides to walk on his farm with birders in search of special species such as Rudd's and Botha's Lark.

Fire

Six farmers reported burning once per year, and one farmer reported burning every second year. Not all farmers burned the same proportion of their farm at each burn, though this was not explicitly quantified. Four farmers reported burning after the first winter rainfall, and all seven reported burning between August and October. The variation in the timing of the burn ranged from two weeks to more than a month, but was generally one month (four out of seven farmers). Two farmers reported the burning of fire breaks in July. Each farmer was asked to rank a list of six reasons for burning in order of importance (1 = most important, 6 = least important), and these scores were then aggregated for each factor (Table 7). Other reasons cited include the nature of a specific part of the farm (e.g. vleis), grass "dormancy" in winter and suitably dry conditions. One farmer burned half of his farm before the first winter rainfall, and half after.

Table 7: A supplied list of reasons for burning ranked in order of importance by farmers in the Wakkerstroom farming community (n=7)

Reason for burning	Aggregate score
Remove unpalatable/moribund grass	1.43
Improve veld condition	2.14
Take advantage of rainfall	2.29
Reduce tick load	3.00
Avoid runaway fires	4.29

Impressions

Some of the interviewed farmers offered other ideas relating to farm management and Rudd's Lark in the area. One farmer reported an increasing proliferation of a fynbos-type plant that was capable of greatly reducing carrying capacity, likely the *Vernonia* shrub noted in the 2016 study. This farmer also stated that burning regimes varied between veld managed for cattle and veld managed for sheep, with farmers in the area burning earlier for the former. With regards to Rudd's Lark, no farmer could specifically recall the work done in 2002, though one farmer stated that he had inherited a practice from his father of not burning a specific hilltop to maintain a breeding site for small grassland birds. After I informed one farmer where I had located Rudd's Lark on his farm, he revealed that for over 40 years, this area had been burned earlier in the year (June/July) than the rest of the farm, as a fire break. The same farmer also stated that certain plateaus "above the granite line" created a different veld type than the rest of the farm, and that this could be important to the habitat selection of Rudd's Lark.

Discussion

The persistence of Rudd's Lark in the Wakkerstroom area is a critical question to consider if we are to assess the remaining metapopulation and how best to conserve it. My results show that there has been a decline in the number of Rudd's Larks detected along transects surveyed in 2002 and 2016. No environmental factors were able to explain Rudd's Lark habitat selection at either a coarse or fine scale in 2016. However, both forb and dead vegetation cover had significantly increased along the same transects between 2002 and 2016. Rudd's Lark territories surveyed in 2016 had significantly shorter grass, more grass cover and dead vegetation cover and less bare ground cover, than territories surveyed in 2002. I found that bird diversity increased significantly with an increase in dead vegetation and a decrease in stone cover. In the specific case of other threatened grassland specialists, the habitat selection of Botha's Lark, Southern Bald Ibis and Black-winged Lapwing could not be predicted by environmental factors in 2016. However, I did find that Yellow-breasted Pipits were present on transects with taller grass and significantly higher elevation than those where they were absent. Analysis of landcover data recorded in 1990 and 2013 suggests that there are far more early season fires than late season fires in the core area. These data also show an increase in "grassland", high-intensity irrigated crops and urban cover, but a decrease in rain-fed crops.

Decline

Assessing the decline of a species both low in abundance and cryptic in nature is a significant challenge, as it is difficult to detect such a species everywhere that it occurs (McArdle 1990, Garza et al. 2005). Moreover, Rudd's Lark occurs in a mosaic of farmland without discrete boundaries in terms of habitat or uniform ownership status and management strategies. It is difficult to track population trends and distribution shifts without intensive ground surveys (Serrano & Astrain 2005), motivating the present study. Rudd's Lark has long been suspected to be in decline in the Wakkerstroom area (and, indeed, in its greater South African range) (Maphisa et al. 2009). However, some sources are difficult to gauge in terms of reliability. Bird guides based in Wakkerstroom, for example, concur that they are finding far fewer Rudd's Larks than a decade ago. But this is based in part on repeated visits to a small number of historically reliable sites such as Fickland Pan (27° 13' 56"S, 30° 2' 27"E). Birds may simply have moved from this site to another one, without actually decreasing in number. Similarly, comparisons between SABAP1 (1987–1991) and SABAP2 (2007–present) suggest a significant range retraction, but could be the result of artefacts such as birder effort or site-bias (Snäll et al. 2011). In the specific case of Rudd's Lark, it is difficult to make inferences from citizen science data, as these birds are often difficult to detect and were found on private farms during my survey where it is unlikely that citizen birders would be atlassing. We might observe trends in pentads that are well-covered, but as with the bird guide observations, these may belie geographic shifts.

However, the data I have collected do suggest that a decline has occurred, that needs to be further investigated with some urgency. I replicated the exact methods employed in 2002, and so any issues of imperfect detection should at least be consistent within both the 2002 and the 2016 surveys. Controllable factors such as time of day, time of year and transect location were kept as similar as possible. Upon arrival in Wakkerstroom in mid-November 2016, I visited the popular birding site, Fickland Pan, and discovered three pairs of Rudd's Larks that had already begun nesting, raising a concern that birds may have started breeding earlier in 2016 than in 2002. If singing consistently declines after breeding commences then we would expect detectability of this species to also decline (de Juana et al. 2004). However, when repeating a subset of the transects an average of 12 days after my initial survey, I detected larks on the same number of transects (n=5). These observations suggest that larks did not appear to be singing less as the season progressed.

Not only did the probability of encountering Rudd's Lark along the replicated transects decrease between 2002 and 2016, but seven entire transects that previously existed as grassland (and where Rudd's Lark was present in 2002 in two cases) have been lost to crop production. By their own admission, some farmers in the area have converted large tracts of fallow land into crop fields. This could be reflected by the 127% increase in high intensity irrigated crops picked up when comparing land use data across the overall core range when comparing 1990 and 2013. However, these same data showed a 7% increase in grassland and a 30% decrease in rain-fed crops. Such landscape scale data can be misleading as it does not capture the dynamic state of the area but rather two discrete points in time. These proportions may be strongly affected by farmers' response to fluctuating climatic and economic factors. Furthermore, these data are a summary of the whole core area and are not necessarily specific to where Rudd's Lark occurs.

Taken together, the evidence suggests that the detected decline in the Wakkerstroom Rudd's Lark population is likely to be genuine.

Rudd's Lark habitat

One of my main objectives was to contribute to the current knowledge of Rudd's Lark habitat selection. The better we understand what habitat Rudd's Lark prefers, the more effectively we can select which areas to conserve or maintain to benefit the species. However, the model sets considering Rudd's Lark habitat selection at both a coarse and a fine scale in 2016 did not produce any models where environmental variables explained the presence of Rudd’s Lark better than the null models. This means that habitat in the study area was not statistically different between where Rudd’s Lark was detected and where it was not. Unless habitat variation exists at a more subtle or fine scale than what was captured by the sampling approach used (as has been suggested by Maphisa et al. 2009), it appears that suitable habitat is available for Rudd’s Lark that is not being currently utilized by the species.

While I did not detect any significant habitat predictors of lark incidence in 2016, I did find that forb and dead vegetation cover had increased significantly along the replicated transects between 2002 and 2016. Previous studies have reported that Rudd’s Lark selects habitat with minimal forb invasion (BirdLife International 2016b), which would suggests that the increase in forb cover could represent habitat deterioration for the species along the transects surveyed. Conversely, dead vegetation (which includes dry grass) has been linked to earlier breeding in the species, which reportedly favours nestling survival (Maphisa et al. 2009). The increase in dead cover along transects would therefore be potentially beneficial to Rudd’s Lark. Grass cover and average grass height have also been cited as being important to Rudd’s Lark habitat selection (Coppedge et al. 2008, Maphisa et al 2016), but I found that they had not significantly changed between 2002 and 2016, so appear not to assist in explaining the decline of Rudd’s Lark in the surveyed area.

I tested whether habitat selected by Rudd’s Lark has changed since the 2002 study of the Wakkerstroom population, because this could indicate habitat degradation or adaptation. Although I did not detect any preference for specific habitat traits by Rudd’s Lark in 2016, my fine-scale comparison of Rudd’s Lark territories recorded in 2002 and 2016 produced a “best” model that featured both Principal Components as well as average grass height. This means that in 2016 Rudd’s Lark occupied territories with less bare ground and more grass and dead vegetation, as well as territories with significantly shorter grass height, than they did in 2002. Three interpretations of this finding are possible. First, these findings could be the result of some variation between surveys in how the vegetation was recorded, or the mis-assigning of territories that can occur with species such as Rudd’s Lark where an individuals’ location can be difficult to pinpoint (Garza et al. 2005). Second, this could reflect an artefact of sampling design and sample size: my data only accounted for vegetation from territories discovered along transects or discovered while surveying these initial territories, while the 2002 study included vegetation from sites far removed from the transects and based on prior knowledge of where Rudd’s Lark occurred. Suspected decline of the population aside, this undoubtedly contributed to why 81 Rudd’s Lark territories were recorded in 2002 compared to 17 in 2016, even considering that in some cases vegetation was recorded more than once for a single bird when it moved its territory in 2002. This disparity presents a new conundrum: if Rudd’s Lark really does have very specific habitat preferences (as suggested by Maphisa et al. 2009), then a larger number of territories should not greatly increase the variation in habitat selection, and the apparent fine-scale shift in habitat selection since 2002 would be genuine. This is the third interpretation. However, it is also possible that the 81 territories were clustered in a way that obliged some males to use marginal habitat, leading to greater variation in habitat selection, whereas an apparently smaller population size in 2002 may have allowed all males to use a more consistent habitat type. This effect was proposed by Garza et al. (2005) in their work on the ecologically similar Dupont's Lark *Chersophilus duponti*. The change in territory habitat revealed by the model may be an artefact, therefore, of a greatly reduced sample size, or of a genuine ecological change relating to lower population density.

Other grassland specialists

While this research was focused on the Rudd's Lark, the greater context includes the state of South Africa's high-elevation grasslands and the endemic birds that occur there. Any management interventions for the conservation of a single species should ideally consider the habitat needs of other key species in the area. I therefore also investigated the abundance and habitat selection of other grassland specialists in the Wakkerstroom. Three of these, like Rudd's Lark, were detected along my 52 transects at low abundance: Botha's Lark (n=4 transects), Black-winged Lapwing (n=6 transects) and Southern Bald Ibis (n=6 transects). Similarly, analysis of these species' habitat selection failed to produce models with better explanatory power than the null. By contrast the fourth species, Yellow-breasted Pipit, was found on 18 transects, and analysis showed that these had taller grass and significantly higher altitude than transects where it was not recorded. This is consistent with our understanding that Yellow-breasted Pipits select particularly high elevation habitat in this region (Tarboton et al. 1987), and the finding by Maphisa et al. (2016) that this species occupied sites with only moderate levels of grazing. Although the ecology of the species mentioned above is different in many ways, these data do suggest that the Yellow-breasted Pipit is the species of least concern in this particular suite.

I found that general species diversity was affected by average grass height and Principal Component 2, which loaded positively for dead vegetation and negatively for stones. That higher bird diversity was found on transects with a greater abundance of dead vegetation and less stones may be explained by the need for grassland birds to select habitat with suitable cover and materials for nest construction at this time of the year (Maphisa et al. 2016).

Fire

Burning and grazing regimes play an important role in structuring habitat for grassland birds (Jansen et al. 1999, Maphisa et al. 2009, Jarzyna et al. 2015). Late burning (November onwards) has been cited as a potential reason for the suspected decline in Rudd's Lark numbers (Maphisa et al. 2009) and was a focus of my research in 2016. Reasons for burning given by farmers were consistent with the findings of Muchai (2002) and included to the removal of poor foraging material, taking advantage of rainfall and the control of ticks. I found that roughly half of all transects surveyed had been burned within the last year, and half had not. This was similar for transects where Rudd's Lark was present, suggesting that the species did not seem to discriminate between transects that had been burned and those that had not. However, "burned" transects needed only to show some evidence of fire from within the previous 12 months to be scored as such. As a rough estimate, none of these transects had been burned within the last two to three months, judging by the abundance of burned stumps or moribund vegetation. This is consistent with the response that burning takes place between August and October given by most of the farmers interviewed. According to the analysis of remotely-sensed fire data, these early season fires occur seven times more frequently than the harmful late season fires between November and December (0.361 per km^2 per year compared to 0.051). Late season fire frequency has been low and fairly stable over the past 14 years, except for one spike in 2013/2014. Early fires appear to be decreasing in frequency over the past four years, but there is no sign of the consistent pattern that might be expected if fire were a significant driver of Rudd's Lark decline or habitat degradation.

If the coarse scale analysis masked Rudd's Lark preference for certain burning regimes, the fine scale analysis was expected to rectify this by analyzing specific Rudd's Lark territories. However, analysis of fine-scale data did not produce strikingly different results. Both Rudd's Lark territories (n=17) and the random sample points (n=356) were divided almost exactly in half in terms of burned and unburned scoring. Fire did explain some of the variation in ground cover variables: predictably, grass cover and average grass height were greater at unburned than burned sites. However, no model set analyzing Rudd's Lark habitat preference showed any significant effect of burning regimes at either the coarse or the fine scale. It thus appears that a) fire was not as important a factor as it has previously been reported to be by Maphisa et al. (2009), and b) there is no evidence that contradicts the current thinking that optimal Rudd's Lark breeding habitat can be either burned or unburned, if burning is not late (BirdLife South Africa 2015). It is worth noting, however, that the territories of six Rudd's Larks (the highest number recorded for any single transect) were recorded in an area that for decades had been burned earlier in the year than the rest of the farm. While a single case such as this is not in itself conclusive, this could merit further investigation. Furthermore, rainfall was cited by farmers as one of the most important cues used to initiate for the start of the burning season. By this reasoning, a shift in the timing of rainfall would dictate a shift in the timing of burning, with potential consequences for Rudd's Lark.

Grazing

Impressions of grazing-regime effects on Rudd's Lark in the literature are mixed, and grazing was thus a factor of interest in my study. Hockey et al. (1988) reported that Rudd's Lark prefers habitat that is moderately to heavily grazed. Muchai (2002) found that where heavy grazing was accompanied by annual burning, ground-nesting birds such as Rudd's Lark were negatively affected. Maphisa et al. (2009) suggested that Rudd's Larks can occur in heavily grazed areas, but that the species generally preferred lightly grazed territories, particularly for breeding. The overall impression is that Rudd's Lark is most benefited by mixed stocking rates that result in moderate to light grazing cover (BirdLife South Africa 2015). I found Rudd's Lark predominantly on lightly grazed transects (80%) in 2016, though this largely corresponded to the large overall proportion (88%) of transects scored as lightly grazed. At the fine scale, a similarly high proportion of sites were found to be lightly grazed both where Rudd's Lark was present and where it was absent. I never recorded Rudd's Larks at entirely ungrazed sites, and this is consistent with previous suggestions that they avoid ungrazed grassland (Maphisa et al. 2009, Hockey et al. 1988). As with fire, no models considered at either the coarse or the fine scale indicated grazing to be a statistically significant factor in predicting Rudd's Lark presence.

Limitations

A study such as this is limited in scope and made difficult by small sample sizes. Several questions need to be addressed in this regard. First, what can we infer from these results about the population of Rudd's Lark in the Wakkerstroom area? My survey of Rudd's Lark in the Wakkerstroom grasslands was not exhaustive. It is highly likely that an unknown number of Rudd's Lark sites exist within this area beyond the 1 km that my transects generally penetrated into the farmland. Even since returning from my fieldwork in December 2016, I have heard reports of Rudd's Lark within the core range that we did not detect (though not in areas where transects were located). Thus, while it seems reasonable to report a decline in the population based on the data available, it is difficult to offer estimates of the Rudd's Lark population in the area. The lack of sufficient sample sizes needed for effective distance sampling was also a shortfall in this regard.

Second, are these findings a fair reflection of a declining trend in Rudd's Lark abundance? My study only presented a single "snapshot" in time. It is impossible to tell whether the perceived decline has been a steady, annual trend or something more infrequent and stochastic. It is also beyond the scope of this project to determine whether the decline is limited to factors within the sites that were surveyed, as the distribution of Rudd's Lark in the early and late season, as well as between breeding seasons, remains unclear. It is suggested in Maphisa 2004 that Rudd's lark does not move much between seasons. However, if Rudd's Lark is moving between the Wakkerstroom area and other sites, this would a critical factor in understanding the extent of the perceived decline. Even short-range movement within farms or between neighbouring could shed light on habitat use and population density.

Third, how robust are the findings that relate to habitat selection? My primary objective was to compare the transects surveyed in 2002 and 2016 in terms of vegetation and number of larks detected rather than search for Rudd's Lark territories. One outcome of this was a low number of Rudd's Lark territories (n=17), which are perhaps the best indicator of this species' habitat preference and were surveyed more extensively by Maphisa et al (2009) who instead found and surveyed 81. My results do support some previous findings such as Rudd's Lark absence from ungrazed sites, but I was unable to extract specific habitat preferences that differed from the general environment that was surveyed. Such a paucity of conclusive information on habitat selection continues to be a concern in an area where rapid anthropogenic change is taking place (Serrano & Astrain 2005). Furthermore, I failed to detect an upward shift in altitude consistent with the climate change effects predicted by Huntley & Barnard (2012). However, work is currently underway by Robin Colyn and Birdlife South Africa to develop a habitat niche model for the species' overall distribution as part of the Threatened Grassland Species Project (Robin Colyn, *in litt.* 2016), which is hoped to greatly improve our knowledge base for Rudd's Lark with regards to the aspects mentioned above.

Recommendations and conservation implications

The apparent decline of Rudd's Lark documented in this thesis merits urgent attention, and argues that Rudd's Lark should be considered within the suite of species most at risk of becoming Africa's first avian extinction. Land transformation in the Wakkerstroom area has led to direct habitat loss for this species, and represents accelerating human pressure. The remaining available habitat does not appear to be fully utilized by the current Rudd's Lark population in the area, or is unsuitable for reasons too subtle or complex to be determined by this study. If we are to effectively conserve this species, a more robust understanding of its habitat preferences is required. Future studies should consider landscape data at a fine-scale, as well as specific floristic features, to determine if changes have occurred at specific sites where Rudd's Lark was recorded in previous studies.

According to farmer interviews, a significant proportion of the Rudd's Lark individuals detected in my survey occur where land management has not changed in recent history and is set to continue as such.

Considering that three to six Rudd's Lark males with territories were detected along a single transect in a few cases (essentially "micro-populations"), such areas could offer critical refuges for the species. I recommend long-term or continuous, non-invasive studies of the groups of individuals found during the 2016 study (and potentially 2002, as well). Such focused monitoring would require relatively little effort and could be used to gain valuable insights into the nature and validity of the perceived decline, as well as whether or not the threats to these birds are confined to the sites where they breed.

It is especially important for wild species to be preserved within agricultural landscapes when livestock play the ecological role formerly carried out by now-extinct large grazers (Tscharntke et al. 2005). Non-intensive grassland management (livestock removed after light to moderate grazing or single camp systems with few animals), as was observed on some of the farms where Rudd's Lark was present, is an important aspect of grassland species conservation (Bignal & McCracken 1996). Based on our current knowledge, including this study, Rudd's Lark tends to prefer gently sloping or flat grassland that has been lightly grazed and not burned late in the year, nor featuring more than a low proportion of forbs, bare ground or stones; these preferences were more evident in 2002 than in 2016, when only a subset of sites with these characteristics were occupied. These aspects, ideally combined with the results of the niche model, need to be communicated as key themes when mediating the necessary inclusion of landowners as active stakeholders in the conservation of this species. Rudd's Lark has already disappeared from sections of its former range (Birdlife International 2016a, N. Theron *in litt*. 2016); Wakkerstroom is one of the key remaining sites where conservationists and landowners must collaborate if this species is to survive.

As with any species in decline, the question of the appropriate IUCN threat category for Rudd's Lark must be carefully considered. Three findings during my study in the Wakkerstroom core area in 2016 correspond to the IUCN criteria that define a species as "Endangered" using the following criteria (IUCN SSC 2000): A2, an observed population size reduction of $\geq$ 50% over the last 10 years where the reduction or its causes may not have ceased OR may not be understood OR may not be reversible, based on (a) direct observation and (c) a decline in area of occupancy and extent of occurrence. First, the 72% decline in detected individuals along transects between the 2002 and 2016 survey; second, the failure to detect the species at sites where previously individuals were present; and third, the irreversible loss (to cultivation) of previously occupied sites in the Wakkerstroom area. Therefore my findings support the tentatively proposed uplisting in the Rudd's Lark's IUCN threat status from Vulnerable to Endangered, consistent with the regional assessment by BirdLife South Africa in the Eskom Red Data Book (Taylor et al. 2015).

Conclusion

My survey of Rudd's Lark in the Wakkerstroom area is the first dedicated research on this species involving both habitat assessment and bird counts in this specific area since the work by David Maphisa in 2002. I found a decline in both Rudd's Lark incidence and absolute numbers along replicated transects between 2002 and 2016. In attempting to explain this apparent decline in the population, I analyzed environmental factors in relation to the presence and absence of Rudd's Lark, but failed to detect any specific habitat predictors. While sites occupied by Rudd's Larks shared common characteristics, these characteristics were also found at sites where Rudd's Larks were not detected, obscuring a general pattern.

However, vegetation had changed along transects overall since 2002 (more forbs and dead vegetation) and the vegetation within Rudd's Lark territories had also changed between the two study periods (preference for more but shorter grass cover, more dead vegetation and less bare ground in 2016 compared to 2002). What this means for Rudd's Lark specifically is still unclear, however. Current fire and grazing regimes seem to favour the species, and landscape data suggest that harmful late season fires have not increased dramatically in the past decade. Similarly, grassland in the core study area has actually increased according to the landscape data. On the other hand, habitat has been lost directly to land conversion, leading to the loss of specific sites occupied by Rudd's Lark in 2002.

Taken together, these patterns suggest that the remaining habitat was not fully occupied by the existing Rudd's Lark population; that is, many sites where Rudd's Larks were not detected shared the landscape and vegetation features common to sites where they were detected. It is possible, however, that fine-scale preferences exist that were not detected in this study.

It is important that the global and regional statuses of Rudd's Lark are aligned by combining the work of BirdLife South Africa and the IUCN. My findings suggest that the listing of Rudd's Lark as "Endangered" by BirdLife South Africa is appropriate. Further research is required in areas such as Memel in the Free State and the Stormberg region of the Eastern Cape to determine priority areas for conservation, though Wakkerstroom is undoubtedly one of them. Conservationists must continue to build partnerships with farmers that will benefit threatened grassland species. Several remaining Rudd's Lark micro-populations occur on land in the Wakkerstroom area that appears to be managed consistently in a way that favours the species; such cases must be monitored and supported where possible. There is much yet to learn, but I hope that this thesis will contribute to protecting one of Africa's currently most vulnerable avian species.

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Appendix A

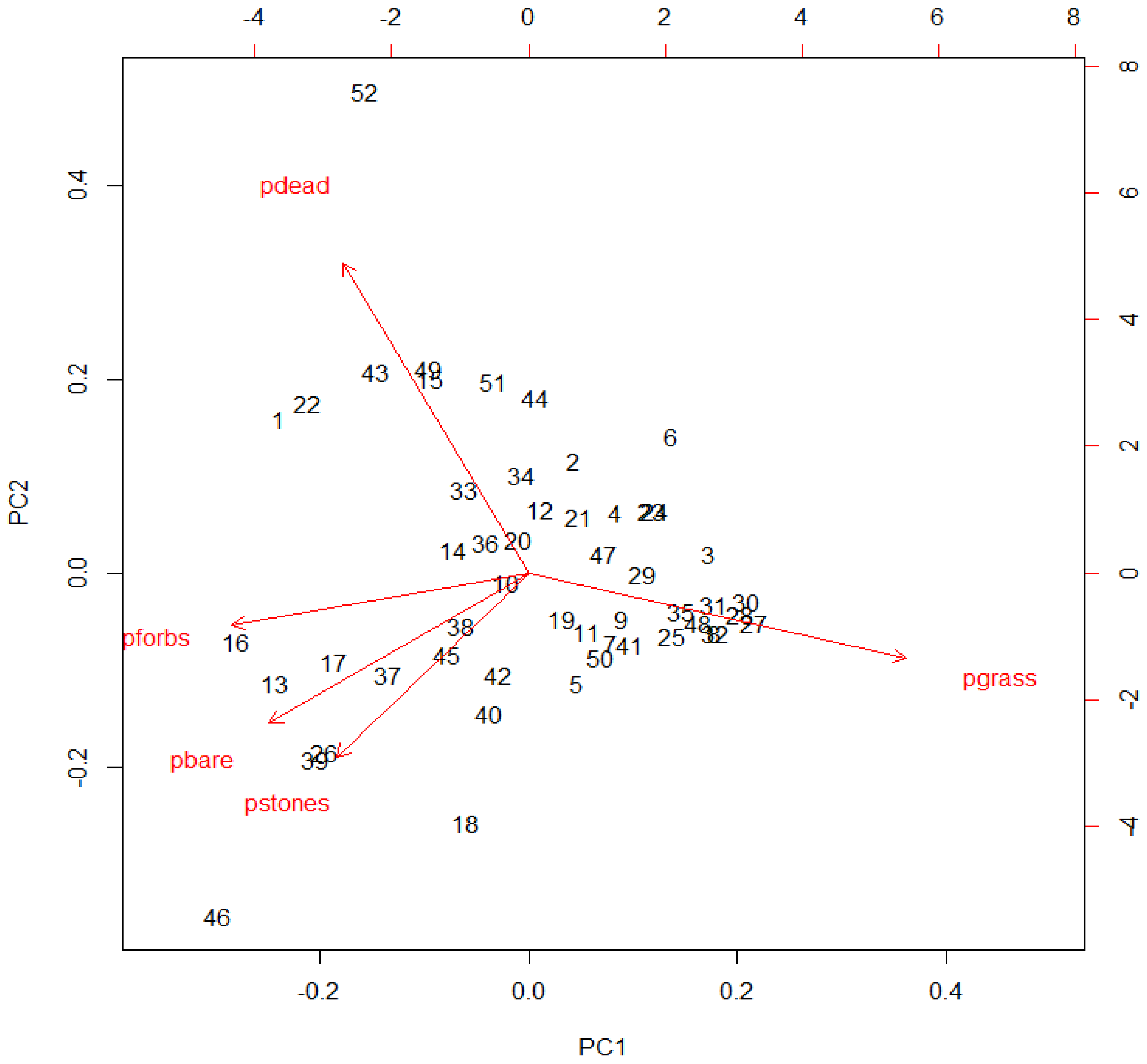

Figure A1: The distribution of transects (n=52) according to ground cover variables as they were accounted for by the first two Principal Components.

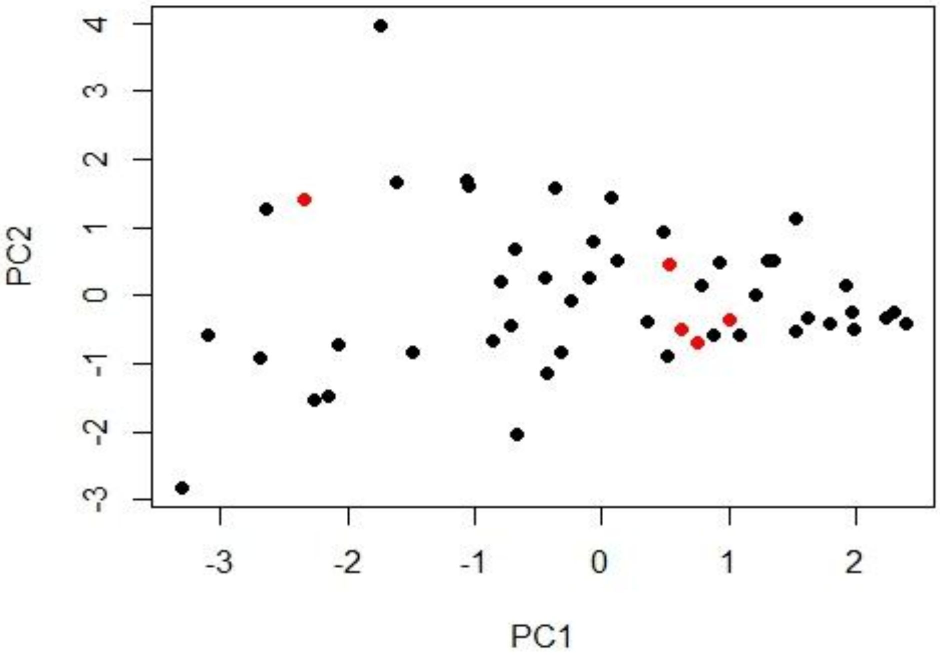

Figure A2: The distribution of transects (n=52) according to ground cover variables as they were accounted for by the first two Principal Components. Transects where Rudd’s lark was present are coloured red.

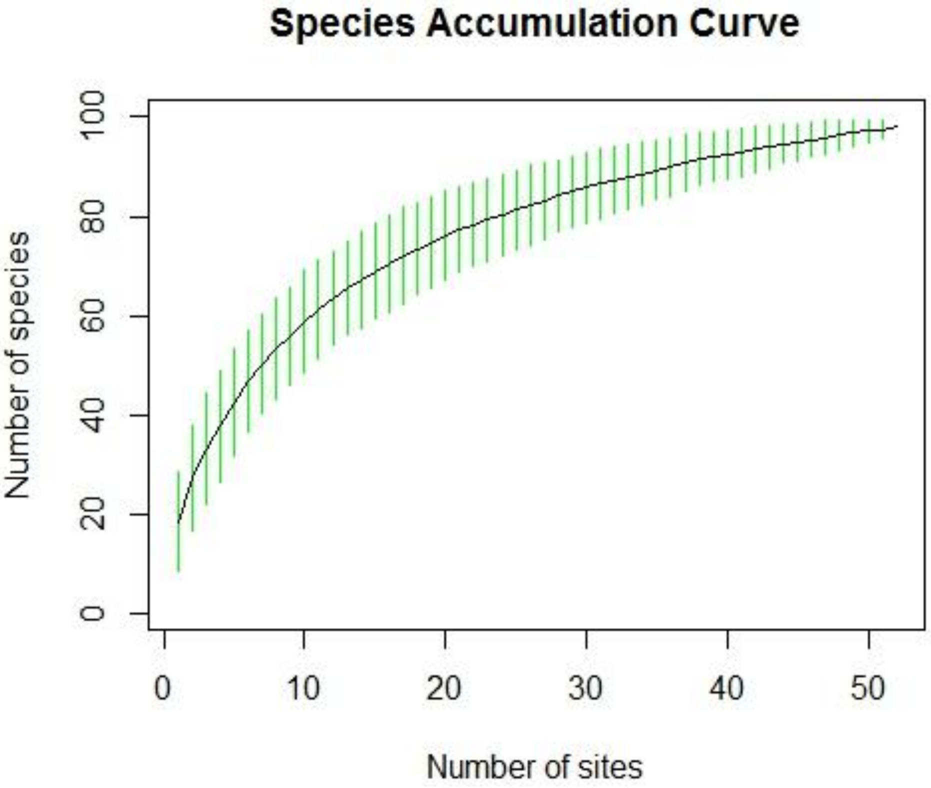

Figure A3: The species accumulation curve for all bird species detected along transects (n=52) in 2016 (n=52).

Table A1: Model selection analysis relating Rudd's Lark presence and absence with environmental variables along transects (n=52). The models were generalized mixed effects models assuming a binomial response and logit link function. Transect ID was treated as a random effect in all models. The five best models are presented here, though none improved on the null model.

Models	Log likelihood	Delta AIC	Akaike weight
Null	-21.376	0.00	0.191
Average grass height	-21.149	1.70	0.081
Altitude	-21.259	1.92	0.073
PC2	-21.376	2.16	0.065
PC1	-21.376	2.16	0.065
Altitude + Average grass height	-21.077	3.78	0.029

Table A2: Model selection analysis relating Rudd's Lark presence and absence with environmental variables at the 100 m scale (17 Rudd's Lark territories compared to 356 random samples along transects. The models were generalized mixed effects models assuming a binomial response and logit link function. Transect ID was treated as a random effect in all models. The five best models are presented here, though none improved on the null model.

Models	Log likelihood	Delta AIC	Akaike weight
Null	-26.992	0.00	0.141
PC2	-26.929	1.91	0.054
Average grass height	-26.987	2.02	0.051
PC1	-26.988	2.02	0.051
Altitude	-23.578	3.45	0.025
Altitude + PC2	-26.752	3.60	0.023

Table A3: Model selection analysis comparing ground cover variables along transects between 2002 and 2016. The models were generalized mixed effects models assuming a binomial response (using a weights function) and logit link function. Transect ID was treated as a random effect in all models. All models that improved on the null are presented. Daggers † denote the best models that were used in model averaging process.

Models	**Log likelihood**	**Delta AIC**	**Akaike weight**
Grass Cover			
Year + Fire†	-374.30	0.0	0.38
Fire†	-375.71	0.55	0.29
Fire + Grazing	-374.53	2.80	0.09
Null	-377.94	2.81	0.09
Average Grass Height			
Fire + Grazing†	-136.36	0.00	0.48
Year + Fire + Grazing†	-136.01	1.81	0.19
Fire	-140.05	2.62	0.13
Grazing	-139.58	4.01	0.06
Year + Fire	-138.70	4.68	0.06
Year + Grazing	-143.17	6.58	0.05
Null	-140.05	2.62	0.02
Forb Cover			
Year†	-205.06	0.00	0.47
Year + Grazing†	-203.28	1.05	0.28
Year + Fire	-205.02	2.19	0.16
Year + Fire + Grazing	-203.12	3.16	0.10
Fire	-210.81	11.49	0.00
Null	-212.59	12.86	0.00
Dead Vegetation Cover			
Year + Grazing†	-249.72	0.00	0.39
Year†	-252.13	0.19	0.36
Year + Fire + Grazing	-249.69	2.36	0.12
Year + Fire	-252.08	2.37	0.12
Fire	-256.52	8.98	0.00
Null	-259.07	11.88	0.00

Table A4: Model selection analysis comparing Rudd's Lark territories in 2002 (n=17) and 2016 (n=81) in terms of environmental variables. The models were generalized linear models assuming a binomial response and logit link function. All models that improved on the null are presented. Dagger † denotes the best model.

Models	**Log likelihood**	**Delta AIC**	**Akaike weight**
Average grass height + PC1 + PC2†	-8.851	0.00	0.743
Altitude + Average grass height + PC1 + PC2	-8.851	2.22	0.245
PC1 + PC2	-14.480	9.08	0.008
Altitude + PC1 + PC2	-14.467	11.23	0.003
Average grass height + PC1	-16.632	13.39	0.001
Altitude + Average grass height + PC1	-16.623	15.54	0.000
PC1	-30.908	39.81	0.000
Altitude + PC1	-30.855	41.83	0.000
Average grass height + PC2	-34.864	49.85	0.000
Altitude + Average grass height + PC2	-34.825	51.95	0.000
PC2	-37.622	53.24	0.000
Altitude + PC2	-37.590	55.30	0.000
Null	-45.212	66.33	0.000

Table A5: Model selection analysis relating bird species diversity with environmental variables along transects (n = 52), including 28 repeated transects. The models were generalized mixed effects models assuming a poisson response and log link function. Transect ID was treated as a random effect in all models. The eleven best models and the null model are presented. Daggers † denote the four best models that were used in model averaging.

Models	Log likelihood	Delta AIC	Akaike weight
Average grass height + PC2†	-235.885	0.00	0.209
Altitude + Average grass height + PC2†	-234.906	0.32	0.178
PC2†	-237.583	1.18	0.116
Altitude + Average grass height + PC1 + PC2†	-234.518	1.88	0.082
Average grass height + PC1 + PC2	-235.764	2.03	0.076
Altitude + PC2	-236.980	2.19	0.070
PC1 + PC2	-236.989	2.21	0.069
Altitude + PC1 + PC2	-235.894	2.29	0.066
Average grass height	-238.380	2.77	0.052
Altitude + Average grass height	-238.072	4.37	0.024
Average grass height + PC1	-238.337	4.90	0.018
Null	-240.768	5.39	0.014

Table A6: Model selection analysis relating the presence and absence of other grassland endemic birds with environmental variables along transects (n = 52) including 28 repeated transects. The models were generalized mixed effects models assuming a binomial response and logit link function. Transect ID was treated as a random effect in all models. For Botha's Lark, Black-winged Lapwing and Southern Bald Ibis, the five best models are presented though none improved on the null model. For Yellow-breasted Pipit, the two models that improved on the null model are presented. Daggers † denote the best models that were used in model averaging.

Models	Log likelihood	Delta AIC	Akaike weight
Botha's Lark			
Null	-6.287	0.00	0.327
PC1	-6.268	2.22	0.108
PC2	-6.268	2.22	0.108
Average Grass Height	-6.28	2.24	0.106
Altitude	-6.284	2.25	0.106
PC1 + PC2	-6.234	4.50	0.034
Black-winged Lapwing			
Null	-9.345	0.00	0.274
PC2	-9.248	2.06	0.098
PC1	-9.328	2.22	0.090
Altitude	-9.341	2.25	0.089
PC1 + PC2	-9.239	4.39	0.031
Average Grass Height + PC2	-9.243	4.40	0.030
Southern Bald Ibis			
Null	-9.345	0.00	0.327
PC2	-9.271	2.11	0.136
Altitude	-9.345	2.25	0.126
PC1 + PC2	-9.267	4.45	0.042
Altitude + PC2	-9.271	4.46	0.042
Altitude + PC1 + PC2	-9.266	6.90	0.012
Yellow-breasted Pipit			
Altitude + Average Grass Height†	-249.72	0.00	0.39
Altitude + Average Grass Height + PC2†	-252.13	0.19	0.36
Null	-249.69	2.36	0.12

Table A7: The complete list of birds seen on transects in Wakkerstroom between 20 November and 17 December 2016

Common Name	Scientific Name	Prevalence (% of transects)	Rank
African pipit	*Anthus cinnamomeus*	100.00	1
Wing-snapping cisticola	*Cisticola ayresii*	94.23	2
Cape longclaw	*Macronyx capensis*	86.54	3
Banded martin	*Riparia cincta*	78.85	4
Red-capped lark	*Calandrella cinerea*	75.00	5
Long-tailed widowbird	*Euplectes progne*	73.08	6
Southern ant-eating chat	*Myrmecocichla formicivora*	71.15	7
Southern red bishop	*Euplectes orix*	67.31	8
Barn swallow	*Hirundo rustica*	63.46	9
Spike-heeled lark	*Chersomanes albofasciata*	55.77	10
Pale-crowned cisticola	*Cisticola cinnamomeus*	50.00	11
Yellow-crowned bishop	*Euplectes afer*	48.08	12
Greater-striped swallow	*Hirundo cucullata*	38.46	13
Yellow-breasted Pipit	*Anthus chloris*	34.62	14
Cape canary	*Serinus canicollis*	32.69	15
African quailfinch	*Ortygospiza atricollis*	26.92	16
Cape wagtail	*Motacilla capensis*	26.92	16
Common quail	*Coturnix coturnix*	26.92	16
Zitting cisticola	*Cisticola juncidis*	26.92	16
Blue crane	*Anthropoides paradiseus*	25.00	20
South African cliff-swallow	*Hirundo spilodera*	25.00	20
Crowned lapwing	*Vanellus coronatus*	23.08	22
Eastern long-billed lark	*Certhilauda semitorquata*	23.08	22
Southern masked weaver	*Ploceus velatus*	21.15	24
Egyptian goose	*Alopochen aegyptica*	19.23	25
White-rumped swift	*Apus caffer*	19.23	25
Pied starling	*Lamprotornis bicolor*	17.31	27
Cape weaver	*Ploceus capensis*	15.38	28
Eastern clapper lark	*Mirafra fasciolata*	15.38	28
African stonechat	*Saxicola torquatus*	13.46	30
Cape crow	*Corvus capensis*	13.46	30
Hadeda ibis	*Bostrychia hagedash*	13.46	30
Pink-billed lark	*Spizocorys conirostris*	13.46	30
Pin-tailed whydah	*Vidua macroura*	13.46	30
Yellow-billed duck	*Anas undulata*	13.46	30
Blue korhaan	*Eupodotis caerulescens*	11.54	36
Grey-crowned crane	*Balearica regulorum*	11.54	36
Southern Bald Ibis	*Geronticus calvus*	11.54	36
Spur-winged goose	*Plectropterus gambensis*	11.54	36

Black-headed heron	*Ardea melanocephala*	9.62	40
Bokmakierie	*Telophorus zeylonus*	9.62	40
Southern fiscal	*Lanius collaris*	9.62	40
Fan-tailed widowbird	*Euplectes axillaris*	9.62	40
Malachite sunbird	*Nectarinia famosa*	9.62	40
Rudd’s lark	*Heteromirafra ruddi*	9.62	40
White-throated swallow	*Hirundo albigularis*	9.62	40
Black-winged Lapwing	*Vanellus melanopterus*	7.69	47
Botha’s Lark	*Spizocorys fringillaris*	7.69	47
Cape sparrow	*Passer melanurus*	7.69	47
Cape turtle dove	*Streptopelia capicola*	7.69	47
Helmeted guineafowl	*Numida meleagris*	7.69	47
Speckled pigeon	*Columba guinea*	7.69	47
Wattled lapwing	*Vanellus senegallus*	7.69	47
White-bellied korhaan	*Eupodotis senegalensis*	7.69	47
African spoonbill	*Platalea alba*	5.77	55
Black-throated canary	*Serinus atrogularis*	5.77	55
Cloud cisticola	*Cisticola textrix*	5.77	55
Denham's bustard	*Neotis denhami*	5.77	55
Grey-winged francolin	*Scleroptila africanus*	5.77	55
Lanner falcon	*Falco biarmicus*	5.77	55
Red-winged francolin	*Scleroptila levaillantii*	5.77	55
Southern grey-headed sparrow	*Passer diffusus*	5.77	55
Steppe Buzzard	*Buteo buteo*	5.77	55
Black sparrowhawk	*Accipiter melanoleucus*	3.85	55
Cape Robin-chat	*Cossypha caffra*	3.85	55
Dark-capped bulbul	*Pycnonotus barbatus*	3.85	55
Diederik cuckoo	*Chrysococcyx caprius*	3.85	55
Levaillant's cisticola	*Cisticola tinniens*	3.85	55
Little swift	*Apus affinis*	3.85	55
Marsh owl	*Asio capensis*	3.85	55
Mountain wheatear	*Oenanthe monticola*	3.85	55
Sacred ibis	*Threskiornis aethiopicus*	3.85	55
South African shelduck	*Tadorna cana*	3.85	55
Spotted thick-knee	*Burhinus capensis*	3.85	55
Whiskered tern	*Chlidonias hybrida*	3.85	55
African snipe	*Gallinago nigripennis*	1.92	76
Amur falcon	*Falco amurensis*	1.92	76
Brown-throated martin	*Riparia paludicola*	1.92	76
Cape rock-thrush	*Monticola rupestris*	1.92	76
Cattle egret	*Bubulcus ibis*	1.92	76
Drakensberg prinia	*Prinia hypoxantha*	1.92	76

Ground woodpecker	*Geocolaptes olivaceus*	1.92	76
Hamerkop	*Scopus umbretta*	1.92	76
House sparrow	*Passer domesticus*	1.92	76
Long-billed pipit	*Anthus similis*	1.92	76
Marsh harrier	*Circus ranivorus*	1.92	76
Red-billed quelea	*Quelea quelea*	1.92	76
Red-collared widowbird	*Euplectes ardens*	1.92	76
Reed cormorant	*Microcarbo africanus*	1.92	76
Rock dove	*Columba livia*	1.92	76
Rufous-chested sparrowhawk	*Accipiter rufiventris*	1.92	76
Sentinel rock-thrush	*Monticola explorator*	1.92	76
Swainson's spurfowl	*Pternistis swainsonii*	1.92	76
Three-banded plover	*Charadrius tricollaris*	1.92	76
Wailing cisticola	*Cisticola lais*	1.92	76
White stork	*Ciconia ciconia*	1.92	76

Table A8: The six land-cover classes that were used in my analysis of land cover in the Wakkerstroom area, generated from multi-seasonal Landsat 8 imagery.

Parent	Class	Description	
GRASSLAND	Grassland	Natural / semi-natural grass dominated areas, where typically the tree and / or bush canopy densities are typically < ± 20 %, but may include localized denser areas up to ± 40 %, (regardless of canopy heights). Includes open grassland, and sparse bushland and woodland areas, including transitional wooded grasslands. May include planted pasture (i.e. grazing) if not irrigated. Irrigated pastures will typically be classified as cultivated, and urban parks and golf courses etc under urban.	
CULTIVATED	Commercial Annuals (rain-fed crops)	Cultivated lands used primarily for the production of rain-fed, annual crops for commercial markets. Typically represented by large field units, often in dense local or regional clusters. In most cases the defined cultivated extent represents the actual cultivated or potentially extent. NDVI-modelled sub-divisions, based on seasonal NDVI maximum and standard deviation ranges, which can be used a qualitative indications levels of cultivation activity, crop rotations and / or productivity, with "low" representing areas of low maximum biomass growth and least seasonal variation; and "high" representing areas of high maximum biomass growth and greatest seasonal variation.	NDVI profile High
			NDVI profile Med
			NDVI profile Low
	Commercial Pivot (High intensity irrigated crops)	Cultivated lands used primarily for the production of centre pivot irrigated, annual crops for commercial markets. . In most cases the defined cultivated extent represents the actual cultivated or potentially extent. NDVI-modelled sub-divisions, based on seasonal NDVI maximum and standard deviation ranges, which can be used a qualitative indications levels of cultivation activity, crop rotations and / or productivity, with "low" representing areas of low maximum biomass growth and least seasonal variation; and "high" representing areas of high maximum biomass growth and greatest seasonal variation.	NDVI profile High
			NDVI profile Med
			NDVI profile Low
	Commercial Permanent (Orchards)	Cultivated lands used primarily for the production of both rain-fed and irrigated permanent crops for commercial markets. Includes both tree, shrub and non-woody crops, such as citrus, tea, coffee, grapes, lavender and pineapples etc. In most cases the defined cultivated extent represents the actual cultivated or potentially extent. NDVI-modelled sub-divisions, based on seasonal NDVI maximum and standard deviation ranges, which can be used a qualitative indications levels of cultivation activity, crop rotations and / or productivity, with "low" representing areas of low maximum biomass growth and least seasonal variation; and "high"	NDVI profile High
			NDVI profile Med
			NDVI profile Low

		representing areas of high maximum biomass growth and greatest seasonal variation.	
FOREST PLANTATION	Forest Plantations: Mature Trees	Planted forestry plantations used for growing commercial timber tree species. The class represents mature tree stands which have approximately 70% or greater tree canopy closure (regardless of canopy height), on all the multi-date Landsat images in the 2013-14 analysis period. The class includes spatially smaller woodlots and windbreaks with the same cover characteristics.	
	Forest Plantations: Young Trees	Planted forestry plantations used for growing commercial timber tree species. The class represents young tree stands which have approximately 40 - 70% tree canopy closure (regardless of canopy height), on all the multi-date Landsat images in the 2013-14 analysis period. The class includes spatially smaller woodlots and windbreaks with the same cover characteristics. Note that young saplings are very difficult to identify on 30 metre resolution Landsat imagery if the actual tree canopy cover density is below ± 30 - 40%, because the background cover, for example, grassland, then dominates the spectral characteristics in that pixel area.	
BUILT-UP	Informal	Areas containing high density buildings and other built-up structures typically associated with informal, often non-regulated, residential housing. Note that in some areas this class may include new formal developments within township areas that appear on Landsat imagery as primarily non-vegetated areas with limited infrastructure development.	

Appendix B

Burning practices and awareness of Rudd's Lark in the Wakkerstroom area

Please make sure respondent has read and signed a copy of the informed consent form before continuing.

Interview number:

1. In what year did you begin farming? (on this farm)

2. What is your position on the farm? (e.g. manager, owner, etc.) Do you farm with anyone else, such as a partner or family member?

3. When were you born?

4. How big is your farm? (Hectares)

5. Please give a breakdown of what you farm. What is the land cover of each type of land use? (E.g. 1000 ha cattle, 2000 ha sheep, 500 ha wheat, 100 ha natural)

Crop type/land use	**Hectares**

6. Have you changed any of your primary land uses since 2003? If so, why?

7. Do you think the weather pattern has changed in the last decade? How has it changed? (e.g. less rainfall, higher summer temperatures)

8. Have you had contact with conservation or stewardship programs in the area?
   a) No
   b) Yes (please elaborate)

9. Are you formally involved in a conservation or stewardship program?
   a) No
   b) Yes (please specify)

Rudd's Lark

10. Are you aware of a species of bird called Rudd's Lark? (please circle the appropriate answer)
    a) Yes
    b) No

    If yes:

    i) Have you seen Rudd's Lark on your farm?
       a) Never

    b) Rarely
    c) Sometimes
    d) Often
    e) I don’t know

ii) Have you noticed a change in the population of Rudd’s Lark on your farm? (Do you see it more or less often than in the past?)

    a) Yes, it has increased
    b) Yes, it has decreased
    c) No, it has stayed the same
    d) I don’t know

iii) Are you interested in the conservation of this bird?

    a) Yes
    b) No

11. Have you previously been contacted about the conservation of this species? If so, what was the outcome?

____

____

____

12. Are you aware of any other rare or interesting birds that live on your farm?

____

____

____

Fire

13. How often do you burn each camp on your farm?

    a) More than twice a year
    b) Twice a year
    c) Once a year

d) Once every two years
e) Less than once every two years
f) Never

14. Please explain the reason for your answer above

15. In which month or months of the year do you typically burn?

16. How much variation is there in the timing of each burn? That is, do you burn at exactly the same time each year or can it be different according to the veld?
a) None
b) 1 week
c) 2 weeks
d) 1 month
e) More than 1 month

17. What are the main reasons for burning? (please rank their importance in the block provided. E.g. if you choose three, then the most important = 1 and the least important = 3)

☐ To take advantage of good rainfall
☐ To reduce tick abundance
☐ To prevent a buildup of moribund/unpalatable grass
☐ To improve grass condition
☐ To take advantage of conditions that are not likely to cause runaway fires
Other (please specify)

Additional Comments

~

Thank you for your time!

For further information please contact:
Wesley Gush (research student): wesgush@gmail.com