The influence of agricultural transformation on the breeding performance of a top predator: Verreaux's Eagles in contrasting land use areas

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RESEARCH ARTICLE

The influence of agricultural transformation on the breeding performance of a top predator: Verreaux's Eagles in contrasting land use areas

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ABSTRACT
Breeding productivity frequently shows variation across a species' range or locally between different habitat types. Agricultural transformation generally has negative effects on biodiversity and often results in reduced prey abundance or increased foraging effort in top predators and, consequently, often reduces breeding productivity. Major factors that affect reproductive success also include climatic variables, breeding density, and timing of breeding. We explored the influence of agricultural transformation on a specialist raptor, Verreaux's Eagle (*Aquila verreauxii*). From 2011 to 2014, we examined productivity in 2 adjacent populations in the Western Cape Province, South Africa: an unspoiled area of Fynbos vegetation with little human development (the Cederberg Mountains) and an agriculturally transformed area (the Sandveld region). Counterintuitively, breeding productivity was higher in the agricultural than in the natural site. In particular, the proportion of pairs that attempted to breed (i.e. breeding rate) was higher in the Sandveld (0.94 ± 0.07 attempts pair^{-1} yr^{-1}) than in the Cederberg (0.48 ± 0.14 attempts pair^{-1} yr^{-1}). Nesting success was also higher in the Sandveld (0.80 ± 0.05 fledged young attempt^{-1} yr^{-1}) than in the Cederberg (0.57 ± 0.13 fledged young attempt^{-1} yr^{-1}), and the probability of nesting successfully was related to the lay date (decreased success with later laying) and to the total cumulative rainfall up to 28 days after hatching (decreased success with increasing rainfall). Using the site-specific breeding rates to produce a population model, we found that in isolation, the Cederberg population is unlikely to be self-sustaining, but Verreaux's Eagles breeding in the agriculturally developed Sandveld region are likely to be an important source population, despite occurring at a much lower density. These results, contrary to our expectations, suggest that Verreaux's Eagle may be more adaptable to agricultural transformation than previously thought, with breeding performance in the agricultural site adequate to maintain the population.

Keywords: agriculture, breeding productivity, land use, PVA, raptor

Influencia de la transformación agrícola en el desempeño reproductivo de un depredador tope: *Aquila verreauxii* en áreas contrastantes de uso del paisaje

RESUMEN
La productividad reproductiva frecuentemente varía a lo largo del rango de una especie o localmente entre diferentes tipos de hábitat. La transformación agrícola generalmente tiene efectos negativos en la biodiversidad y usualmente produce una reducción en la abundancia de presas o un aumento en el esfuerzo de forrajeo de los depredadores tope, y consecuentemente usualmente reduce la productividad reproductiva. Los principales factores que afectan el éxito reproductivo también incluyen variables climáticas, la densidad de crías y la sincronización de la reproducción. En este estudio analizamos la influencia de la transformación agrícola sobre una rapaz especialista, *Aquila verreauxii*. Examinamos la productividad en dos poblaciones adyacentes, un área prístina de vegetación de Fynbos con poco desarrollo humano (las Montañas Cederberg) y un área agrícola transformada (la región Sandveld), en la Provincia Cabo Oeste, Sud África, desde 2011 a 2014. De modo contra intuitivo, la productividad reproductiva fue más alta en el sitio agrícola que en el sitio natural. En particular, la proporción de parejas con intentos reproductivos (tasa reproductiva) fue mayor en Sandveld (0.94 ± 0.07 intentos/pareja/año) que en Cederberg (0.48 ± 0.14 intentos/pareja/año). El éxito de anidación fue también más alto en Sandveld (0.80 ± 0.05 jóvenes emplumados/intento/año) que en Cederberg (0.57 ± 0.13 jóvenes emplumados/intento/año) y la probabilidad de anidar exitosamente estuvo relacionada con la fecha de puesta (disminuyendo el éxito con una fecha más tardía de puesta) y con la precipitación acumulada total hasta 28 días luego de la eclosión (disminuyendo el éxito con un incremento en la precipitación). Usando las tasas reproductivas específicas para cada sitio para producir un modelo poblacional, encontramos que es improbable que la población de Cederberg sea auto suficiente en un estado de aislamiento, mientras que es probable que los individuos que se reproducen en la región Sandveld, que se encuentra desarrollada agrícolamente, sean una fuente poblacional importante, a pesar de presentarse a una densidad mucho menor. Nuestros resultados sugieren,
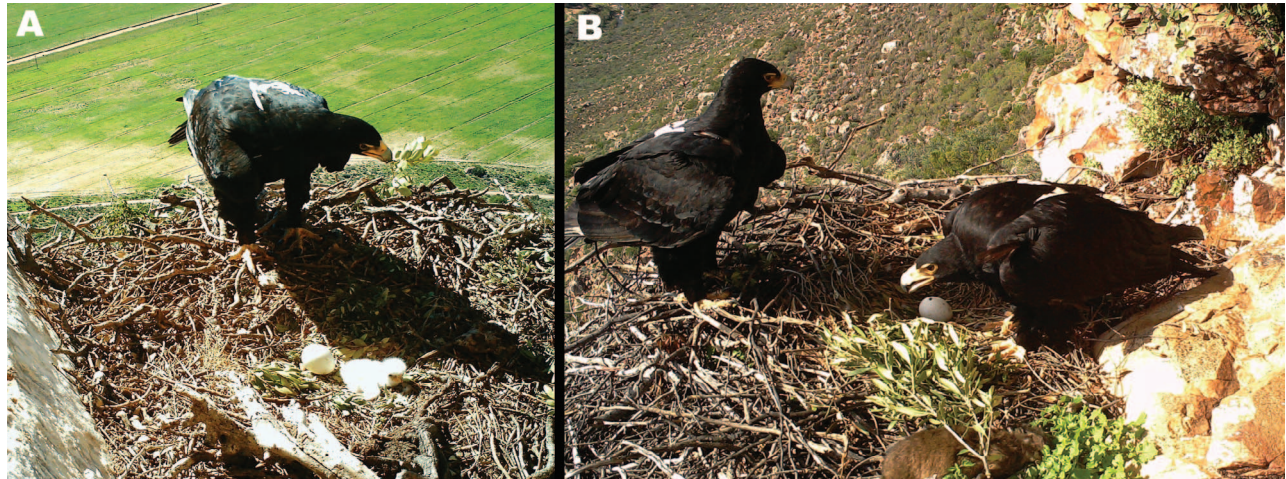
FIGURE 1. Typical active Verreaux's Eagle nests in (**A**) the agriculturally developed Sandveld region and (**B**) the Cederberg Mountains, South Africa.

contrariamente con nuestras expectativas, que los individuos de *A. verreauxii* pueden ser más adaptables a la transformación agrícola de lo que se pensó previamente, con un desempeño reproductivo en el sitio agrícola adecuado para mantener a la población.

Palabras clave: agricultura, AVP, productividad reproductiva, rapaz, uso del suelo

INTRODUCTION

Transformation of land for agriculture is a key driver of biodiversity loss (Haines-Young 2009). However, the effects of agriculture on biodiversity depend largely on the intensity of land use (Reidsma et al. 2006) and the ability of a species to adapt to changes in resource availability (Butet et al. 2010). A well-documented example of the negative effects of agriculture on biodiversity has been the collapse of farmland bird populations in Europe during the late 20th century, a period characterized by agricultural intensification (Fuller et al. 1995, Donald et al. 2001). However, some species apparently benefit from cultivated landscapes, often associated with the provision of food or breeding resources in areas where they were previously scarce or unavailable (Wolff et al. 2001, Moreno-Mateos et al. 2009, Cardador et al. 2011).

Raptors are considered good indicators of ecosystem health because of their position as apex predators and their sensitivity to a changing environment (Sergio et al. 2006). Agricultural transformation can degrade or destroy preferred habitats and deplete prey resources (Donázar et al. 1993, Amar and Redpath 2005, Jenkins et al. 2013), resulting in decreased breeding productivity (Arroyo et al. 2002), reduced offspring condition (Almasi et al. 2015), or delayed egg laying (Costantini et al. 2014). Breeding performance can be further influenced by climatic variables. In a study of Mauritius Kestrels (*Falco punctatus*), agricultural transformation exacerbated negative impacts of high rainfall on nesting success by reducing the availability of native prey species around nest sites (Cartwright et al. 2014). However, for some raptorial species, there is evidence that agricultural land use can increase breeding performance, perhaps linked to increases in prey availability or the abundance of suitable nesting areas (Coates et al. 2014). Cultivation of oilseed rape (*Brassica napus*) has been positively correlated with vole abundance and with breeding productivity of Common Buzzards (*Buteo buteo*; Panek and Hušek 2014). In Western Marsh-Harriers (*Circus aeruginosus*), increases in breeding productivity, egg size (Sternalski et al. 2013), and nest-site occupancy (Cardador et al. 2011) have been correlated with increased agricultural land use.

Verreaux's Eagle (*Aquila verreauxii*) is a long-lived raptor that reproduces slowly, producing a maximum of 1 young yr^{-1} (Gargett 1990; Figure 1). Verreaux's Eagle is generally considered a specialist predator, with a single prey type (hyraxes: *Procavia* and *Heterohyrax* spp.) comprising 88–98% of their diet in most studies (Gargett 1977, Tarboton and Allan 1984, Davies 1994), although this varies between biomes (Boshoff et al. 1991). Breeding productivity has been monitored in several regions of the southern African range of Verreaux's Eagle (Tarboton and Allan 1984, Allan 1988, Gargett 1990, Davies 1994); however, factors affecting productivity have rarely been investigated (but see Gargett 1990, Gargett et al. 1995). Gargett et al. (1995) found an inverse relationship between Verreaux's Eagle reproductive performance and the

FIGURE 2. Map of southern Africa, showing locations of the study sites for this study (Cederberg and Sandveld) and previous studies (Matopos: Gargett 1900; Magaliesberg: Allan 1988; Karoo National Park: Davies 1994).

volume of rainfall in the preceding summer. However, their results may have been distorted by interference from egg collectors, and this pattern broke down following severe drought. It was speculated that low rainfall reduces vegetation cover, thereby increasing hyrax vulnerability and accessibility to Verreaux's Eagles, whereas prolonged drought may cause prey population crashes (Gargett et al. 1995).

In light of declines in the population of Verreaux's Eagles indicated by the Southern African Bird Atlas Projects (Loftie-Eaton 2014) and the recent up-listing of the conservation status to "vulnerable" in southern Africa (Taylor 2015), the present study aimed to evaluate the productivity of 2 adjacent populations (~20 km) nesting in contrasting habitats in the Western Cape, South Africa. The first population is located in a predominantly natural habitat, the Cederberg Mountains. The second population breeds in the nearby Sandveld, which has been heavily transformed for agriculture. Both of these sites are in the relatively moist Fynbos biome (Rutherford et al. 2006), where rain falls predominantly in the winter months (May–September), coinciding with laying, incubation, and much of the nestling stage. By contrast, previous studies of Verreaux's Eagles in southern Africa (Allan 1988, Gargett 1990, Davies 1994) have been conducted in summer rainfall regions (October–March) outside of the most sensitive breeding period; therefore, effects of rainfall on nesting success are expected to be more pronounced in the present study.

Comparative studies of subpopulations in contrasting environments can be useful in exploring the relative ecological importance of distinct populations (Pulliam 1988, Pulliam and Danielson 1991, Boal and Mannan 1999, Amar et al. 2003). To assess whether agriculture negatively affects Verreaux's Eagle demographics, we tested the hypothesis that productivity is lower in the Sandveld than in the Cederberg. We also compared our productivity measures to those of previous studies in southern Africa. We tested the effects of weather on breeding performance; increased rainfall during the nestling stage was expected to have a negative impact on nesting success. Finally, we used our demographic data from both sites to construct a simple population model of the long-term population viability of these 2 populations, assuming both open- and closed-population scenarios.

METHODS

Study Site
The 2,570 km^2 Sandveld study site (Figure 2) stretches from the coast of the Western Cape Province, South Africa, inland through agricultural plains and hills (0–1,078 m a.s.l.). There is little formal conservation in the Sandveld, and extensive agricultural conversion since the 1980s has transformed this region into an important area for the production of potatoes (Heydenrych 1993, Low et al. 2004, Franke et al. 2011). There is an average density of 1.2 pairs of Verreaux's Eagles per 100 km^2 ($n = 30$), generally

clustered around the available cliff habitat (M. Murgatroyd personal observation).

The Cederberg Mountains are located to the east of the Sandveld region (Figure 2). Covering 1,178 km^2 (altitude range: 200–2,027 m a.s.l.), this study site is dominated by natural Fynbos vegetation and is largely protected by provincial conservation authorities (Maree and Vromans 2010). There are a similar number of Verreaux's Eagles breeding here ($n = 42$) as in the Sandveld, but they occur at nearly 3× the density (3.0 pairs per 100 km^2; M. Murgatroyd personal observation).

Study Species and Breeding Terminology

Despite usually laying 2 eggs (Gargett 1990), Verreaux's Eagles almost invariably rear a single young per successful breeding attempt. Obligate siblicide occurs if both eggs hatch successfully (Rowe 1947, Gargett 1978, 1990, Steyn 1982). Consequently, breeding productivity is directly determined by the breeding rate and by whether or not a nesting attempt produces a fledgling; variation in brood size is irrelevant. The terminology we use is as follows: breeding rate is the proportion of monitored occupied nests that make a breeding attempt, nesting success is the proportion of breeding attempts that successfully rear a nestling, and breeding productivity is the proportion of monitored pairs that successfully rear a nestling (Steenhof and Newton 2007, Virani and Harper 2009).

Surveys and Monitoring

Nests were monitored in 4 breeding seasons (2011–2014). Good prior knowledge of nest locations was available in the Sandveld, supplemented through additional ground surveys. Knowledge of nest locations in the Cederberg was relatively limited, and nests were located through ground surveys beginning in March 2011, prior to the first breeding season.

Helicopter surveys were carried out in 2012 and 2013, at the end of the breeding season. The interior of the Cederberg and the peripheries of both study sites were covered by aerial surveys along cliffs to ensure good coverage of nest locations in less accessible areas. These peripheral nests were not monitored for breeding productivity, but this information was important for accurately determining nest proximities (see below). GPS locations and photographs were taken of all nests. A nest was considered occupied if Verreaux's Eagles were seen close to it (<200 m; $n = 11$), if there was a nestling on it ($n = 1$), if there was greenery on it ($n = 1$), if there was bright white wash on the cliff wall or a flattened nest platform indicative of a recent breeding attempt ($n = 8$), or if occupation was confirmed postsurvey ($n = 6$).

We observed nest sites from a distance of 0.5–1.5 km, approximately every 2–3 wk through the breeding season (late May to early November). Observations lasted for a target of 3 hr, although the length varied according to the stage of breeding and the ease of identification of breeding behaviors. Pairs were considered not to have initiated breeding if they were not sighted during observations lasting ≥3 hr or if they were sighted but left the nest unattended regularly or for extended periods. Incubation was assumed when individuals appeared to be sitting (rather than standing) in a nest for the majority of an observation and not leaving the nest unattended for more than ∼15 min. Occasionally ($n = 6$) this was verified by observations of the nest contents. Hatching was assumed when an adult was observed feeding a nestling or moving prey on the nest. Precise hatching dates were obtained at nests that had cameras installed ($n = 8$; Appendix Table 7). Successful breeding was determined by seeing the fledged young close to the nest or a fully feathered nestling on the nest.

Because monitoring of some pairs commenced later in the season, deriving nesting success using these nests could bias our results, owing to potential failure prior to the first visit (Steenhof and Kochert 1982). Therefore, nests that were found with a nestling or that were monitored only after July ($n = 22$) were excluded from analyses. Our analyses were focused on (1) nests that were monitored from or prior to incubation and (2) nonbreeding pairs that were checked at least once in both June and July ($n = 112$).

Explanatory Variables

Lay date. The lay date was estimated to the nearest day by the following methods, listed in order of preference: (1) hatching dates obtained from nest cameras, minus the 44-day incubation period ($n = 8$; Steyn 1982, Gargett 1990); (2) the midpoint of visits <2 wk apart when incubation began between the visits ($n = 12$); (3) back-calculation from hatching dates estimated from observations of nestling size and feather development (Steyn 1982; $n = 31$); (4) a combination of methods 2 and 3 when nest monitoring occurred >14 days apart ($n = 14$); and (5) in cases of nest failure, the earliest possible lay date was assumed to be the last date the nest was recorded as incubating minus 44 days, and the lay date was estimated as the midpoint between the earliest possible lay date and the date incubation was actually first noted ($n = 2$). A small number of failed nests ($n = 6$) could not be assigned a lay date and were excluded from analyses that included this variable.

Nesting variables. The proximity index (PI), which is an index of the population density for each occupied nest, was calculated for each nest annually as the sum of reciprocals of the squared distance to all other occupied nests within 10 km (Amar and Redpath 2005, Arroyo et al. 2009). All nests known by the end of the surveys were included, except when new nests were detected in areas previously surveyed ($n = 1$) and when territory abandonment

occurred ($n = 1$). Nest aspect (nearest of the 4 cardinal directions) was considered to be proxy for nest exposure to prevailing weather conditions and was estimated from 1:50,000 topographical maps.

Weather. Weather data were obtained from the South African Weather Service stations located at Clanwilliam (for Cederberg) and Lambert's Bay (for Sandveld), both ~20 km from the study sites. To investigate the influence of weather on nesting success, we used weather variables around hatching and during the early nestling phase, when nestlings are most vulnerable to climatic extremes (Kostrzewa and Kostrzewa 1990). Hatch date was calculated from our lay date plus 44 days. The influence of weather was explored over 3 temporal scales: 7, 14, and 28 days, starting from 3 days before the hatch date (to account for inaccuracy in the date). During these periods, we calculated the following weather variables for each nest: the maximum number of consecutive days with rain (RainCon, days), the cumulative total rainfall (RainTot, mm), and the average temperature (TempAv, °C).

Statistical Analysis

Breeding rate. All statistical analyses were performed in R 3.1.2 (R Development Core Team 2015). The breeding rate was investigated using a generalized linear mixed effects model (GLMM) specifying a logit link function and binomial response (where $1 =$ a breeding attempt was made, $0 =$ no breeding attempt was made). We included 3 fixed effects: site (Cederberg or Sandveld), year, and PI. Territory was included as a random term to account for pseudoreplication. To explore the most important variables, we analyzed the data by model selection with Akaike's Information Criterion (AIC_c) using the "MuMIn" package (Barton 2014). Models were ranked according to their AIC_c values, and model averaging was performed across the top candidate models ($\Delta AIC_c < 2$). We could not perform a formal test of the effects of weather variables (rain and temperature) on breeding rate because of the lack of territory-specific data.

Nesting success. Nesting success was investigated using a generalized linear model (GLM) specifying a binomial distribution and logit link function, with the response variable being 1 or 0 for whether a pair was successful or not. The following covariates were included: study site, year, PI, nest aspect, lay date, and the 3 levels of RainCon[7, 14, 28], RainTot[7, 14, 28], and TempAv[7, 14, 28]. RainCon and RainTot variables were also entered with an interaction term as a proxy for the intensity of rain. All terms were entered into the GLM, and subsequently we performed model selection using AIC_c ranking methods, with the specification that weather variables from different temporal scales (7, 14, or 28 days) could not appear in the same model. Additionally, we analyzed interactions with

site between abiotic and climate variables (to look for site-dependent effects) in an ad hoc way, but none of the models provided any strong evidence for any such difference; therefore, no interactions with site were included in the analysis presented in the results.

Population viability analysis (PVA). Population viability was modeled using Vortex 10 (Lacy and Pollak 2014), a commonly used software for modeling population dynamics (e.g., Carrete et al. 2009, Jarić et al. 2010, García-Ripollés and López-López 2011). Models were parameterized using our site-specific breeding productivity data and population sizes, assuming stable age distribution. Starting population sizes included all known occupied nests used in calculating PIs plus 5% to account for the possibility of any missed territories. Carrying capacity was defined as the population size plus the few known vacant territories in both study sites. We used survival rates from Vernon's (1972) predictions of life expectancy and survival in a stable population of Verreaux's Eagles to create a baseline model (PVA Baseline). Additionally, we investigated the effects of a 10% increase (PVA+10) in mortality, simulating a plausible low-intensity anthropogenic effect such as the construction and operation of a wind farm nearby (García-Ripollés and López-López 2011), and a comparable 10% decrease (PVA−10) in mortality, to investigate potential population growth around upper and lower bounds of biologically plausible ranges of mortality. Natal dispersal has rarely been investigated in Verreaux's Eagles (but see Goodwin 2000). However, studies of dispersal and natal philopatry in similar-sized raptors have indicated the potential for juvenile dispersal between populations (González et al. 1989, Whitfield et al. 2009, Weston et al. 2013), whereas dispersal of breeding adults is expected to be rare (Newton 1979, Gargett 1990, Whitfield et al. 2009). Therefore, given our limited understanding of these movements, we ran all models assuming closed populations with no dispersal, allowing estimation of population-specific growth rates. We then specified 50% dispersal of subadult birds between the populations to examine the influence of differential productivity on the overall metapopulation in the region, given the potential for juvenile dispersal. The predicted population growth rates are derived from 1,000 iterations over 50 yr for each model (Appendix Table 8).

RESULTS

In 112 occupied breeding years monitored from 2011 to 2014, annual productivity was 0.52 ± 0.27 young pair^{-1} yr^{-1} (Table 1). However, all measures of breeding performance were greater in the Sandveld than in the Cederberg. The breeding rate in the Sandveld was double that in the Cederberg, and nesting success was 1.4× higher in the Sandveld than in the Cederberg. This was followed

TABLE 1. Summary of Verreaux's Eagle pairs monitored and breeding parameters recorded in each area in each year of the study.

	Cederberg					Sandveld					All
	2011	2012	2013	2014	Total ± SD	2011	2012	2013	2014	Total ± SD	Total ± SD
Pairs	13	16	17	18	64	4	9	19	16	48	112
Attempts	8	9	5	8	30	4	9	16	15	44	74
Fledged young	6	4	3	4	17	3	7	13	13	36	53
Breeding rate	0.62	0.56	0.29	0.44	0.48 ± 0.14	1.00	1.00	0.84	0.94	0.94 ± 0.07	0.71 ± 0.27
Productivity	0.46	0.25	0.18	0.22	0.28 ± 0.13	0.75	0.78	0.68	0.81	0.76 ± 0.05	0.52 ± 0.27
Success	0.75	0.44	0.60	0.50	0.57 ± 0.13	0.75	0.78	0.81	0.87	0.80 ± 0.05	0.69 ± 0.15

by overall breeding productivity, which was 2.7× higher in the Sandveld than in the Cederberg.

Breeding Rate

The GLMM analysis of the breeding rate included 3 top candidate models with ΔAIC < 2 (Table 2). Following model averaging, the most important term (with a relative importance of 1.00) was "site" (Table 3), reflecting the consistently higher breeding rate in the Sandveld (0.94 ± 0.07) compared to the Cederberg (0.48 ± 0.14) (Table 1 and Figure 3). There was considerable year-to-year variation in breeding rate, with our "year" term having a high relative importance value (0.72). "PI" had a low relative importance value (0.21), and the confidence intervals for the parameter estimates overlapped zero, suggesting no support for strong density dependence in breeding rates.

Nesting Success

Lay date and RainTot28 featured in all top candidate models explaining nesting success (Table 4), and consequently both contributed the highest relative importance (1.00; Table 5) after model averaging. Nesting success decreased with later laying (Figure 4) and with increasing total rainfall up to 28 days after hatching (Figure 5). Nesting success was consistently higher in the Sandveld (0.80 ± 0.05) than in the Cederberg (0.57 ± 0.13); however, the relative importance of the term "site" (0.55; Table 5) was lower than that of lay date and RainTot28.

TABLE 2. Results from the top GLMMs (ΔAIC$_c$ < 2) comparing model fit for rate of breeding attempts in Verreaux's Eagles (n = 112 observations from 2011 to 2014). Model parameters: site (Cederberg or Sandveld), year (2011–2014), and PI (proximity index: a measure of the density of nests within 10 km).

Model	df	LogLik	AIC$_c$	ΔAIC$_c$	w_i	ER
Site+year	6	−52.35	117.50	0.00	0.50	–
Site	3	−56.22	118.70	1.17	0.28	1.79
Site+year+PI	7	−52.07	119.20	1.71	0.21	2.35

Notes: df = degrees of freedom, LogLik = log liklihood, ΔAIC$_c$ = change in AIC$_c$ in relation to the highest-ranked model, w_i = AIC$_c$ weight, and ER = evidence ratio.

Other terms that featured in our top candidate models had low relative importance values (PI: 0.24; Tempav28: 0.14; RainCon28: 0.11), and none of the weather variables at shorter temporal scales (up to 7 and 14 days) around the hatch date were featured in any of the models with ΔAIC < 2.

Comparison of Breeding Performance in Other Populations

All the breeding parameters in the Sandveld were greater than in any of the previous studies reported, making it the most productive area for Verreaux's Eagles currently known (Figure 6). By contrast, the Cederberg is considerably less productive than all other studied populations (Tarboton and Allan 1984, Allan 1988, Gargett 1990, Davies 1994). Between-site differences are more pronounced for breeding rate than for nesting success.

Population Viability

Stochastic growth rates (λ) indicated that as a closed population, in all survival scenarios, the Cederberg population would be unlikely to sustain itself (λ = 0.921–0.951). The Sandveld population was predicted to experience a positive growth rate in the PVA Baseline scenario (λ = 1.011), which increased further with a 10% decrease in mortality (λ = 1.029). However, even within the more productive Sandveld population, negative population growth was predicted when mortality was increased by 10% (λ = 0.990) (Table 6 and Figure 7).

In the open-population models, the PVA Baseline predicted a decrease across all populations (λ = 0.977), where negative growth rates in the Cederberg combined with dispersal between the populations resulted in a metapopulation decrease. This was exacerbated when mortality rates increased (λ = 0.956). Decreased mortality (PVA−10) stabilized the population growth rate in the Sandveld population (λ = 1.000) and slowed the decline in the Cederberg (λ = 0.992). However, because of dispersal between the populations, the overall metapopulation remained slightly in decline (λ = 0.996); but the probability of extinction within the tested time frame was eliminated in this scenario (Table 6 and Figure 7).

TABLE 3. Parameter estimates (β) from model averaging (with shrinkage) of the ranked models in Table 2 explaining the variation in breeding rate in Verreaux's Eagles. Parameters: site (Cederberg or Sandveld), year (2011–2014), and PI (proximity index: a measure of the density of nests within 10 km); RI = relative importance of the variable.

| | β | SE | Adjusted SE | z | P | Confidence intervals | | RI |
						2.5%	97.5%	
(Intercept)	0.38	0.77	0.78	0.49	0.63	−1.14	1.90	–
Site	3.52	1.00	1.01	3.48	0.00	1.54	5.51	1.00
Year 2012	−0.11	0.76	0.77	0.14	0.89	−1.91	1.62	0.72
Year 2013	−1.43	1.19	1.19	1.20	0.23	−3.81	−0.17	0.72
Year 2014	−0.70	0.86	0.87	0.81	0.42	−2.71	0.75	0.72
PI	0.22	0.83	0.84	0.27	0.79	−2.00	4.08	0.21

DISCUSSION

In direct contrast to our predictions, we found a consistently greater breeding performance of Verreaux's Eagles in the agriculturally transformed Sandveld area than in the relatively pristine Cederberg. Breeding parameters for these 2 sites also differed markedly from those in previous studies of this species. Despite the limitations of our study—sample size in some years of monitoring, and not knowing the productivity of the Sandveld prior to agricultural conversion—these results indicate that some raptors can achieve high breeding productivity in agricultural areas. Furthermore, in the scenario presented, this is sufficient to maintain population viability.

Site Effects

Differences in breeding performance between the sites were more prominent for the breeding rate than for nesting success, with less than half of the resident pairs making a breeding attempt annually in the Cederberg, but with >90% of pairs attempting to breed in the Sandveld. The greater breeding rates in the Sandveld than in the Cederberg could not be attributed to nesting densities or annual fluctuations. Nesting success was affected by rain and timing of laying, and it remained consistently greater

in the Sandveld than in the Cederberg. Rainfall during our study was greater in the Cederberg (213.8 ± 47.8 mm) than in the Sandveld (177.8 ± 51.0 mm), and this might be a mechanism for the observed differences between the sites. When compared with previous studies, the Sandveld is noted for being the most productive area for Verreaux's Eagles currently known, whereas the Cederberg is the least productive area. This demonstrates the potential value of some agriculturally transformed areas to breeding Verreaux's Eagles and suggests two questions: What is so good about the Sandveld, and what is so bad about the Cederberg?

Territory and individual adult quality are important in determining the probability of making a breeding attempt (Drent and Daan 1980, Sergio and Newton 2003), and this can be regulated by a balance between food availability and daily energy requirements (Widén 1994, Lõhmus and Väli 2004, Shepard et al. 2011). Consequently, it may be that in the Cederberg, either food availability is limited or the topography requires greater energy consumption for daily movements compared with the Sandveld, resulting in the substantially lower breeding rate. The opposite might be true in the Sandveld, where agricultural transformation may be responsible for providing greater diversity or availability of prey (Ogada and Kibuthu 2009, Kross et al.
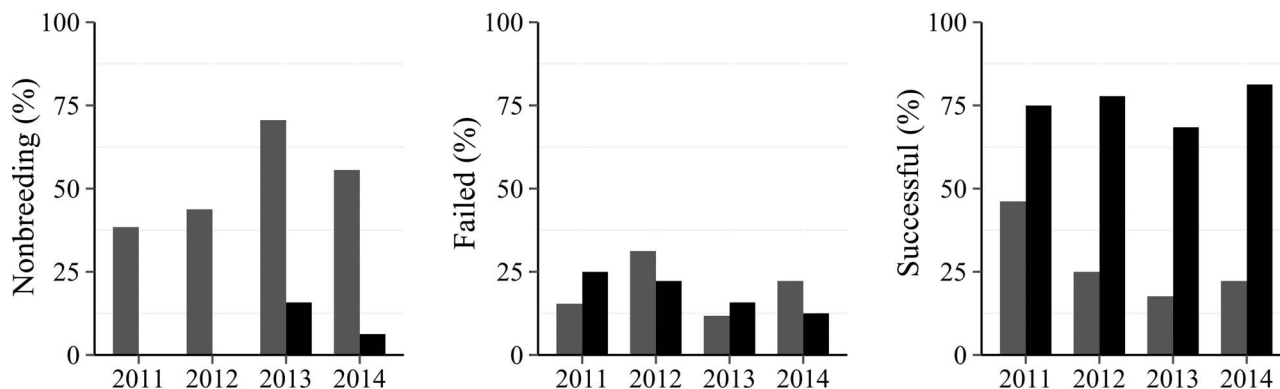

FIGURE 3. Breeding performance of Verreaux's Eagles in the Cederberg (gray, n = 64) and Sandveld (black, n = 48) regions, South Africa, 2011–2014.

TABLE 4. Results from the top GLMs ($\Delta AIC_c < 2$) comparing model fit for nesting success of Verreaux's Eagles ($n = 68$ observations from 2011 to 2014). Model parameters: LD (lay date), site (Cederberg or Sandveld), year (2011–2014), PI (proximity index: a measure of the density of nests within 10 km), RainTot28 (total rainfall, mm), RainCon28 (number of consecutive rain days), and TempAv28 (average temperature, °C), all during 28 days around hatching (starting 3 days before the estimated date of hatching).

Models	df	LogLik	AIC$_c$	ΔAIC_c	w_i	ER
Site+LD+RainTot28	4	−27.47	63.60	0.00	0.28	–
LD+RainTot28	3	−28.83	64.00	0.45	0.22	1.26
Site+LD+RainTot28+Temp28	5	−27.00	65.00	1.38	0.14	1.96
Site+LD+RainTot28+PI	5	−27.09	65.10	1.57	0.13	2.21
LD+RainTot28+PI	4	−28.37	65.40	1.80	0.11	2.52
LD+RainTot28+RainCon28	4	−28.39	65.40	1.83	0.11	2.52

Notes: df = degrees of freedom, LogLik = log likelihood, ΔAIC_c = change in AIC$_c$ in relation to the highest-ranked model, w_i = AIC$_c$ weight, and ER = evidence ratio.

2013) or the topography may be more conducive to a low-energy life style, although further research is clearly required to explore this explanation further. Davies (1994) observed that the apparently optimal habitat along upper cliff escarpments in the Karoo harbored high densities of Verreaux's Eagle pairs but these pairs experienced far lower breeding rate and success than pairs that had a greater proportion of bottom plains and farmland within their territories, resulting in breeding productivity being 66% lower in upper-escarpment pairs than in lower-escarpment pairs. This was attributed to a less reliable single-species (rock hyrax [*Procavia capensis*]) prey base in the upper escarpments than in the farmlands where there are alternate species available. Dietary differences or relative prey availability in each study site should be further investigated to assess the contribution it might have on breeding parameters.

Some raptors are known to exhibit fluctuating patterns in breeding productivity, whereby productivity follows patterns in prey abundance (Steenhof et al. 1999, McIntyre et al. 2006, Moss et al. 2012) or the favorability of climatic conditions (Redpath et al. 2002, McDonald et al. 2004). However, our findings are likely to be representative of local trends, owing to (1) the similarity of rainfall patterns during our study (Cederberg: 213.8 ± 47.8 mm; Sandveld: 177.8 ± 51.0 mm) and in the preceding decade (Cederberg: 204.8 ± 46.1 mm; Sandveld: 185.9 ± 53.9 mm) in both regions; (2) the slow life history of hyrax (Hoeck 1989, Barry et al. 2015); and (3) the absence of obvious cyclic trends in a 31-yr study of Verreaux's Eagles (Gargett et al. 1995). Considering these factors, and even with the addition of occasional "good" years, the Cederberg is unlikely to become more productive than the Sandveld.

Other Variables Affecting Breeding Performance

We expected lower breeding productivity in our study areas compared with previous studies, owing to the contrasting rainfall seasonality. The Cederberg and the Sandveld are both located in a winter rainfall region, whereas the previous studies were all undertaken in summer rainfall regions. Despite this, the breeding rate in the Sandveld exceeded that in summer rainfall regions, whereas the breeding rate of Cederberg Verreaux's Eagles was substantially lower than those reported in all other studies (Figure 6), showing that Verreaux's Eagles can breed successfully in winter rainfall regions.

Increased rainfall during chick rearing invariably causes reduced nesting success in raptors (Rodríguez and

TABLE 5. Parameter estimates (β) from model averaging (with shrinkage) of the ranked models in Table 4 explaining the variation in nesting success in Verreaux's Eagles. Parameters: LD (lay date), site (Cederberg or Sandveld), PI (proximity index: a measure of the density of nests within 10 km), RainTot28 (total rainfall, mm), RainCon28 (number of consecutive rain days), and TempAv28 (average temperature, °C), all during 28 days around hatching (starting 3 days before the estimated date of hatching); RI = relative importance of the variable.

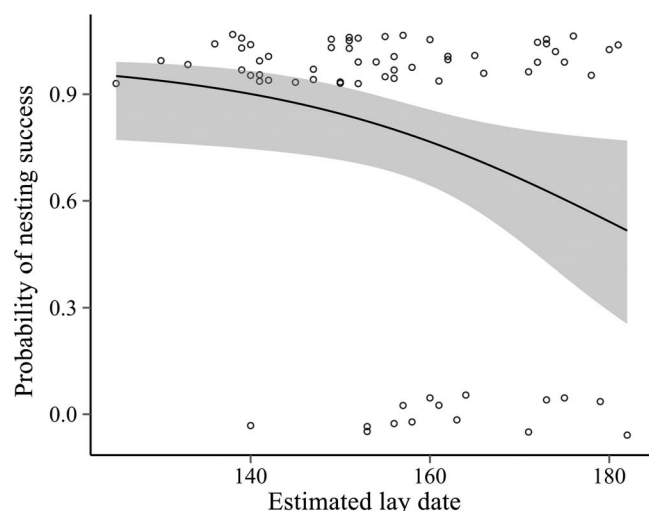|	β	SE	Adjusted SE	z	P	Confidence intervals 2.5%	97.5%	RI
(Intercept)	15.87	6.70	6.82	2.33	0.02	2.51	29.23	–
LD	−0.08	0.03	0.03	2.31	0.02	−0.14	−0.01	1.00
RainTot28	−0.09	0.04	0.04	2.15	0.03	−0.18	−0.01	1.00
Site	0.63	0.77	0.77	0.81	0.42	−0.25	2.53	0.55
PI	−0.20	0.56	0.57	0.36	0.72	−2.60	0.91	0.24
TempAv28	0.05	0.20	0.20	0.27	0.79	−0.39	1.16	0.14
RainCon28	−0.03	0.13	0.13	0.23	0.82	−0.84	0.31	0.11

FIGURE 4. Line fitted from a binomial generalized linear model showing the probability of Verreaux's Eagle nesting success against the estimated lay date (with confidence intervals) in the Cederberg and Sandveld regions of South Africa.

Bustamante 2003, McDonald et al. 2004, Amar et al. 2012, Bionda and Brambilla 2012, Zabala and Zuberogoitia 2014). During heavy rainfall, a nestling is more susceptible to starvation from decreased food provisioning and hypothermia, particularly until it has developed the first insulating feathers. Furthermore, food requirements of nestlings increase during cold weather (Gargett 1990, Redpath et al. 2002), and rainfall is likely to reduce adult hunting success (McDonald et al. 2004). The total rainfall up to 28 days after hatching was significant in predicting
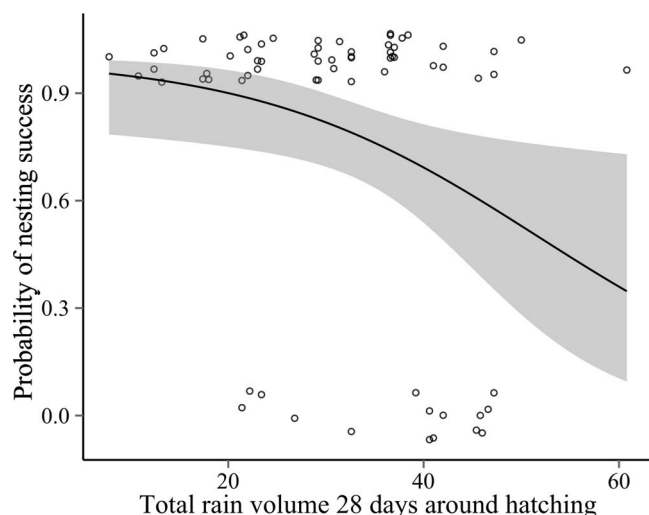

FIGURE 5. Line fitted from a binomial generalized linear model showing the probability of Verreaux's Eagle nesting success against total rainfall (mm) recorded up to 28 days after hatching with confidence intervals, in the Cederberg and Sandveld regions of South Africa.
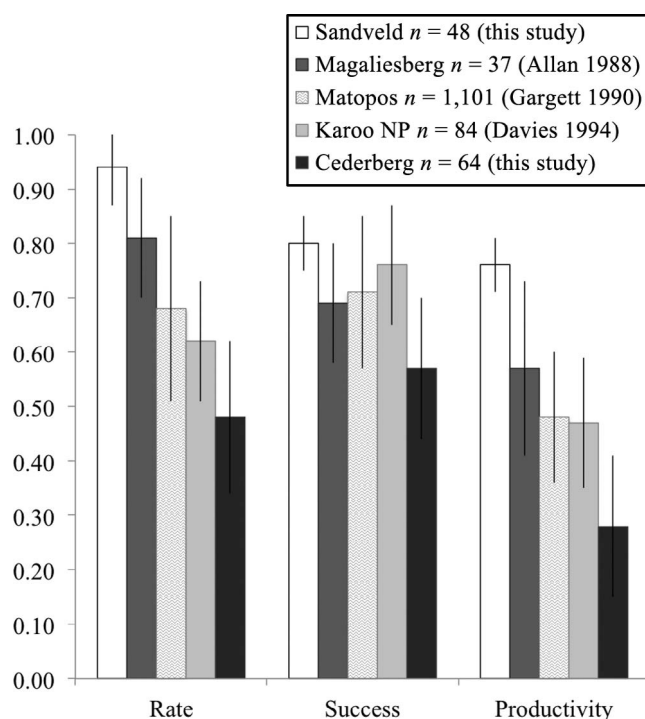

FIGURE 6. Mean annual breeding performance (± SD) of Verreaux's Eagles in 5 areas of southern Africa (Allan 1988, Gargett 1990, Davies 1994): breeding rate = proportion of monitored pairs that initiated incubation; success = proportion of breeding attempts that were successfully rearing a nestling; and productivity = proportion of monitored pairs that were successful. Sample sizes of monitored occupied breeding years (n) are given in the legend. Study durations: this study, 2011–2014; Magaliesberg, 1982–1984; Matopos, 1959–1984; Karoo National Park, 1986–1990.

the outcome of a breeding attempt, whereas rainfall during shorter periods after hatching was less important, demonstrating the susceptibility to nest failure beyond just the first few weeks of chick rearing. From a recent review of brooding behavior in raptors, the allometric relationship predicts that for a bird of this size, intensive brooding requirements should occur until the young are ~27 days old (Katzenberger et al. 2015), which links well with our findings.

Our finding that timing of breeding influences success is in agreement with multiple studies of raptorial species (Newton and Marquiss 1984, Margalida et al. 2003, McDonald et al. 2004, Martin et al. 2014). Increased rainfall as the breeding season progresses has been identified as a mechanism explaining this seasonal decline in nesting success in some species (Senapathi et al. 2011, Cartwright et al. 2014). However, lay date and rainfall were not correlated in our study; therefore, we assume that these act independently with the greater success of early-breeding pairs potentially related to individual and/or territory quality. Although these effects are often difficult

TABLE 6. Stochastic estimates of annual rate of population growth (λ) for Verreaux's Eagles over a 50-yr period in the Cederberg and the Sandveld, South Africa: $\lambda = 1$ represents a stable population, $\lambda < 1$ is declining, and $\lambda > 1$ is increasing. Metapopulation (Meta) growth rates are not included for closed populations because of the complete separation of the populations; therefore, only the sum of individuals in the 2 populations is relevant. Also shown are the probability of extinction (PE) and predicted extant population size (N-extant) of Verreaux's Eagles in the 50-yr time frame. All variables are modeled as both closed (no dispersal between sites) and open (50% dispersal of juveniles) populations with area-specific breeding rates derived from this study. Population viability analysis (PVA) model scenarios: "PVA Baseline" is a model with mortality rates derived from Vernon (1972); "PVA−10" incorporates a 10% decrease in mortality; and "PVA+10" is modeled on a 10% increase in mortality.

Model	Population	$\lambda \pm$ SD	PE	N-extant $\pm$ SD
PVA−10				
Closed	Cederberg	0.951 ± 0.10	0.19	10 ± 5.6
	Sandveld	1.029 ± 0.06	0.00	70 ± 4.5
	Meta	–	0.00	78 ± 7.6
Open	Cederberg	0.992 ± 0.08	0.00	56 ± 13.3
	Sandveld	1.000 ± 0.09	0.00	54 ± 12.2
	Meta	0.996 ± 0.04	0.00	110 ± 23.4
PVA Baseline				
Closed	Cederberg	0.935 ± 0.12	0.54	6 ± 3.0
	Sandveld	1.011 ± 0.06	0.00	64 ± 9.3
	Meta	–	0.00	68 ± 10.0
Open	Cederberg	0.975 ± 0.11	0.01	26 ± 10.2
	Sandveld	0.979 ± 0.11	0.01	26 ± 10.9
	Meta	0.977 ± 0.05	0.00	52 ± 20.1
PVA +10				
Closed	Cederberg	0.921 ± 0.13	0.84	4 ± 1.6
	Sandveld	0.990 ± 0.07	0.01	42 ± 15.8
	Meta	–	0.00	42 ± 16.0
Open	Cederberg	0.954 ± 0.14	0.09	10 ± 5.4
	Sandveld	0.958 ± 0.15	0.13	10 ± 5.6
	Meta	0.956 ± 0.07	0.03	19 ± 10.5

FIGURE 7. Graphical output for the population viability analysis (PVA) models: simulated population sizes ($\pm$ SD) of Verreaux's Eagles over 50 yr for the Cederberg population (solid lines), the Sandveld population (dashed line), and the metapopulation across both areas (dotted lines), modeled as both closed and open populations with area-specific breeding rates derived from the presnt study. "PVA Baseline" is a model with mortality rates derived from Vernon (1972), "PVA−10" incorporates a 10% decrease in mortality, and "PVA+10" is modeled on a 10% increase in mortality. Lines show the mean output for 1,000 simulations.

to separate, higher-quality individuals or those inhabiting better-quality territories can attain breeding condition earlier than poorer individuals or territories, and these pairs often have a greater probability of nesting success (Verhulst and Nilsson 2008, Zabala and Zuberogoitia 2014).

Population Viability

Unfortunately, reliable survival estimates were not available for our populations. Differences in population trends between the modeled scenarios highlight the need to be cautious when assigning these predictions to real-life scenarios. Furthermore, although productivity was higher in the Sandveld, survival of adults or juveniles (Millsap et al. 2004) or the quality of offspring (Almasi et al. 2015) could be lower in this human-altered habitat; therefore, the balance between productivity and survival may not be
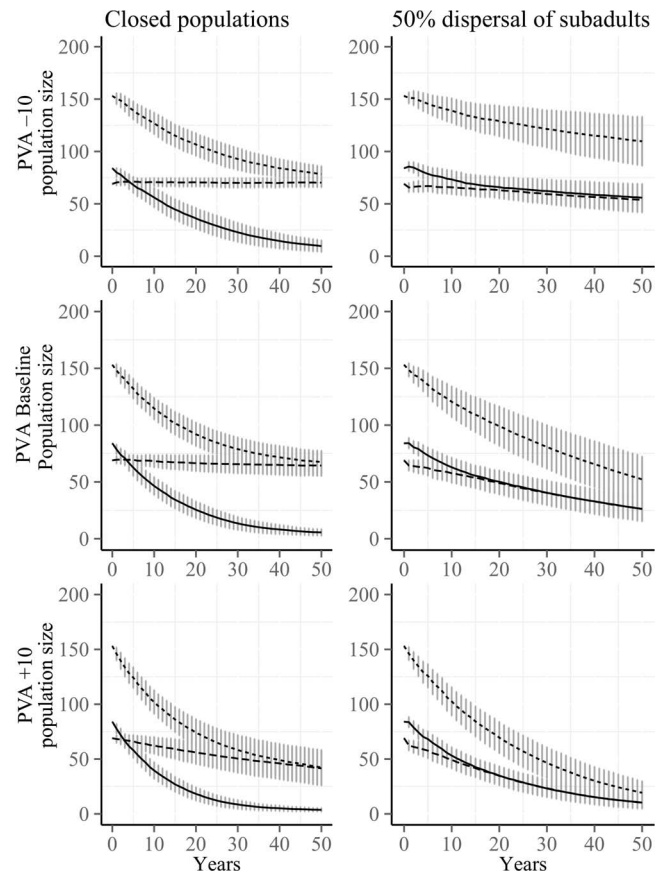
equal between the 2 sites. Accepting this limitation, population modeling indicated that differences in breeding productivity could have a profound effect on the long-term stability of each study population. In contrast to expectations of negative impacts of agricultural land use on breeding productivity of top predators, the closed PVA Baseline model shows an apparently healthy population in the Sandveld. On the other hand, it is unlikely the Cederberg population would be self-sustaining. Although little is known about juvenile dispersal and philopatry in Verreaux's Eagles, the potential for dispersal from natal areas has been seen in the closely related Adalbert's Eagle (*Aquila adalberti*; González et al. 1989), Golden Eagle (*A. chrysaetos*; Weston et al. 2013, Ogden et al. 2015), and Bonelli's Eagle (*A. fasciata*; Real and Mañosa 2001,

Cadahía et al. 2010). Dispersal between subpopulations can drive source–sink dynamics and often leads to a combined higher metapopulation than just the "source" would alone (Pulliam 1988, Pulliam and Danielson 1991). However, dispersion from a productive population into decreasing populations can cause an ecological trap (Purcell and Verner 1998, Battin 2004) and result in the decline of the metapopulation, as seen in the open PVA Baseline model.

The scenario-based approach highlights how any increment in mortality would be detrimental to the metapopulation, which is consistent with modeling in other long-lived raptors (Katzner et al. 2006, Carrete et al. 2009, García-Ripollés and López-López 2011, Rushworth and Krüger 2014). Although density-dependent effects are usually expected to result in increased breeding performance as the population declines (Fasce et al. 2011), we did not include these effects in our models and consider it unlikely that there would be a significant change, given that our breeding analysis showed no relationship with the proximity index.

Conclusions

The measured differences in breeding performance between the natural and agriculturally developed study sites were opposite to our predictions based on the fundamental idea that top predators are largely associated with natural and undisturbed ecosystems (Sergio et al. 2005, 2006). Our results challenge the assumption that the Cederberg represents prime habitat for this species and suggest that the Sandveld, in its current agriculturally transformed state, is in fact a more suitable area. Although agricultural intensification is often blamed for the loss of ecological heterogeneity (Benton et al. 2003, Flynn et al. 2009, Herrera et al. 2015), it can also provide resource opportunities that can be beneficial under some circumstances (Cardador et al. 2011, Buij et al. 2013). Despite not knowing whether (1) breeding performance has changed in the Sandveld following agricultural development and a changing prey base or (2) the differences in breeding productivity between the sites already occurred prior to agricultural transformation of the Sandveld, our findings support the notion that Verreaux's Eagles can maintain good breeding productivity in agriculturally transformed areas. However, there is likely to be a threshold of transformation tolerance whereby functional diversity and prey availability are not compromised (Magioli et al. 2015). Land use and climate change are the 2 major pressures facing biodiversity loss globally. There are potentially synergetic effects between these factors, and understanding these is important for effective conservation strategies (Opdam and Wascher 2004, Mantyka-Pringle et al. 2015). Our results highlight the Sandveld as a regionally important site for conservation and preservation of Verreaux's Eagles. Management actions should aim to identify and eliminate or avoid any current or future sources of unnatural mortality in this area. This may be particularly relevant to the growing wind-energy industry in South Africa, which has been identified as a cause of mortality (De Lucas et al. 2008, Drewitt and Langston 2008) and of disturbance-related decreases in breeding productivity of similar eagle species (Dahl et al. 2012). The maintenance of suitable heterogeneous conditions in the Sandveld is also likely to be important to secure viable populations in this region.

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APPENDIX TABLE 7. Supplementary information on camera deployments at Verreaux's Eagle nests in the Cederberg and Sandveld study sites.

Area	Year	Camera make	Setup	Frame interval	Start date	End date	Photos (n)
Cederberg	2012	Scoutguard 560	Motion-sensing	NA	July 11	July 22	302
Cederberg	2012	Scoutguard 560	Motion-sensing	NA	July 14	July 15	32
Sandveld	2012	Scoutguard 560	Motion-sensing	NA	July 5	July 20	475
Cederberg	2013	Ltl Acorn 6210MG/C	Time-lapse	3 min	June 29	September 25	18,576
Cederberg	2013	Ltl Acorn 6210MG/C	Time-lapse	3 min	July 22	August 13	5,610
Sandveld	2013	Ltl Acorn 6210MG/C	Time-lapse	3 min	July 10	September 7	5,268
Sandveld	2013	Ltl Acorn 6210MG/C	Time-lapse	3 min	July 5	July 11	1,468
Sandveld	2013	Ltl Acorn 6210MG/C	Time-lapse	3 min	July 4	August 26	5,287

APPENDIX TABLE 8. Input parameters from the simulated population viability analysis (PVA) scenarios for Verreaux's Eagles in the Cederberg and Sandveld study sites as modeled in Vortex. Scenarios: "PVA Baseline" is a model with mortality rates derived from Vernon (1972); "PVA−10" incorporates a 10% decrease in mortality; and "PVA+10" is modeled on a 10% increase in mortality.

Parameter	PVA−10		PVA Baseline		PVA+10	
	Cederberg	Sandveld	Cederberg	Sandveld	Cederberg	Sandveld
Model settings						
Number of iterations	1,000	1,000	1,000	1,000	1,000	1,000
Number of years	50	50	50	50	50	50
Extinction definition	Only 1 sex remains		Only 1 sex remains		Only 1 sex remains	
Number of populations	2	2	2	2	2	2
Inbreeding depression	No	No	No	No	No	No
Reproductive system						
Pair system	Long-term monogamous		Long-term monogamous		Long-term monogamous	
Age at first breeding (female)	4	4	4	4	4	4
Age at first breeding (male)	4	4	4	4	4	4
Maximum age of reproduction	30	30	30	30	30	30
Maximum number of broods yr^{-1}	1	1	1	1	1	1
Maximum number of progeny yr^{-1}	1	1	1	1	1	1
Sex ratio at birth (M/F)	50/50	50/50	50/50	50/50	50/50	50/50
Density-dependent reproduction	No	No	No	No	No	No
Adult females breeding successfully yr^{-1} (%) [a]	28	76	28	76	28	76
EV adult females breeding successfully yr^{-1} (%) [a]	13	5	13	5	13	5
Mean number of offspring $female^{-1}$ yr^{-1} (± SD) [a]	1 ± 0.00	1 ± 0.00	1 ± 0.00	1 ± 0.00	1 ± 0.00	1 ± 0.00
Mortality rates						
Percent mortality from age 0–1 (juvenile) ± SD	36.9 ± 2.0	36.9 ± 2.0	41 ± 2.0	41 ± 2.0	45.1 ± 2.0	45.1 ± 2.0
Percent mortality from age 1–2 (subadult) ± SD	16.2 ± 2.0	16.2 ± 2.0	18 ± 2.0	18 ± 2.0	19.8 ± 2.0	19.8 ± 2.0
Percent mortality from age 2–3 (subadult) ± SD	16.2 ± 2.0	16.2 ± 2.0	18 ± 2.0	18 ± 2.0	19.8 ± 2.0	19.8 ± 2.0
Percent mortality from age 3–4 (subadult) ± SD	16.2 ± 2.0	16.2 ± 2.0	18 ± 2.0	18 ± 2.0	19.8 ± 2.0	19.8 ± 2.0
Percent mortality from age 4+ (adult) ± SD	8.1 ± 2.0	8.1 ± 2.0	9 ± 2.0	9 ± 2.0	9.9 ± 2.0	9.9 ± 2.0
Initial population structure						
Initial population size	84	69	84	69	84	69
Stable age structure	Yes	Yes	Yes	Yes	Yes	Yes
Carrying capacity	92	73	92	73	92	73

[a] Results from this study.