RESEARCH ARTICLE

African Grass Owl nest site use and nest survival in fragmented grassland landscapes

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Studies of nest site use in owls rarely involve species utilizing dynamic nest substrates such as grasses or sedges. We studied nest site use and nest survival in African Grass Owls (*Tyto capensis*) in the Highveld Grasslands of South Africa by monitoring 41 nests found in Gauteng and Mpumalanga between 2009 and 2017. We also placed radio- and GPS-tracking devices on seven nesting females to collect information about habitat use within their home ranges. Nest site use was investigated at the home range scale under three hypotheses related to how they select nest patches with respect to predator avoidance, namely the total foliage, potential-prey-site, and edge-effect hypotheses. Nest patch metrics and land-cover characteristics were modelled for differences between African Grass Owl nest patches and 41 random patches, using matched-pairs logistic regression. African Grass Owls used nest patches that were larger ($\bar{x}$ = 3.6 ha *vs* $\bar{x}$ = 1.9 ha) and older ($\bar{x}$ = 2.9 years *vs* $\bar{x}$ = 2.3 years) than random patches, and that had more *Imperata cylindrica* in closer proximity to the focal patch within the home range. They also used patches with a greater percentage wetland ($\bar{x}$ = 7.4% *vs* $\bar{x}$ = 4.3%) and a lower percentage developed land-cover ($\bar{x}$ = 0.5% *vs* $\bar{x}$ = 2.1%) within the home range than random patches. Multivariate models supported the total foliage hypothesis over potential-prey-site and edge-effect alternatives. Percentage developed land-cover was the most significant driver of nest survival, with daily nest survival decreasing with an increase in developed land-cover. The results of this study confirm that African Grass Owls are highly selective in terms of nesting habitat and emphasize their vulnerability with respect to habitat loss and fragmentation.

Keywords: African Grass Owl, nest site use, Highveld Grasslands, nest survival, owl, *Tyto capensis*, *Imperata cylindrica*.

INTRODUCTION

Changes in local land use and associated habitat loss is the greatest driver of the global extinction of species (Bibby, 1995; BirdLife International, 2018; Groombridge, 1992). Habitat loss and destruction is also the greatest threat to breeding birds worldwide (König, Becking & Weick, 2008; Mikkola, 2014). To mitigate this threat, an understanding of the breeding and foraging habitat requirements of a species is required (Underwood, Chapman & Crowe, 2004). Nest site selection is the hierarchical process of animal behaviour related to the use of breeding habitats disproportionate to their availability (Hutto, 1985; Jones, 2001; Thomas & Taylor, 2006). Natural selection should influence an individual's choice of nest site by favouring habitat conditions that improve reproductive success, and

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this behaviour could be adaptive because the choice of nesting site may influence parental fitness (Collias & Collias, 1984). However, sometimes nest site selection may have the opposite result, when seemingly ideal locations act as ecological traps, especially when birds fail to demonstrate behavioural plasticity in light of significant anthropogenic changes to their environments (Dwernychuk & Boag, 2011; Ma *et al.*, 2019).

Habitat influences nest site selection at two scales, namely the nest site scale and the nest-patch scale (Martin & Roper, 1988). At the nest site scale, the factors selected for include microclimate (*e.g.* Maclean, 1970; O'Connor, 1984; Vuňuela & Sunyer, 1992), food availability, nest predation (*e.g.* Forstmeier & Weiss 2004; Lima, 2009; Martin, 1993; Ricklefs, 1969), or any combination of these at and around the nest (Simmons & Smith, 1984). Nest predation is likely to be a strong determinant of nest site use for ground-nesting birds, as they are known to incur higher nest predation rates than off-ground nesters (Martin, 1993). At the nest-patch scale, landscape characteristics around a nest site may be especially important in heterogeneous habitats. Distance from the nest to the nearest ecotone may be, for example, a crucial factor as mammalian predators favour edge habitats (Møller, 1989; Paton, 1994). Moreover, habitat patch sizes are of critical importance as nest predation increases with decreasing patch size (*e.g.* Martin & Roper, 1988; Stanevičius, 2004).

Finding a suitable nest site is further limited by their availability (Goodenough, Elliot & Hart, 2009; Malan, 2009). For birds that do not construct their own nests, *e.g.* most Strigidae (owls), suitable nest sites are even more limited (König *et al.*, 2008; Rockweit, Franklin, Bakken & Gutiérrez, 2012). Studies of nest site use by ground-nesting owls (*e.g.* Holt, 1992; Keyes, Gahbauer & Bird, 2016), are few in comparison to those of nest site use by cavity-nesting owls (*e.g.* Hershey, Meslow & Ramsey, 1998; LaHaye, Gutiérrez & Call, 1997; May, Petersburg & Gutiérrez, 2004; Severinghaus, 2007; Stralberg *et al.*, 2009).

The African Grass Owl (*Tyto capensis*) is a poorly studied species that inhabits moist grasslands in South Africa. Here, it is one of two species of owl that lays its eggs on the ground in nests sheltered by grass and/or sedges, the other being the sympatric Marsh Owl (*Asio capensis*) (Kemp & Calburn, 1987; Kemp, 2005; Steyn, 1982). Nest site use by African Grass Owls is poorly documented (Pretorius, 2019), causes of nest failure are underreported, and the species is rare and secretive by nature (Ansara, 2004; Lepage, 1999). Tarboton & Erasmus (1998) suggested that African Grass Owl nests are vulnerable in fire-prone grasslands because of the timing of their breeding attempts. From the above, it is clear that knowledge of African Grass Owl nest site use and breeding habitat requirements at different scales is required to ascertain the impact that current and future anthropogenic changes in land-use practices might have on the species.

The aim of this study was to quantify nest site use and assess the habitat features influencing nest survival of African Grass Owls in fragmented Highveld Grassland landscapes. To do this, we tested three alternative hypotheses considered the main drivers of nest site use in response to predation risk (Chalfoun & Martin, 2009). These included the edge-effect, potential-prey-site and total foliage hypotheses. The total foliage hypothesis suggests that increased vegetation density may hamper predator search effort (Martin & Roper, 1988; Martin, 1993). It is linked to the degree of nest concealment by vegetation (Martin, 1992), and is associated with the following patch attributes: vegetation density (*e.g.* Martin & Roper, 1998), patch age (*e.g.* Storch, 1991), patch size (*e.g.* Clark & Shutler, 1999) and patch shape. The potential-prey-site hypothesis is based on the prediction that the probability of discovery (*e.g.* of a nest) decreases with an increase in the number of unoccupied sites (*e.g.* nest habitat patches). It is explained by patch metrics such as patch diversity and the percentage of land-cover variables (Magaňa, Alonso, Martín, Bautista & Martín, 2010). We also predicted that African Grass Owl nests favoured habitat features that decrease the amount and proximity of ecotones (the edge-effect hypothesis). It is well known that nest predation risk is higher close to ecotones such as woodland–grassland edges (Gates & Geysel, 1978; Schneider, Low, Arlt & Pärt, 2012; Söderström, Pärt & Rydén, 1998; Storch, Woitke & Kriege, 2005). To test these hypotheses, our specific objectives were to (1) describe habitat use of African Grass Owls by means of radio- and GPS-tracking of individuals, (2) to assess nest site use of African Grass Owls using patch metrics and land-cover data, and (3) to investigate how habitat features influence nest survival, testing the proposition that African Grass Owl nest site use is adaptive.

METHODS

Study area

The Highveld Grasslands (Olson *et al.*, 2001) is a terrestrial ecoregion restricted to the inland plateau of South Africa, ranging in elevation from 1400 to 1800 m a.s.l. Our study area was located in the Mesic Highveld Grasslands (Mucina & Rutherford, 2006), a vegetation type found within this ecoregion (Fig. 1). This area is largely transformed by urban development, afforestation and agriculture, with a noteworthy increase in mining and urban areas over the study area since 1994 (Neke & du Plessis 2004; Schoeman *et al.*, 2013). Land ownership of the different study sites varied from state-owned land in the form of Suikerbosrand Nature Reserve, a Gauteng provincial nature reserve run by the Gauteng Department of Agriculture and Rural Development (GDARD), to private land.

The study area included African Grass Owl territories in two South African provinces, Gauteng and Mpumalanga. The area is characterized by cold, dry winters and hot summers (Kruger & Mbatha, 2021). Mean annual rainfall during the study period (2008–2017) was 593.34 ±

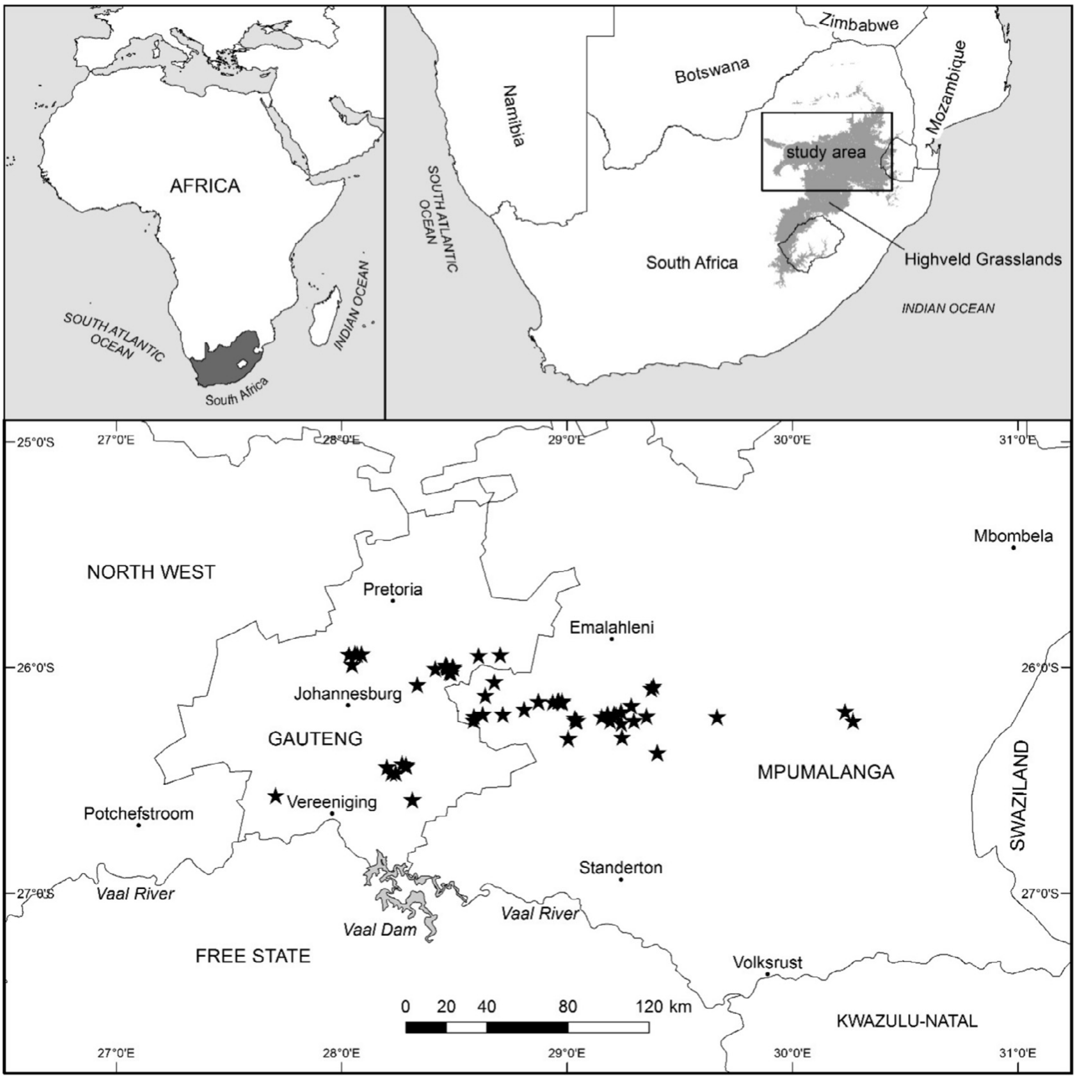

Fig. 1. Map of the study area on the Mesic Highveld Grasslands (Mucina & Rutherford, 2006) of South Africa, including the location of African Grass Owl nests (✶) discovered during the period 2009 to 2017.

152.70 mm. Rainfall is distributed between the spring and summer months (October–February), with late rains extending into autumn (March/April). The Highveld regularly experiences violent thunderstorms and fire risk is high, particularly during early spring when the grasslands are still dry (Steyn, 2020). Landowners therefore employ fire through controlled burning regimes to manage grassland health and yield (Tainton, 1999).

Nests and random points

African Grass Owl nests were monitored between 2009 and 2017. A use-*versus*-availability model (Marcum & Loftsgaarden, 1980) was used to compare measured characteristics of African Grass Owl nests to paired random points within the same home range. We assumed that nesting habitat was available to owls if it occurred within a pair's home range (Jones, 2001). Mean home-range size was an area size of 423 ha (range = 32–1527) at the 95% kernel density isopleth, based on telemetry data recorded from captured adults fitted with tracking devices (Pretorius, 2019). At least one habitat patch containing random points was surveyed within each African Grass Owl home range to confirm that they were not using them for nesting. Procedures for delineating nest habitat patches are described in the Supplementary material.

To reduce spatial autocorrelation, we considered only one nest for pairs with more than one nest record from the same patch, selected using a random-number generator in Microsoft Excel. This restriction limited the sample to 41 nests. Because not all pairs were fitted with tracking devices, we constructed theoretical home ranges of a circular shape around each nest and random site, with a radius of 1160.36 m, resulting in 423 ha polygons from which to extract information about nest site use model parameters per territory. Centroids were extracted from polygons representing *Imperata* patches to standardize the placement of random points within their respective patches. This assumption was deemed to be a reasonable as African Grass Owl nests were usually located in the centre of a patch.

Data collection

Seven African Grass Owls were captured and fitted with tracking devices. The devices fitted to owls included three VHF radio and four Global Positioning System (GPS)-enabled devices. The owls were captured at the nest using a specially designed walk-in trap (see Pretorius (2019) for more details about trapping and tracking African Grass Owls).

Circular statistics were performed on azimuths of nest entrances recorded at African Grass Owl nests to describe nest orientation, following Batschelet (1981). The trigonometrical method (Batschelet, 1981) was used to obtain a mean nest orientation and corresponding angular deviations. Rayleigh's test for randomness was performed in order to detect directedness, and the data were tested for fit to the Von Mises distribution (analogous to the normal distribution).

Variables recorded at nests and random sites included various patch metrics and land-cover characteristics. Twelve different patch metrics were derived from the *Imperata cylindrica* vector. The choice of patch metrics included in the analyses was based on those proposed by Bender, Tischendorf & Fahrig (2003) and McGarigal, Cushman & Ene (2012). Land-cover classes were derived from 72 types given by the 2013–2014 South African national land-cover dataset version 5.0 (Geoterraimage, 2015), reducing them to six consolidated, broader classes. A description of the patch metrics and their formulae is presented in the supporting material. Data collection was desktop-based, using a graphical information system (GIS) and remote sensing tools. Age of patch burn was taken to be the time in years since the last burn. This information was obtained using the Collection 6 moderate resolution imaging spectrometer (MODIS) burned area product (MCD64A1, Giglio, Boschetti, Roy, Humber & Justice, 2018), by summing all the available images covering the study area for each year between 2001 and 2017.

Data analyses

Habitat use by radio- and GPS-tracked African Grass Owls

To determine habitat use by African Grass Owls, we compared habitat available to owls within the home range to habitat used by radio and GPS-tracked owls (n = 7). This comparison was done by means of compositional analysis (Aebischer, Robertson & Kenward, 1993) of different land-cover types. The 72 different land-cover types were reclassified into the following nine land-cover types mapped within African Grass Owl home ranges: (1) exotic tree plantations, (2) woodland, (3) shrubland, (4) cultivated fields, (5) open water, (6) wetlands, (7) grassland, (8) developed and (9) mining. Compositional analysis of habitat use was a two-step process; first, the significance of habitat use was assessed using Wilk's lambda and then a ranking matrix was constructed to illustrate the extent of habitat use of one land-cover type over another (Calenge, 2017). This process was repeated for two levels of habitat use, as classified by Johnson (1980), and recommended by Aebischer *et al*. (1993), namely: (1) 2nd-order habitat use, *i.e.* home range used within the study area and (2) 3rd-order habitat use, *i.e.* land-cover type used within the home range. In the case of zero values for a complete lack of habitat use, a value of 0.01% was used as a substitute, as used by Aebischer *et al*. (1993).

Nest site use

A focal-patch analysis strategy (McGarigal *et al*., 2012) was used to model African Grass Owl nest site use. To select significant variables for multivariate analyses, univariate analyses were conducted on all recorded variables to determine the difference between African Grass Owl nests and random points. Continuous habitat variables were compared between used (active nests) *versus* available sites (paired random points) using the 1:1 and matched-pairs (case-control) logistic regression (MPLR) method of Hosmer & Lemeshow (1989). A sampling unit was thus an African Grass Owl nest and paired random point. African Grass Owl nests (case) were coded as 1, and random points (control) were coded as 0.

The Wald statistic, z-value and probability values from univariate MPLR analyses were used to screen variables for inclusion in multivariate models. Mickey & Greenland (1989) proposed that any variable with a univariate test P-value of $P <$ 0.25 should be included in the initial multivariate model, since they showed that the use of $P < 0.05$ often fails to include variables known to be important. In this study we selected to omit variables with P-values ≥ 0.1 to minimize the restrictive influence of less important variables on more important variables. The number of variables added to the multivariate analyses was reduced by removing certain independent variables that were strongly correlated using the variable reduction method proposed by Green (1979). This method is widely used in similar studies of nest site use in birds of prey (*e.g.* Sergio & Bogliani, 2000; Sergio, Pedrini & Marchesi, 2003; Warketin & James, 1988). Spearman's rank correlations were performed to investigate correlation between variables. Variables were deemed to be strongly correlated when $r > 0.7$. Correlated variables were then reduced to a single variable by selecting the one that was perceived to be more ecologically important to African Grass Owls. When there was no clear difference in the ecological importance of correlated variables, the one which had the lower P-value in explaining the difference between African Grass Owl nests and random points was retained.

An information-theoretical approach was used to compare and rank candidate models with the small-sample correction for Akaike's Information Criterion (AIC_c, Burnham & Anderson, 2002; Hurvich & Tsai, 1989,). Akaike weights (Buckland, Burnham & Augustin, 1997) and delta AIC_c (ΔAIC_c) were also calculated to show model likelihood and uncertainty. Only those models appearing within the 95% confidence set based on Akaike's weights were used as candidate models. Competing models within $\Delta AIC_c \leq 2$ were considered to be well supported by the data (Burnham & Anderson 2002).

Influence of nest site use on nest survival

The above-mentioned patch metrics and land-cover variables were included in nest survival models, using the methodology contained within Rotella (2017). Because it is an altricial species, the nesting period for the African Grass Owl is assumed to be the number of days from the laying of the first egg to the fledging of the first nestling, *i.e.* the egg laying + incubation + nestling period, estimates for which were described in the results. Nest survival was determined using an extension of Bart & Robson's (1982) generalized likelihood using the nest survival function of the program MARK, procedures for which are described by Rotella (2017). The same sets of multivariate models for investigating hypotheses related to nest site use in general were used to model the influence of nest site use on nest survival.

Analysis software

All data analyses related to nest site use were performed using the R statistical language and environment (version 3.5.1, R Core Team, 2018). The *Imperata cylindrica* patch-delineation model (see Supplementary material) was evaluated using the 'confusionMatrix' function of the package 'caret' (version 6.0-80, Kuhn, 2018). Compositional analysis of habitat use was conducted using the R package 'adehabitatHS' (version 0.3.13, Calenge, 2017). The MPLR analyses were performed using the 'clogit' function of the package 'survival' (version 2.42-6, Thoreau, 2018). Unless otherwise stated, data are presented as mean ± 1 standard deviation (S.D.) or range in brackets.

RESULTS

African Grass Owls nested significantly more in *Imperata cylindrica* than in other species of grass or sedge ($\chi^2 = 265.08$, d.f. = 5, $P < 0.001$). *Imperata cylindrica* was used for 88% of all nests ($n = 41$). African Grass Owl nest orientation data fitted a Von Mises distribution and were concentrated around an apparent favoured direction. The distribution of nest orientation azimuths was significantly different than expected from random (Rayleigh's $Z = 17.56$, $r = 0.48$, $P < 0.001$). Mean nest orientation was 102.16°. These data indicated a preferred east-southeast orientation of African Grass Owl nests on the Highveld Grasslands.

Nest site use

Patch metrics and land-cover features of African Grass Owl nest sites and random sites are presented in Table 1. Results of univariate matched-pairs logistic-regression models investigating the differences between African Grass Owl nest and random patches are given in Table 2. The differences between African Grass Owl nest and random patches for significant variables is illustrated in Fig. 2. African Grass Owls used nest sites with greater percentage wetland (Wald $\chi^2 = 6.50$, $P = 0.01$), lower percentage developed (Wald $\chi^2 = 3.82$, $P = 0.05$) and greater percentage cultivated (Wald $\chi^2 = 3.31$, $P = 0.07$) land-cover than random sites. Patch metrics used for nesting included a greater mean patch size (Wald $\chi^2 = 9.13$, $P < 0.01$) and greater patch radius (Wald $\chi^2 = 8.08$, $P < 0.01$). African Grass Owls also favoured older patches (Wald = 6.86, $P < 0.01$), bigger patches (Wald $\chi^2 = 5.69$, $P = 0.02$), a smaller mean nearest-neighbour distance (Wald $\chi^2 = 5.04$, $P = 0.03$) and more alternative patches (Wald $\chi^2 = 5.00$, $P = 0.03$) than random sites. All other variables showed insignificant differences ($P > 0.1$) between African Grass Owl nest sites and random sites and were thus excluded from multivariate nest site use models.

Habitat use at the 2nd- and 3rd-order scale

Land-cover types within African Grass Owl home ranges included mostly grassland and cultivated fields. There was much heterogeneity among other types of land-cover, with varying

Table 1. Patch metrics and land-cover characteristics of African Grass Owl nest and random *Imperata cylindrica* patches within the home range (423 ha). Estimates in the table are mean values with standard deviation in brackets.

Variable name	Nest patch	Random patch
Patch metrics		
age (years)	2.86 (1.09)	2.27 (1.11)
number of patches	11.23 (5.60)	10.03 (5.03)
size (ha)	3.59 (4.23)	1.92 (1.84)
area–perimeter ratio	26.33 (12.76)	29.38 (21.53)
shape index	1.87 (0.80)	1.68 (1.32)
Voronoi polygon (ha)	104.25 (101.07)	100.72 (72.57)
radius (m)	217.08 (151.08)	128.19 (122.39)
mean patch size (ha)	1.25 (0.85)	0.75 (0.72)
nearest neighbour distance (m)	338.85 (344.06)	450.01 (366.27)
mean nearest neighbour distance	458.92 (319.66)	606.63 (344.05)
proximity index	2.27 (4.07)	1.482 (2.57
Land-cover variables		
cultivated (%)	61.8 (16.2)	55.4 (19.3)
grassland (%)	24.3 (13.1)	29.6 (17.4)
mining (%)	1.2 (3.9)	2.3 (6.9)
woodland (%)	2.1 (2.3)	3.8 (4.8)
developed (%)	0.5 (0.7)	2.1 (3.6)
wetlands (%)	7.4 (3.8)	4.3 (3.9)
diversity (Shannon diversity)	1.0 (0.2)	1.0 (0.2)

Table 2. Univariate matched-pairs logistic-regression models for variables used to assess the difference between patch metrics and land-cover variables at African Grass Owl nest sites ($n = 41$) and random points ($n = 41$). Variables selected for inclusion in multivariate models are indicated by an asterisk (*). β = model coefficient. AIC_c= Akaike's Information Criterion adjusted for sample size, Wald = Wald χ^2 test statistic.

Variable	β	S.E.	Z	P-value	AIC_c	Wald
Patch metrics						
mean patch size (*)	2.26	0.75	3.02	<0.01	34.60	9.13
radius (*)	0.01	0.01	2.84	<0.01	35.25	8.08
age (*)	1.69	0.64	2.62	<0.01	37.11	6.86
size (*)	0.86	0.36	2.39	0.02	37.46	5.69
mean nearest neighbour distance (*)	–0.00	0.00	–2.25	0.03	42.22	5.04
number of patches (*)	0.35	0.16	2.24	0.03	43.86	5.00
nearest neighbour distance	–0.01	0.00	–1.58	0.11	42.87	2.51
proximity index	0.30	0.21	1.44	0.15	47.15	2.09
shape index	0.35	0.34	1.01	0.31	49.41	1.03
area–perimeter ratio	–0.02	0.02	–0.93	0.35	49.61	0.86
Voronoi polygon	0.00	0.00	0.17	0.87	50.49	0.03
Land-cover variables						
wetlands (*)	21.35	8.38	2.55	0.01	40.76	6.50
developed (*)	–55.28	28.28	–1.95	0.05	41.46	3.82
cultivated (*)	3.80	2.09	1.82	0.07	46.54	3.31
mining	–25.87	19.21	–1.35	0.18	46.80	1.81
grassland	–3.21	2.00	–1.60	0.11	47.65	2.57
diversity	–1.12	1.40	–0.80	0.42	49.86	0.65
woodland	–0.77	11.61	–0.07	0.95	50.52	0.00

percentages of urban, mining, and open water areas. Woodland land-cover was present within all owl home ranges, while the presence of exotic tree plantations and shrubland varied. Despite the heterogeneity in land-cover composition, selectivity by African Grass Owls was not random (Wilks lambda, $\lambda = 0.079$, $P < 0.01$). Compositional analysis of 3rd-order habitat use (habitat use within the home range of individuals) revealed a strong preference for wetlands over other land-cover types, followed by grassland and shrubland (Table 3). The owls also showed a general avoidance of woodland, mining, and cultivated fields. The latter result was particularly interesting because of the

Table 3. Ranking matrix describing 3rd-order habitat use, based on a comparison of the proportions of African Grass Owl telemetry locations within each land-cover type with the proportions of land-cover types within home ranges. The symbols + and – denote preference and avoidance, respectively, and the number of + or – symbols is related to the significance of the preference or avoidance, as determined by means of compositional habitat analysis.

Land-cover type	Plantation	Woodland	Shrubland	Cultivated fields	Open water	Wetlands	Grassland	Urban	Mining	Rank
Plantations	0	+	–	+	–	– – –	– – –	–	+	3
Woodland	–	0	– – –	–	–	– – –	– – –	–	–	0
Shrubland	+	+++	0	+	+	– – –	– – –	+	+	6
Cultivated fields	–	+	–	0	–	– – –	– – –	–	+	2
Open water	+	+	–	+	0	– – –	–	–	+	4
Wetlands	+++	+++	+++	+++	+++	0	+	+++	+++	8
Grassland	+++	+++	+++	+++	+	–	0	+	+++	7
Urban	+	+	–	+	+	– – –	–	0	+	5
Mining	–	+	–	–	–	– – –	– – –	–	0	1

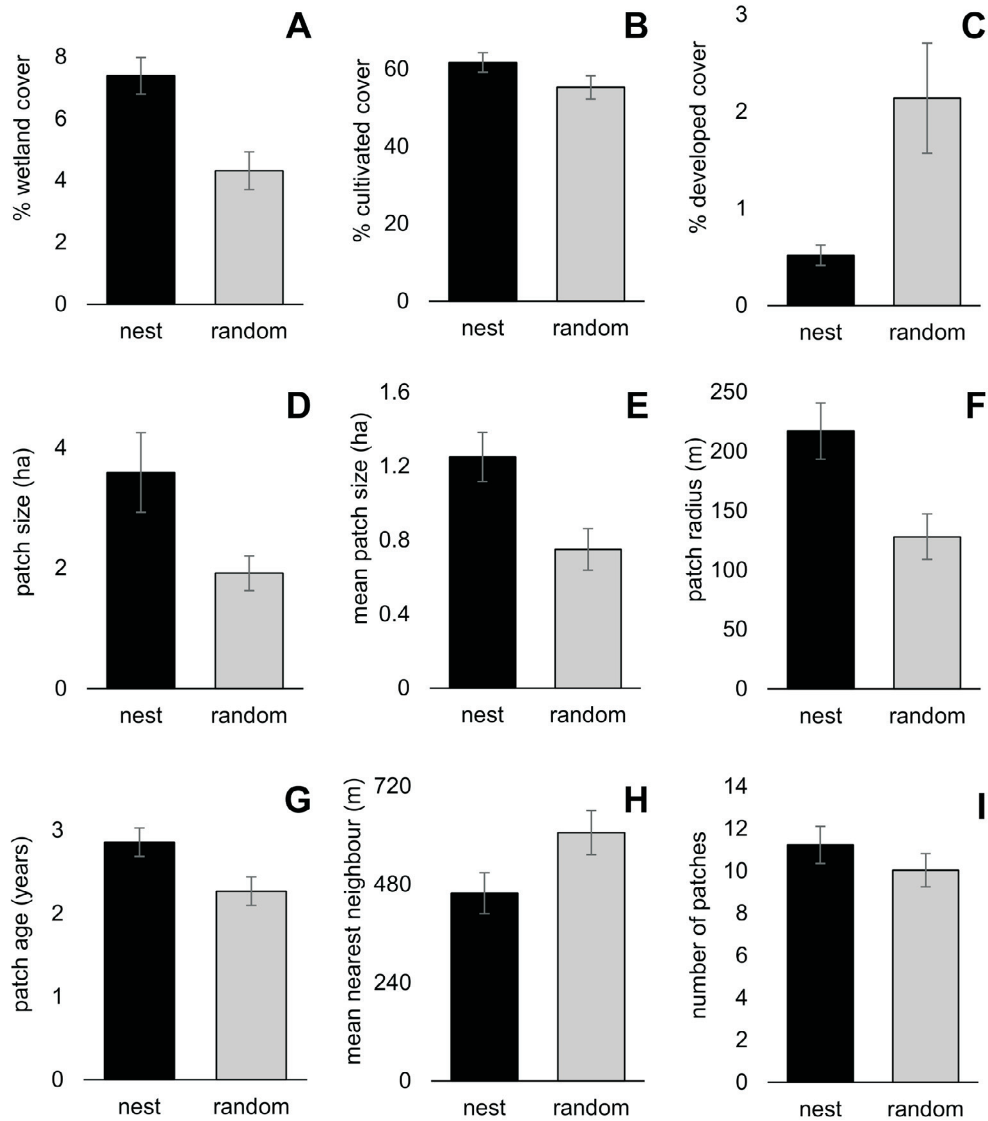

Fig. 2. Habitat variables separating African Grass Owl nest sites and random points on the Highveld Grasslands of South Africa. African Grass Owls used nest sites with a greater % wetland (**A**), greater % cultivated (**B**) and a lower % developed (**C**) land-cover than random sites. Patch metrics used for nesting included a greater patch size (**D**), greater mean patch size (**E**) and greater patch radius (**F**). They also favoured older patches (**G**), smaller mean nearest-neighbour distance (**H**) and more patches (**I**) than random sites.

general availability of cultivated fields and the rodent prey they attract.

Compositional analysis of 2nd-order habitat use (use of home ranges within the study area) contrasted with that of 3rd-order habitat use, as cultivated fields were the third-most used land-cover type (after grasslands and wetlands), and showed a general avoidance for urban, mining and shrubland land-cover (Table 4).

Multivariate models: nest site use and nest survival

There was little support for multivariate models testing the potential-prey-site and edge-effect hypotheses; all the candidate models within the 95% confidence set and $\leq 2\ \Delta AIC_c$ of the top-ranked model supported the total foliage hypothesis (Table 5). The candidate models included different combinations of four variables separating African

Table 4. Ranking matrix describing 2nd-order habitat use, based on a comparison of the proportions of land-cover types within African Grass Owl home ranges with the availability of habitat types within the study area. The symbols + and – denote preference and avoidance, respectively, and the number of + or – symbols is related to the significance of the preference or avoidance, as determined by means of compositional habitat analysis.

Land-cover type	Plantation	Woodland	Shrubland	Cultivated fields	Open water	Wetlands	Grassland	Urban	Mining	Rank
Plantations	0	–	+	– – –	–	– – –	– – –	+++	+	3
Woodland	+	0	+++	–	–	– – –	– – –	+++	+++	4
Shrubland	–	– – –	0	– – –	– – –	– – –	– – –	+	+	2
Cultivated fields	+++	+	+++	0	+	+	–	+++	+++	6
Open water	+	+	+++	–	0	– – –	– – –	+++	+++	5
Wetlands	+++	+++	+++	–	+++	0	–	+++	+++	7
Grassland	+++	+++	+++	+	+++	+	0	+++	+++	8
Urban	– – –	– – –	–	– – –	– – –	– – –	– – –	0	–	0
Mining	–	– – –	–	– – –	– – –	– – –	– – –	+	0	1

Table 5. The 95% confidence set of multivariate models describing nest site use in African Grass Owls. Candidate models within ≤ 2 ΔAIC_c are indicated by an asterisk (*). 95% Confidence sets of models are limited to models of $\Sigma\omega_i$ ≤ 0.95. AIC_c = Akaike's Information Criterion adjusted for sample size; ΔAIC_c = difference in AIC_c between the *i*th and the best model; ω_i = Akaike weight for the *i*th model; *K* = number of model parameters; $\Sigma\omega_i$ = sum of Akaike weights.

Model	AIC_c	ΔAIC_c	ω_i	Likelihood	*K*	$\Sigma\omega_i$
age + radius (*)	19.94	0.00	0.32	1.00	2	0.32
age + radius + wetlands (*)	19.98	0.04	0.32	0.98	3	0.64
age + size + radius + wetlands (*)	21.50	1.56	0.15	0.46	4	0.79
age + size + wetlands (*)	21.89	1.96	0.12	0.38	3	0.91
age + size + radius	23.82	3.88	0.04	0.14	3	0.95

Grass Owl nest sites from random sites. These included patch age, radius of gyration, patch size and percentage wetland land-cover within the home range. Patch age was represented in all of the candidate models.

A total of 20 models were included in the 95% confidence set describing the influence of nest site use variables on African Grass Owl nest survival. Seven of these were considered candidate models ≤ 2 ΔAICc (Table 6), including a mixture of variables supporting mainly the edge-effect hypothesis. The percentage developed land-cover within the home range was the only model scoring higher than the constant daily nest survival rate model (the null model – *S* (~1)). As with the difference between African Grass Owl nest and random patches (univariate MPLR model coefficient β = –55.28), the relationship between African Grass Owl nest survival and the percentage developed land-cover within the home range was negative.

DISCUSSION

In this study, we investigated three hypotheses related to African Grass Owl nest site use, restricting the analyses to the preferred nest substrate on the Highveld Grasslands of South Africa, *Imperata cylindrica*. At the home range scale of 423 ha, nine patch metrics and land-cover variables separated African Grass Owl nest patches from random patches. Patch metrics of the focal patch (*e.g.* patch age, size and radius) indicate that African Grass Owls used patches that provide better cover than others available in the home range (total foliage hypothesis). Other significant patch metrics, including mean patch size, mean nearest neighbour distance and the number of patches, supported the hypothesis that nest sites were located

Table 6. The 95% candidate set of models explaining the influence of nest site use on African Grass Owl nest survival (*S*). Candidate models within ≤ 2 ΔAIC_c are indicated by an asterisk (*). 95% confidence sets of models are limited to models of $\Sigma\omega_i \leq 0.95$. AIC_c = Akaike's Information Criterion adjusted for sample size, ΔAIC_c = difference in AIC_c between the *i*th and the best model, ω_i = Akaike weight for the *i*th model, *K* = number of model parameters, $\Sigma\omega_i$ = sum of Akaike weights.

Model	AIC_c	ΔAIC_c	ω_i	Model likelihood	*K*	$\Sigma\omega_i$
S developed (*)	137.61	0.00	0.11	1.00	2	0.11
S (~1)	137.81	0.19	0.10	0.90	1	0.22
S proximity index (*)	138.57	0.95	0.07	0.61	2	0.29
S mining (*)	139.08	1.47	0.05	0.47	2	0.35
S developed + proximity index (*)	139.27	1.66	0.05	0.43	3	0.40
S size (*)	139.40	1.78	0.04	0.40	2	0.45
S number of patches (*)	139.52	1.90	0.04	0.38	2	0.49
S radius (*)	139.60	1.99	0.04	0.36	2	0.53
S developed + mining	139.65	2.04	0.04	0.35	3	0.58
S mean patch size	139.68	2.06	0.04	0.35	2	0.62
S mean nearest neighbour distance	139.75	2.14	0.04	0.34	2	0.66
S grassland	139.78	2.16	0.03	0.33	2	0.70
S wetlands	139.78	2.17	0.03	0.33	2	0.74
S cultivated	139.79	2.18	0.03	0.33	2	0.78
S mining + cultivated	140.93	3.32	0.02	0.19	3	0.80
S age + radius	141.24	3.62	0.01	0.16	3	0.82
S number of patches + mean patch size	141.29	3.68	0.01	0.15	3	0.84
S size + grassland	141.38	3.76	0.01	0.15	3	0.86
S radius + size	141.39	3.78	0.01	0.15	3	0.87
S number of patches + mean nearest neighbour distance	141.45	3.84	0.01	0.14	3	0.89
S mean nearest neighbour distance + mean patch size	141.50	3.89	0.01	0.14	3	0.91

in patches that are more difficult for predators to locate, because of the greater search effort required (potential-prey-site hypothesis). African Grass Owls thus used nest patches with both greater total foliage and potential nest site density. Multivariate nest site use models supported the former. This result contrasts with experiments conducted by Chalfoun & Martin (2009), who tested the same hypotheses, although the species studied differed greatly in terms of life history traits and their position on the trophic scale.

Our results suggested that not all random *Imperata cylindrica* patches within the home range may have been available to African Grass Owls as alternative nesting sites, as patch age and size influenced foliage density, which was critical to providing the cover and structure for building the roofed tunnels typical of nests. African Grass Owls thus probably used nest patches based on total foliage, and there may only be one suitable patch within the home range. This finding was supported by our observations of nest site fidelity by African Grass Owl pairs in this study. The condition of an *Imperata* patch is dynamic over time because of periodic fires or other disturbances. Our observations have shown that nesting females left the territory during such times, ignoring other, undisturbed patches within the home range, and returned to nest in the original patch when it again became suitable. Quantity and quality of the foliage within the nest patch was thus favoured over quantity of other patches within the home range.

Land-cover characteristics were also important drivers of both nest site use and nest survival, although specific land-cover types were not consistent in their influence on these two aspects. African Grass Owls preferred patches with a greater percentage wetland-cover within the home range; however multivariate models indicated that the percentage developed land-cover influenced nest survival to a greater extent than other variables. Being a ground-nesting species, African Grass Owl nests are inheritably vulnerable to predation by mammals. Assuming the owl possesses some defensive capability against smaller predators, introduced mammals such as feral/domestic cats and dogs probably play a significant role in nest predation. More developed land-cover close to nests increases the probability of contact and places them at a greater risk to predation by these species.

How birds alter their choice of nest site in light of significant environmental changes is variable, depending largely on the species and type of habitats involved (Woodward, Fink & Thompson, 2001). The relationship between nest site use and nest survival is also inconsistent within species and local populations (Davis, 2005; Reilly & Benson, 2019). The consequences to fitness (*e.g.* Mitchell, Warner & Jansen, 2013) may therefore not always be clearly interpreted as nest site use being adaptive. There could be several explanations for the disparity between habitat features used for nesting and those that drive nest survival rates, as was the case with this study. One explanation is the ecological-trap hypothesis, which is demonstrated particularly in reference to edge-effects (*e.g.* Černý, Rymešová & Šálek, 2020) and density-dependent predation (*e.g.* Purcell & Verner, 1998). According to Donovan & Thompson (2001), ecological traps require that an organism exhibits a preference for certain habitats and that selecting preferred (trap) habitat leads to lower fitness. In this study, African Grass Owls have certainly shown a preference for certain habitat features, and this preference was repeated despite having territories with significantly different combinations of land-cover types. The difference between features that improved nest survival and those that were chosen as a nest site was not clearly interpretable as an edge-effect, although human development and the impact of concomitant shrinking habitat was evident. We did not study edge-effects and the ecological trap theory for all life stages that influence fitness. Even when nest survival rates lead to no apparent conclusion that nesting near habitat edges influences fitness, the survival of offspring may yet be impacted in the post-fledging stage (Shipley, Murphy & Elzinga, 2013). This aspect has not yet been investigated sufficiently in the case of the African Grass Owl because of poor success in monitoring marked birds.

Habitat use by radio- and GPS-tracked African Grass Owls was addressed for 2nd-and 3rd-order scales. There was a contrast in preferred and avoided land-cover types between the two different scales of use, although wetlands were generally preferred over other land-cover types. Preference for wetlands was particularly significant within the home range, confirming previous observations of this species' dependence on this land-cover type for nesting and hunting habitat (*e.g.* Kemp, 2005; Kemp & Calburn, 1987; Mendelsohn, 1989; Whittington-Jones & Peacock 2015). The avoidance of cultivated fields at the home-range scale may be attributed to prey preference, as this land-cover type supports granivorous rodents (*e.g.* the Highveld gerbil *Gerbilliscus brantsii*) considered to be pests to farmers, while wetlands harbour larger, herbivorous species (*e.g.* the vlei rat, *Otomys auratus*), which have been identified as the preferred prey of the African Grass Owl (Pretorius 2019). Larger crops such as maize may also provide a challenging structure for hunting owls to navigate when coursing over and stooping down on prey. Avoidance of urban, woodland and mining land-cover types was not unexpected, as African Grass Owls have rarely been seen utilizing such habitats. This observation points to a lack of niche overlap between African Grass Owls and their congener, the Barn Owl (*Tyto alba*). It is the adaptation of the latter to transformed environments that has made it one of the most successful and widespread species of bird in the world (König *et al.*, 2008).

In general, the ranking of land-cover types in terms of habitat use was expected, considering their preference of prey and nest site use, however subtle differences between 2nd-and 3rd-order results illustrate the influence of scale. The use of cultivated fields at the 2nd-order scale appeared to be driven by differences in agricultural land use. At this larger scale, African Grass Owl presence reflected the latitudinal gradient in agricultural potential within the study area, characterized by a predominance of livestock farming to the south and to the north of a belt of grain production situated between 25.5°S and 26.5°S (see Waldner *et al.*, 2017 for cropland mapping). The negative impact of trampling by livestock may thus have been an important driver of nest site use not captured by the analyses in this study, because grassland land-cover was not separated into natural, fallow and grazed pastures. There may also be a positive impact of fallow land lying between cultivated fields, which are usually well protected from burning by firebreaks. Protection from livestock, fire and predators would create the most suitable habitat for breeding African Grass Owls, given the sources of nest mortality. Unfortunately, South African farmers often employ a mixed crop/livestock strategy to improve resilience against climate instability, and crops such as maize (*Zea mays*) are opened to livestock post-harvest to provide supplementary feed from waste grain. Conversely, land that is solely used for grain production may offer better protection from livestock, but also provide better opportunities for nest predators since farmers have less need to control them.

Testing these predictions may lead to more useful estimates of habitat suitability at larger spatial scales. Indeed, the scale of analysis is shown to influence results in studies of both habitat use (*e.g.* Thompson & McGarigal, 2002) and nest survival (*e.g.* Huhta, 1995). Scale determines the degree of habitat fragmentation, and the impacts of habitat fragmentation on avian nest site use and nest survival are more likely to be detected at a landscape scale and over a period of several years (Stephens, Koonsa, Rotella & Willey, 2003) than at the patch-level analyses conducted in this study. Patch metrics used in the matched-pairs logistic regression of this study can be applied to larger scales, although patch definition and delineation may be more difficult to achieve compared with our simple *Imperata cylindrica* binary vector.

The African Grass Owl is thought to be a habitat specialist regarding its preference for wetlands and adjacent moist grasslands (Whittington-Jones & Peacock, 2015). In this study we have illustrated how the species is restricted by nest site availability, despite being able to construct its own nest cavities. The fragmentation of breeding habitat has long been considered a significant driver of decreased annual reproductive success in birds (Robinson & Wilcove, 1994, Winfree 2004). We argue that this influence is two-fold in African Grass Owls: 1) suitable nest patches become more limited, and 2) an increase in developed land-cover increases predation risk from feral/domestic animals. To further substantiate these results, and because resource use is affected by scale, we recommend that future studies examine the influence of the spatial correlation of resource availability (*e.g.* Backwell, 2007). Identifying African Grass Owl nest-predator species should also be prioritized, and we suggest using more sophisticated/sensitive camera trapping technologies than what has been employed thus far.

CONCLUSIONS

The main findings of this study indicated that the quality of breeding territories occupied by African Grass Owls on the Highveld was based on habitat characteristics that improve the overall fitness of individuals, and that their choice of breeding habitat was influenced by cover from predators. To maintain the integrity of current African Grass Owl territories and provide adequate habitat to promote the establishment of new sites, we propose the following guidelines for the Highveld Grasslands: 1) Maintain a wetland/moist-grassland matrix with an area totalling at least 42 ha (50% 'core area' of the plugin kernel density estimate). 2) Include in this area a main nest patch of *Imperata cylindrica* of ≥ 3.6 ha. 3) Protect the core area from fire by means of firebreaks that are maintained annually. 4) Burn the core area at an interval of between three and six years to maintain adequate cover and structure of the *Imperata cylindrica* and prevent the grass from becoming too moribund. 5) If possible, maintain a second patch within the 423-ha home range, burnt alternately with the main core area to ensure that the territory holders always have an alternative patch available to them. 6) Limit development within the home range area. 7) Exclude livestock from the core area and do not overstock the whole home range area, thereby maintaining functional drainage lines. 8) Remove alien vegetation as much as possible, especially highly invasive species such as the pompom weed (*Campuloclinium macrocephalum*).

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Supplementary material to:

African Grass Owl nest site use and nest survival in fragmented grassland landscapes

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Supplementary Figure and Tables

Fig. S1. Delineation (yellow polygons) of *Imperata cylindrica* patches on dry-season Google Earth images.

Table S1. Patch metrics used to describe African Grass Owl nest sites and random *Imperata cylindrica* patches.

Table S2. Land-cover variables used to describe landscape features within 423 ha buffers around African Grass Owl nest sites and random points. Land-cover classes were taken from the 2013–2014 South African national land-cover dataset (Geoterraimage, 2015).

Table S3. Hypotheses about nest site selection in African Grass Owls and the variables used in matched-pairs logistic-regression models.

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Delineation of *Imperata cylindrica* patches

The dark red leaf-frond colour of *Imperata cylindrica* makes patches of this grass species clearly visible on satellite imagery, and its rhizomatous nature results in patches characterized by circular shapes (Fig. S1). These properties make it distinguishable from other grass species during the late dry season. To test whether remote sensing can be used as a tool for classifying and delineating *Imperata cylindrica* patches, we drew polygons around patches typical of the shape and colour of the species, using Google Earth images from the late dry season (July to September). A total of 15 342 patch-polygons were identified within the study area. Because patch delineation was unsupervised and subjective, the final shapefile containing individual polygons was validated in the field by means of a driven transect, conducted in May 2017. The route covered 382 km across the centre of the study area. A total of 81 *Imperata* patches intersected the route. We used parameters of the confusion matrix (Stehman, 1997) to gauge the classification performance of the *Imperata* spatial model. Because *Imperata cylindrica* is associated with moist soil conditions (Van Oudtshoorn, 2012), predicted 'no' was taken to be wetlands predicted to not contain *Imperata* ($n = 207$ of 282 wetlands intersecting the transect). The final accuracy of the model was taken to be a balance between sensitivity and specificity, *i.e.* (sensitivity + specificity)/2 (Kuhn, 2018).

The *Imperata cylindrica* spatial model correctly predicted 67 out of 81 patches bisecting the driven transect, resulting in a sensitivity of 83%. Of the wetlands not predicted to contain *Imperata cylindrica*, the model failed to predict absence for only three out of 207 wetlands, resulting in a specificity of 99%. The ratio between correct and incorrect classifications culminated in an overall model accuracy of 94%, and a balanced accuracy ((sensitivity + specificity)/2) of 91%. These statistics indicated a good fit of the delineation of *Imperata cylindrica* patches.

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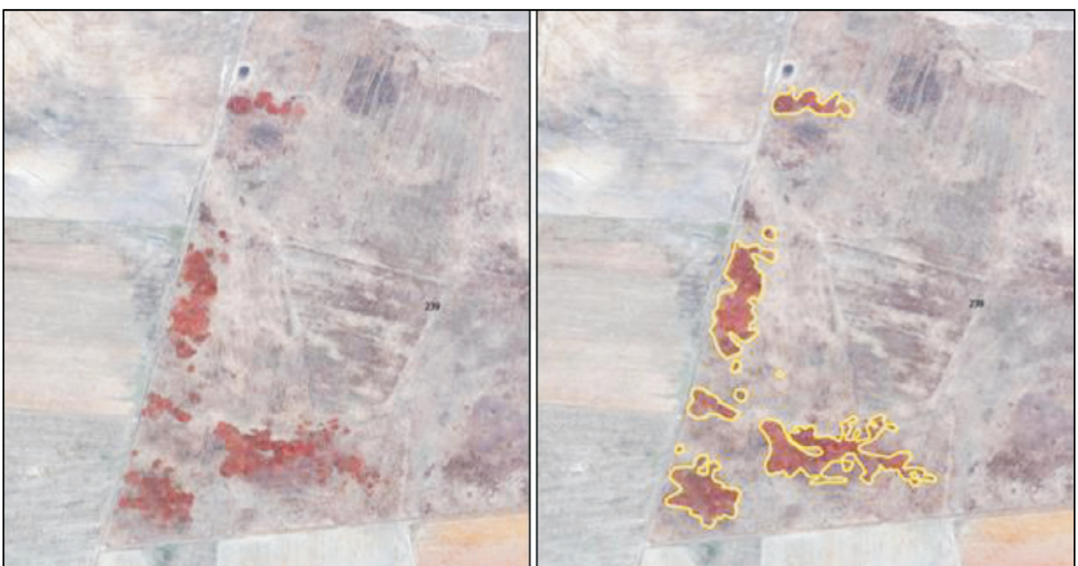

Fig. S1. Delineation (yellow polygons) of *Imperata cylindrica* patches on dry-season Google Earth images.

Table S1. Patch metrics used to describe African Grass Owl nest sites and random *Imperata cylindrica* patches.

Patch metric	Description	Equation
number of patches	Number of patches	
age	Time since last burn in years	
size	Patch area	
area-perimeter ratio	Ratio of patch area to perimeter	$\frac{a}{p}$
shape index	Deviation from a circular shape	$\frac{p}{2\sqrt{\pi . a}}$
Voronoi polygon	Voronoi polygon area	
radius	Radius of circle drawn from the polygon centroid	
mean patch size	Average patch size	$\frac{\sum a}{NP}$
nearest neighbour distance (NND)	Minimal distance to target patch of the same size class	
mean nearest neighbour distance	Mean distance to target patch in the same size class	$\frac{\sum NND}{NSP}$
proximity index	Sum of the ratio of the total size of the focal patch and its neighbours of the same size class to their distances from the focal patch	$\sum \left[\frac{a_{patch_i}}{\left(d_{patch_i}\right)^2} \right]$

a = area; p = perimeter; NP = number of patches; NSP = number of similar patches; d = distance; $patch_i$ = focal patch

Table S2. Land-cover variables used to describe landscape features within 423 ha buffers around African Grass Owl nest sites and random points. Land-cover classes were taken from the 2013–2014 South African national land-cover dataset (Geoterraimage, 2015).

Name	Description	Land-cover classes
cultivated	Percentage area under cultivation within the specified buffer around the nest/point	10–31
grassland	Percentage grassland within the specified buffer around the nest/point	7
mining	Percentage area under mining within the specified buffer around the nest/point	35–41
developed	Percentage urban and/or developed area within the specified buffer around the nest/point	42–72
wetlands	Percentage wetland area within the specified buffer around the nest/point	3
woodland	Percentage woody vegetation within the specified buffer around the nest/point	4, 5, 6, 32, 33, 34

Table S3. Hypotheses about nest site selection in African Grass Owls and the variables used in matched-pairs logistic-regression models.

Hypothesis		Prediction
H_0	Nest patch selection is not different to random	All variables: nest = random
H_1	Total foliage hypothesis	
	African Grass Owls favour nest patches with better nest concealment by vegetation	age_{nests} > $patch\ age_{random}$
		$size_{nests}$ > $patch\ size_{random}$
		$area\text{-}perimeter\ ratio_{nests}$ > $area\text{-}perimeter\ ratio_{random}$
		$shape\ index_{nests}$ > $shape\ index_{random}$
		$radius_{nests}$ > $radius_{random}$
		$grassland_{nests}$ > $grassland_{random}$
		$wetlands_{nests}$ > $wetlands_{random}$
H_2	Potential-prey-site hypothesis	
	African Grass Owls favour nest patches with a larger predator search area	$number\ of\ patches_{nests}$ > $number\ of\ patches_{random}$
		$Voronoi\ polygon_{nests}$ < $Voronoi\ polygon_{random}$
		$nearest\ neighbour\ distance_{nests}$ < $nearest\ neighbour\ distance_{random}$
		$mean\ patch\ size_{nests}$ > $mean\ patch\ size_{random}$
H_3	Edge-effect hypothesis	
	African Grass Owls favour nest patches with habitat features that decrease the amount and proximity of ecotones	$proximity\ index_{nests}$ > $proximity\ index_{random}$
		$mining_{nests}$ < $mining_{random}$
		$developed_{nests}$ < $developed_{random}$
		$woodland_{nests}$ < $woodland_{random}$
		$cultivated_{nests}$ < $cultivated_{random}$
		$diversity_{nests}$ < $diversity_{random}$