


On the brink of extinction—Habitat selection of addax and dorcas gazelle across the Tin Toumma desert, Niger

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Abstract

Aim: To assess the distribution and occurrence of addax (*Addax nasomaculatus*), the most critically endangered ungulate species globally, and dorcas gazelle (*Gazella dorcas*), for which the ecology in the southern Sahara is virtually unknown.

Location: Tin Toumma desert, Niger

Methods: Integrating field surveys, collected over a 7-year period (2008–2014), with remote sensing-derived measures of vegetation productivity (NDVI) and surface roughness, we fit models in a generalized linear regression framework to predict and evaluate the occurrence of addax and dorcas gazelle.

Results: Addax declined significantly over the course of the study, strongly affecting the outcomes of our regression models. Other factors, namely surface roughness and the occurrence of the perennial grass *Stipagrostis acutiflora*, were important in predicting addax occurrence. Dorcas gazelle, inhabiting areas further to the south of our study area, were more positively associated with increases in vegetation productivity than addax. Both species were observed to have a strong negative response to human disturbance. Predictive models, relying only on remotely sensed derived variables, provided insight into areas of habitat suitability and highlighted niche partitioning across the Sahelo-Saharan biome.

Main conclusions: Our results provide improved insight into the factors contributing to the occurrence of this critically endangered (addax) and vulnerable (dorcas gazelle) species and may help guide future field surveys across the region to locate small and geographically isolated populations. Developing statistically based ecological habitat models provide a first-step towards improved management and policy development for the long-term conservation of these species and complement field surveys conducted across the region to monitor species that are increasingly being pushed to extinction.

KEYWORDS

Addax nasomaculatus, *Gazella dorcas*, niche partitioning, Niger, Termit & Tin Toumma National Nature Reserve

1 | INTRODUCTION

The Sahara desert is the largest desert region in the world, supporting a unique and charismatic flora and fauna (Beudels, Devillers, & Lafontaine, 1998; Brito et al., 2014). Most impressive are the ungulate assemblages of the Sahelo-Saharan region, historically including flagship species such as

addax (*Addax nasomaculatus*), dama gazelle (*Nanger dama*), dorcas gazelle (*Gazella dorcas*) and scimitar-horned oryx (*Oryx dammah*). Over the past few decades, however, the Sahara has suffered a catastrophic decline in its megafauna (Durant et al., 2014), a result of overhunting, habitat loss and desertification (Newby, Wachter, Durant, Pettorelli, & Gilbert, 2016). Of the 14 large vertebrates found across the region, four are now extinct in the

wild (including scimitar-horned oryx), while most others persist across a small fraction of their former range (Durant et al., 2014; Ripple et al., 2016).

Systematic scientific research has been severely limited across the Sahelo-Saharan region, due in part to the region's size and political instability, reducing the capacity to adequately assess the ecology and habitat requirements of these desert-adapted species (Belbachir, Pettorelli, Wachter, Belbachir-Bazi, & Durant, 2015; Brito et al., 2014; Durant et al., 2012). Many regions remain data deficient, with most existing data considered circumstantial or the product of merging incomplete records between years and over large areas. Incorporating data from field surveys into statistical frameworks with remotely sensed derived variables can help further our understanding of the factors driving site occupancy and help guide field surveys into unexplored regions (e.g., Pearson, Raxworthy, Nakamura, & Townsend Peterson, 2006; Pettorelli, Owen, Duncan, & Freckleton, 2016).

Once found in large numbers over immense arid areas, addax is now considered one of the rarest antelopes on earth. The International Union for Conservation of Nature (IUCN) classifies the species as critically endangered (IUCN International Union for the Conservation of Nature, 2015). The largest (and perhaps only) population remaining in the wild (~100 individuals at the time of this study) exists in eastern Niger across the Tin Toumma desert and the great erg of Bilma (Actman, 2016; Rabeil, 2016; Rabeil, Garba, Harouna, Abagana, & Bello, 2016). Other sporadic records exist of small isolated groups and individuals from the eastern Air Mountains/western Ténéré desert in Niger, the Eguey region of western Chad, and in the Majabat Al Koubra in Mauritania, although no sightings have been recorded in any of these areas since 2007 (IUCN International Union for the Conservation of Nature, 2015; Rabeil, 2016). While highly adapted and able to survive without drinking water for extended periods (Newby, 2006), addax occasionally move into Sahelian regions during times of prolonged drought. These areas, now progressively occupied by humans, increase the vulnerability of addax to increased hunting/poaching pressure and competition with livestock (Newby, 2006). Even core Saharan areas, formerly refuge for the species, are increasingly accessible by man, further increasing the potential for population extinction (Duncan, Kretz, Wegmann, Rabeil, & Pettorelli, 2014; Edwards et al., 2014).

Dorcas gazelle are more widely distributed across the desert than addax (IUCN International Union for the Conservation of Nature, 2015). Considered a habitat generalist (Chammem, Selmi, Nouria, & Khorchani, 2008), the species may be even more susceptible to displacement from pastoral land uses than addax due to a perceived affinity to Sahelian regions. Dorcas gazelle are classified as vulnerable to extinction (IUCN International Union for the Conservation of Nature, 2015), although the most recent global estimate of 35,000–40,000 individuals remaining across Sahelo-Saharan Africa (East, 1999) is both out of date and likely inflated. In the Tin Toumma desert, the population is estimated to be 1,500–2,000 individuals (Rabeil, Newby, & Harouna, 2008). Dorcas gazelle are assumed to be in rapid decline due to poaching and disturbance from oil activities (Duncan et al., 2014; Rabeil & Newby, 2014; Wachter, Rabeil, & Newby, 2010), factors which have been shown to affect movement and resource use of ungulates in other studies/regions (e.g., Northrup, Anderson, & Wittenmyer, 2015), although quantitative estimates do not exist.

We incorporated data from field surveys collected across the Tin Toumma desert with remote sensing-derived variables of vegetation

quality and surface roughness to identify the factors contributing to habitat suitability for addax and dorcas gazelle. Our focus was geared towards identifying how these species share resources across this harsh landscape and increase our understanding of the factors shaping habitat selection. We predicted (P1) strong spatial separation between the occurrence of both species, with addax occurrence increasing in hyperarid areas to the north of the Tin Toumma desert and dorcas gazelle limited to areas further to the south where higher levels of biomass productivity exist; (P2) human disturbance to have a strong negative effect on the occurrence of both species; and (P3) local vegetation to be important in models predicting species occurrence. In addition to our predictions, we develop predictive surfaces of habitat suitability, providing valuable information to guide future field surveys into unexplored regions and help locate isolated populations which may exist.

2 | METHODS

2.1 | Study area

The Tin Toumma desert and the Great erg of Bilma (~97,000 km²) are located in north central Niger, lying between the erg of Ténéré in the north and the Sahelian zone in the south (Figure 1). Along the region's western boundary, the Tin Toumma is limited by the Termit Massif, one of the most biologically diverse strongholds of large desert vertebrates remaining in the Sahara with several significant desert landscape features. In the north, prevalent north-eastern winds have created dune fields comprising large linear and parallel ("seif") dunes with a NE-SW alignment. Dunes are interspersed by rocky outcrops. To the west and closer to the Termit Massif, the dunes are irregularly spaced, resulting in mobile dunes (i.e., barkhans) separated by deep depressions. In 2012, the Niger government established the Termit & Tin Toumma National Nature Reserve across this desert region, representing the largest protected area in Africa (Figure 1).

Ecologically, the southern Tin Toumma represents the transition zone between Sahelian and Saharan ecosystems. Climate and rainfall patterns throughout the transition zone are modulated by differences in landform, producing unique patterns in seasonal and spatial resource distributions. Large dunes, for example, create shelter from wind and allow for greater moisture retention. Consequently, interdune depressions and flat areas throughout the Tin Toumma can facilitate perennial vegetation growth of grass/bush species such as *Stipagrostis vulnerans*, *Stipagrostis acutiflora*, *Cornulaca monacantha* and *Cyperus conglomeratus* (Wachter et al., 2004). In areas to the south where winds are reduced, smooth linear dunes separated by large flat sandy areas occur. These flat sandy areas are often colonized by annual plants, including *Aristida mutabilis* (Rabeil et al., 2008), emerging at the onset of the rainy season (July). July–September are typically the wettest months of the year. Average annual rainfall is 68 mm/year (Xie & Arkin, 1997; Appendix S1).

2.2 | Field data collection

Between December 2008 and 2014, we conducted 15 transect surveys along nine routes east of the Termit Massif (Figure 1, Table 1). Transects were spaced at ~10-km intervals running west to east. We collected

FIGURE 1 Topography and survey transects throughout the Tin Toumma desert, Niger. See Table 1 for transect survey dates. Image source: Shuttle Radar Topography Mission (SRTM)

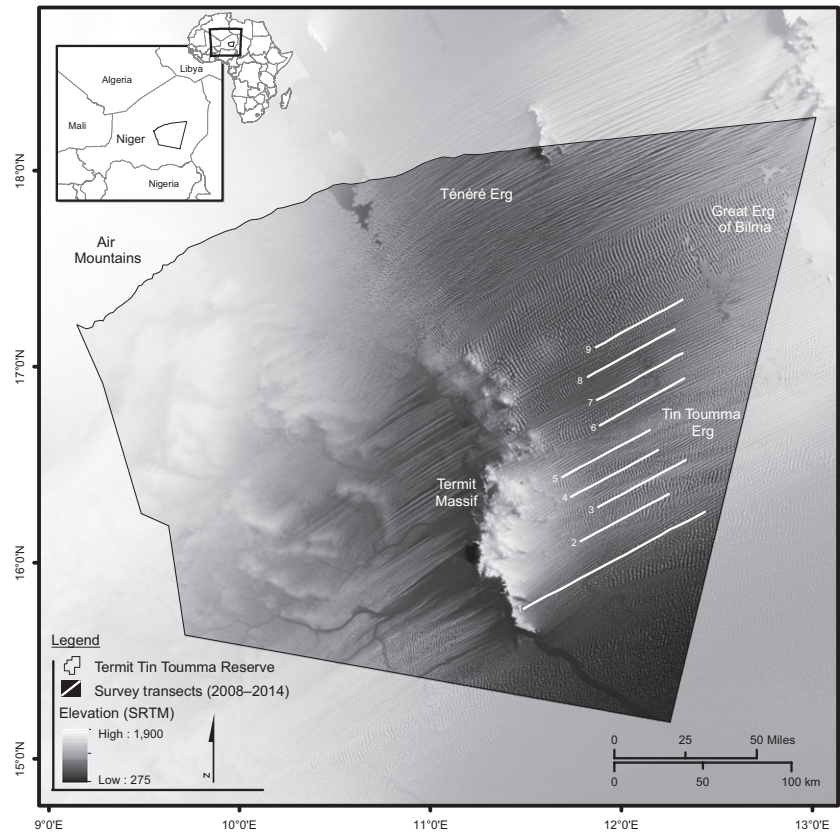


TABLE 1 Occurrence and prevalence for addax (*Addax nasomaculatus*) and dorcas gazelle (*Gazella dorcas*) at sampling locations across the Tin Toumma desert, Niger

Year	Season	Transect ID ^a	Plot Locations	Occurrence (n)		Species Prevalence (%)		Site Prevalence ^b (%)	
				Addax	Dorcas gazelle	Addax	Dorcas gazelle	One	Both
2008	Cold	1–5	66	22	28	33.3	42.4	68.2	7.6
2009	Dry	1–5	66	6	16	9.1	24.2	28.8	4.6
2009	Wet	1–5	66	8	19	12.1	28.8	39.4	1.5
2009	Cold	1–5	66	16	33	24.2	50.0	63.6	10.6
2010	Dry	1–5	66	4	15	6.1	22.7	24.2	4.6
2010	Dry	1–5	66	8	19	12.1	28.8	37.9	3.0
2010	Wet	1–5	66	3	13	4.5	19.7	24.2	0.0
2010	Cold	1–5, 8–9	88	14	29	15.9	33.0	44.3	4.6
2011	Dry	4–5, 8–9	44	7	4	15.9	9.1	15.9	9.1
2011	Wet	1, 4–5, 8–9	66	10	12	15.2	18.2	24.2	9.1
2012	Cold	4–9	66	8	9	12.1	13.6	21.2	4.6
2013	Cold	1–5	66	16	35	24.2	53.0	60.6	16.7
2014	Dry	4–9	66	4	9	6.1	13.6	16.7	3.0
2014	Wet	4–9	66	4	8	6.1	12.1	18.2	0.0
2014	Cold	2–6, 8	66	1	34	1.5	51.5	51.5	1.5
				Mean:		13.2	28.5	35.9	5.4

^aSee Figure 1 for transect ID locations.

^bSite prevalence is calculated as the percentage of the plot locations having at least one (One) or both (Both) species present.

Addax models	K ^a	AIC _c	ΔAIC _c ^b
Rough + Rough ² + NDVI + NDVI ² + Humans + Dorcas gazelle + <i>Stipagrostis vulnerans</i> + <i>Stipagrostis acutiflora</i> + <i>Cornulaca monacantha</i> + Season + Year	18	642.9	0.00
Reduced Model			
Rough + Rough ² + NDVI + NDVI ²	5	744.6	101.7
Dorcas gazelle models	K ^a	AIC _c	ΔAIC _c ^b
Rough + Rough ² + NDVI + NDVI ² + Humans + Addax + <i>S. vulnerans</i> + <i>S. acutiflora</i> + <i>C. monacantha</i> + Season + Year	18	976.9	0.00
Reduced Model			
Rough + Rough ² + NDVI + NDVI ²	5	1105.3	128.4

^aNumber of estimable parameters.

^bDifference in value between Akaike's information criterion for small sample sizes (AIC_c) of the full and reduced variable model.

data across all seasons, including relatively cold (November–February), dry (March–June) and wet (July–October) periods. Transect routes were surveyed by vehicle, driving at a speed of 15–20 km/hour, and were either ~100 km (southernmost transect) or ~50 km (all others) in length. Between four and seven transects were surveyed at each time period (Table 1). Total survey length was 562 km. Along each transect, we counted addax and dorcas gazelle directly via sightings and indirectly via fresh tracks within 500 m of the transect (Newby, Wachter, Monfort, Dixon, & Houston, 2004). We assumed perfect detection due to habitat conditions, survey swath width and animal size. At each observation, we recorded the global positioning system (GPS) location (latitude/longitude, WGS84 datum), date/season and number of individuals. Transects shifted slightly between season and year of survey due to changes in landform (e.g., shifting sands). As a result, we aggregated animal counts within a 2.5 km radius of plot locations spaced 5 km apart, allowing for a conservative broad-scale approach to incorporate low population densities. Evidence of human disturbance (e.g., sighting, vehicle track) was collected and summarized in the same manner.

To automate and standardize data collection, we used a PDA/GPS unit or a tablet and saved records to an open-source survey database (<http://www.cybertracker.org/>). Data were projected to UTM 32N, WGS84. Results were re-coded to a measure of occurrence (presence/absence). Vegetation occurrence information, thought a priori to influence species' distribution, was collected at plot locations. These data included the occurrence of vegetation species *S. vulnerans*, *S. acutiflora* and *C. monacantha* (Beudels et al., 1998; Newby et al., 2004; Rabeil, Beudels-Jamar, & Greth, 2010).

2.3 | Satellite data and data processing

Following methods described by Mueller et al. (2008), we integrated addax/dorcas gazelle occurrence with satellite-derived estimates of primary productivity to develop models predicting habitat suitability. Primary productivity was estimated from Normalized Difference Vegetation Index (NDVI) data from the moderate-resolution imaging spectroradiometer (MODIS). NDVI is known to be strongly correlated with a region's vegetation productivity/greenness (Goward & Prince, 1995; Tucker, 1979) and has been used extensively as an important

TABLE 2 Full vs. reduced variable regression models predicting addax (*Addax nasomaculatus*) and dorcas gazelle (*Gazella dorcas*) occurrence across the Tin Toumma desert, Niger. Parameter descriptions defined in the text

parameter in models predicting animal movement and habitat use (e.g., Boone, Thirgood, & Hopcraft, 2006; Hopcraft et al., 2014; Mueller et al., 2008; Pettorelli, 2013; Pettorelli et al., 2005, 2014) and for quantifying vegetation dynamics in desert ecosystems (Dall'Olmo & Karnieli, 2002).

MODIS NDVI data (MOD13Q1; <https://lpdaac.usgs.gov/>) are provided in 16-day, cloud-free data composites with a 250 m spatial resolution. We matched the date of each transect survey with the NDVI composite date, reprojecting and mosaicking adjoining tiles to UTM Zone 32N, WGS84. Mean NDVI was summarized within a 2.5 km radius and extracted at each plot location. We also calculated the change in local elevation range (referred to as "surface roughness" or "Rough") from 30-m Shuttle Radar Topography Mission (SRTM) data (<https://lta.cr.usgs.gov/SRTM>; SRTM, 2004). Defined as the difference between the minimum and maximum values of a cell and its eight surrounding neighbours (Wilson, O'Connell, Brown, Guinan, & Grehan, 2007), pixels with similar neighbourhood values have a low change in elevation range (e.g., flat areas), whereas highly variable neighbourhoods have a large change in elevation range (e.g., steep slopes).

2.4 | Statistical analysis and validation

We fit generalized linear models (logistic regression, logit link), inclusive of all covariates, with addax or dorcas gazelle occurrence as the response variable to evaluate the relative importance of each parameter. We tested for independence between data points to determine whether we met model assumptions by inspecting spatial semi-variograms and correlograms across an array of lag distances. No violations were observed (Appendix S2). We standardized $([x - \bar{x}] / \sigma_x)$ the continuous predictor variables and included quadratic terms for these parameters to investigate nonlinear relationships. None of the input variables had collinearity issues, assessed via a variance inflation factor analysis (Hair, Anderson, Tatham, & Black, 1995; Appendix S3). The year of survey was included as a factor in models, with 2007 (the first year of our field survey) as the reference class. We created a reduced variable model for each species, inclusive only of NDVI and surface roughness (and their quadratic forms), to evaluate the effectiveness of these continuous variables at predicting habitat suitability across our entire study area and to provide useful information to

guide future field surveys. Reduced variable models were compared with full models using Akaike's information criterion corrected for small sample sizes (AIC_c). Model structure is provided in Table 2. Analyses were conducted in R (version 3.3.1, R Development Core Team, 2013).

To evaluate model fit, we calculated the area under the receiver-operating curve (AUC; DeLeo, 1993; Zweig & Campbell, 1993) and performed 10-fold cross-validation (Fielding & Bell, 1997; Hastie, Tibshirani, & Friedman, 2005). Fit of our reduced variable models was further evaluated by incorporating an independent dataset collected via aerial survey in November 2007 (Wacher, Newby, & Rabeil, 2007). The survey was conducted across the study region using a standard fixed strip-width survey method (Norton-Griffiths, 1978) and extended to the west of the Termit Massif. Survey transects were set 10 km apart, with a sample strip width of 500 m on either side of the aircraft (i.e., 1,000 m effective strip width) as addax, highly visible in the open landscape, were the main target species. Transects were flown at an altitude of 150 m. The aerial survey resulted in the detection of 60 addax in eight groups and 164 dorcas gazelles in 69 groups.

2.5 | Model prediction

To predict addax/dorcas gazelle occurrence across the study area, we applied our reduced variable model by matching a MODIS NDVI 16-day composite (NDVI image date: 17 November 2007) to the aerial survey date. Additional predictive surfaces were created to investigate shifts in habitat suitability during dry (NDVI image date: 06 March 2007) and wet season periods (NDVI image date: 13 August 2007). NDVI and surface roughness were processed

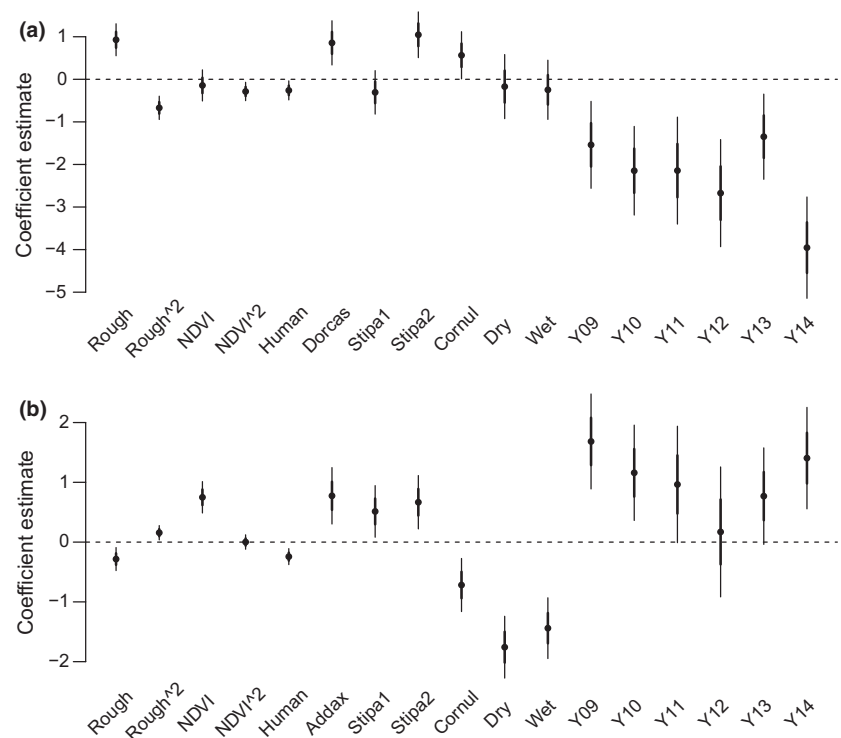
using the same procedures described in data processing (i.e., scaled and centred) after summarizing pixel values within a 2.5-km moving window (function focal, R raster library (Hijmans & van Etten, 2012)). We resampled the NDVI to 30 m using bilinear interpolation to match the resolution of the surface roughness. From the resulting cold season predictive surface, we extracted the predicted value and calculated the mean value where addax and dorcas gazelle were observed during the aerial survey. We compared these values with the prediction means of 1,000 random toroidal shift simulations of the relocation pattern within a boundary box of the surveyed area (Fortin & Dale, 2005). We determined the significance of our model by summarizing how many of the simulated patterns had a higher average probability of occurrence than the mean calculated from the observed addax/dorcas gazelle locations (as in Mueller et al., 2008). We used the prevalence of addax/dorcas gazelle from our line transect surveys (the fraction of survey points with observed occurrence) as the threshold value in classifying presence/absence of each species (addax occurrence threshold: $prevalenceAddax > 0.13$; dorcas gazelle occurrence threshold: $prevalenceDorcas > 0.29$).

3 | RESULTS

3.1 | Habitat suitability models

The parameter "Year" had the largest effect in models predicting addax occurrence, with a strong negative response observed over the time period (2008–2014) of our field surveys (Figure 2a, Appendix S4). Vegetation productivity, approximated by NDVI, and surface roughness ("Rough") were also important factors

FIGURE 2 Coefficient estimates from generalized linear models predicting addax (a) and dorcas gazelle (b) occurrence. Dry and wet seasons (dry/wet) are compared with the cold season reference class. Years 2009–2014 (Y09–Y14) are compared with year 2008 (reference class). The continuous variables NDVI (Normalized Difference Vegetation Index) and Rough (surface roughness) have been standardized $[(x - \bar{x}) / \sigma_x]$. Grass species *Stipagrostis vulnerans* (Stipa1), *Stipagrostis acutiflora* (Stipa2) and *Cornulaca monacantha* (Cornul) compared with absence of each species



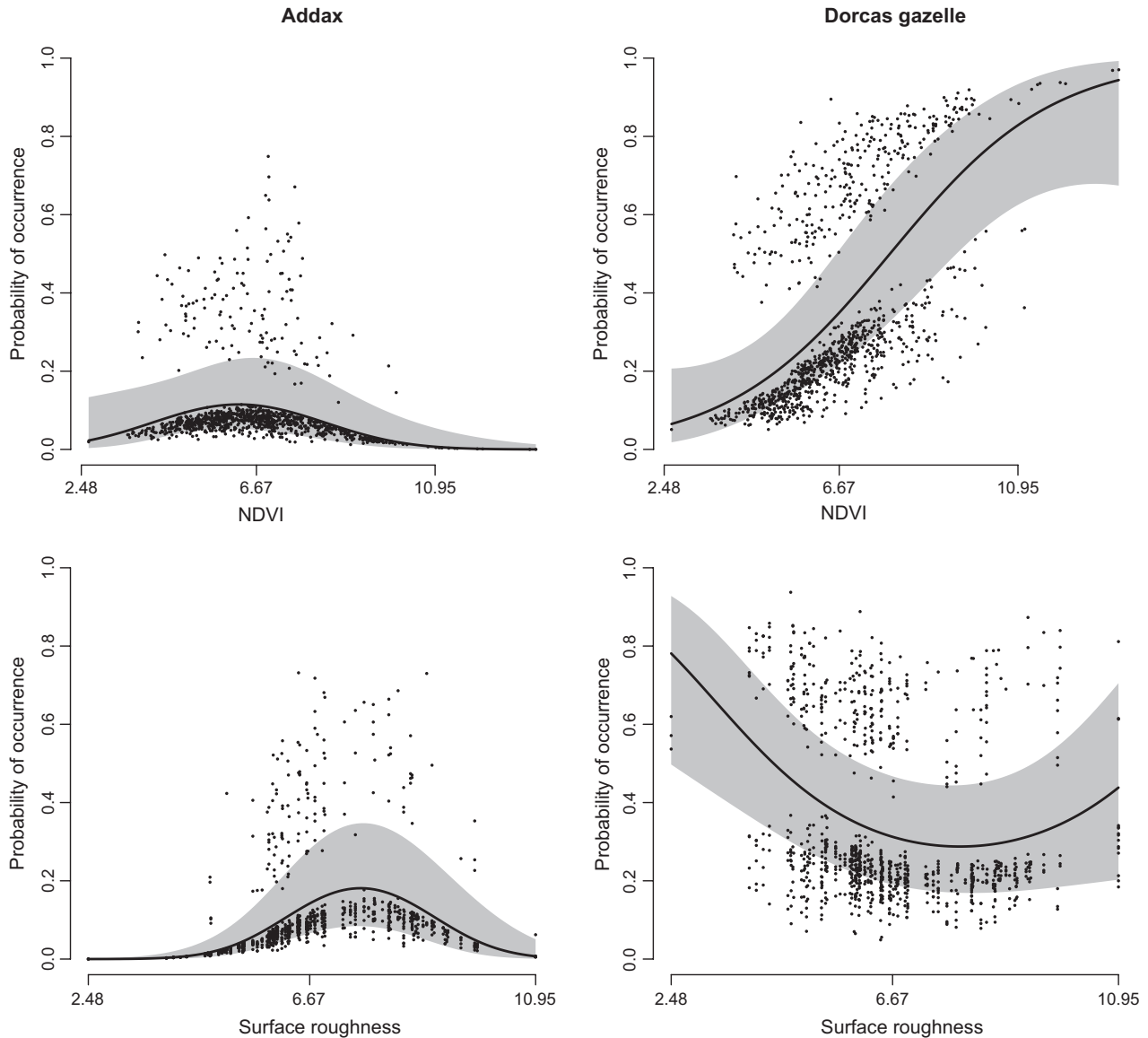


FIGURE 3 Probability of species occurrence for addax (*addax nasomaculatus*) and dorcas gazelle (*Gazella dorcas*) in relation to NDVI (Normalized Difference Vegetation Index) and surface roughness (Rough)

contributing to addax occurrence. Both parameters were significant ($p < .01$), highlighting an intermediate parameter range leading to increased probability of occurrence (Figures 2a and 3). Other factors, namely the occurrence of dorcas gazelle, and perennial grasses *S. acutiflora* and *C. monacantha*, also led to increased addax occurrence probability. Addax avoided areas with increased human disturbance and had no change in occurrence probability across seasonal sampling periods (Figure 2a, Appendix S4). AUC statistics highlight a good fit to the data (0.82), with 10-fold cross-validation providing additional model support (0.87). Coefficient values, Z-scores and confidence intervals for all parameters are provided in Appendix S4.

Contrary to addax, the year of survey had a strong positive effect on dorcas gazelle occurrence in relation to the initial year of our survey (2008). Coefficient estimates also highlight a decrease in dorcas gazelle occurrence from 2009 to 2012 followed

by an increase from 2012 to 2014. The response to vegetation productivity, approximated by NDVI, was also significantly positive (Figures 2b and 3), emphasizing that dorcas gazelle occurrence increases with increased vegetation productivity. Dorcas gazelle occurrence was highest during cold season periods, with significant negative responses observed during dry and wet seasons (Figure 2b, Appendix S4). The response to surface roughness showed clear distinctions to our model of addax occurrence, with dorcas gazelle occurrence probability being highest in areas of low and high surface roughness (Figures 2b and 3). Other positive responses were observed in relation to the occurrence of addax, *S. acutiflora* and *S. vulnerans*. Significant negative responses were observed in relation to human disturbance (similar to addax) and the occurrence of *C. monacantha* (contrary to addax). AUC and 10-fold cross-validation for our dorcas gazelle occurrence model were 0.81 and 0.77, respectively.

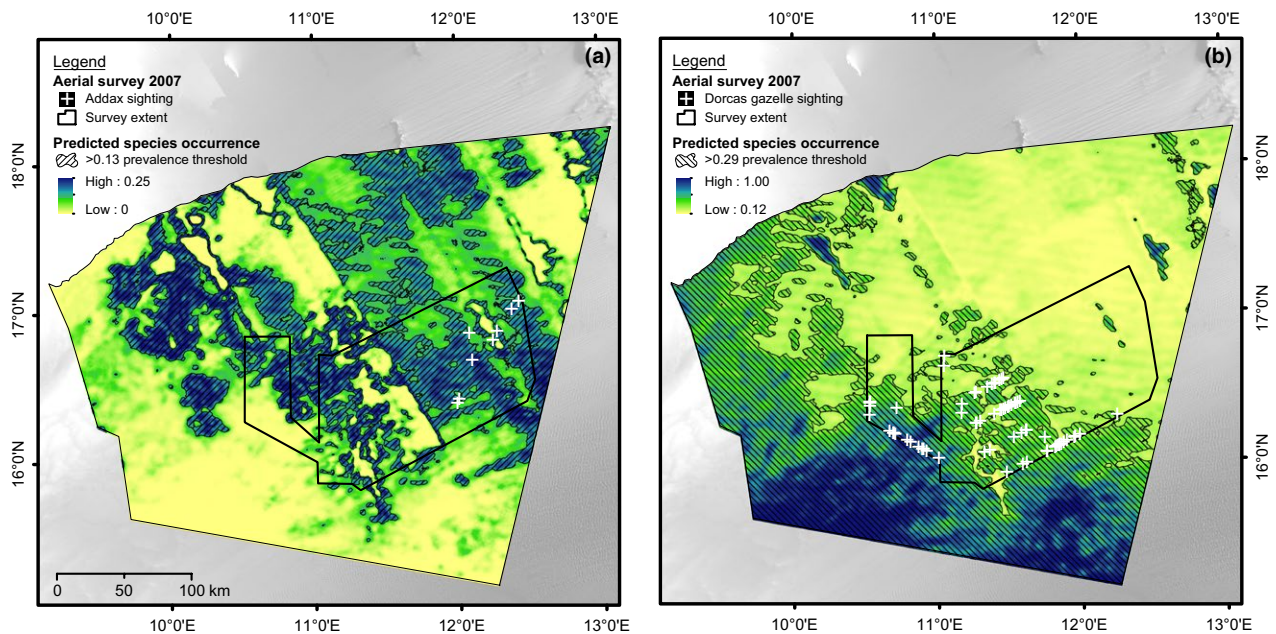


FIGURE 4 Predicted species occurrence for addax (a) and dorcas gazelle (b) across the Termit & Tin Toumma National Nature Reserve. Validation data from a 2007 aerial survey. Note that the prevalence threshold and the range of predicted species occurrence differ between species. [Colour figure can be viewed at wileyonlinelibrary.com]

3.2 | Prediction models

Spatially explicit model predictions from our reduced variable structure revealed significant spatial separation between the occurrence of addax and dorcas gazelle across the Tin Toumma (Figure 4). Similar spatial trends were observed in dry and wet season periods (Appendix S5). The total area of predicted overlap in the cold season was 4,997 km², corresponding to 16% of the predicted occurrence for addax and 11% of the predicted occurrence for dorcas gazelle. Occurrence probability for addax was greatest in the central and northern sections of the study area. Dorcas gazelle occurrence probability was greatest in more mesic regions, primarily in the south and south-west of our study area, seemingly following moisture and vegetation gradients rather than landform. Total area of predicted occurrence during the cold season was 31,183 km² for addax and 45,950 km² for dorcas gazelle, 32% and 47% (respectively) of the study area (Appendix S6). Marginal changes occurred in the total area of predicted habitat suitability between seasonal periods, with the density in predicted suitability increasing in wet and cold season periods (Appendix S5).

Predictive models were significantly weaker in performance than full models, illustrated by the difference in AIC_c (Table 2) and AUC statistics (0.66 for addax; 0.69 for dorcas gazelle). Ten-fold cross-validation results, however, were similar to full models (0.87 for addax; 0.72 for dorcas gazelle). Coefficient estimates remained significant for parameters NDVI (quadratic form) and surface roughness (listed in Appendix S7). Accuracy of our model predictions was high for both species, with random shifts of the survey data having a higher than average prediction in 88 of 1,000 simulations ($p = .09$) for addax and 182 of 1,000 simulations ($p = .18$) for dorcas gazelle. While sample

sizes were low, 50% of addax observations (four of eight groups) were located in areas of predicted occurrence compared with 78% of dorcas gazelle observations (54 of 69 groups). All observations were within 2.3 km of the predicted occurrence threshold, distances easily traversed by each species.

4 | DISCUSSION

We examined field data collected over a 7-year survey period to estimate habitat suitability of a critically threatened and a vulnerable ungulate across Africa's largest protected area. Our results provide ecological insight into the effects of fine-scale information on the probability of occurrence of these desert-adapted species, with a number of locally collected parameters shown to have strong effects (P3), and highlight the effectiveness of remote sensing-derived variables at predicting species occurrence across the Termit & Tin Toumma National Nature Reserve. While expectedly weaker than full models inclusive of local plot-based information, predictive models may help guide future field surveys into unexplored regions and provide a methodology for assessing habitat suitability prior to potential reintroduction efforts.

The strongest effect observed in species occurrence models was year of survey. For addax, this parameter highlights a strong decline in species occurrence over our study period. While not unexpected, it draws attention to the dire situation for this critically endangered ungulate, with the latest survey (March 2016) indicating that there are fewer than 100 individuals across this harsh desert landscape, perhaps the only place left on earth where wild addax still exist (Actman, 2016; Rabeil, 2016; Rabeil, Garba, Harouna, Abagana, & Bello, 2016). For

dorcas gazelle, the fluctuations in species occurrence coincide with the peak in oil prospection across the Tin Toumma (2009–2011), followed by a time of relative quiet until the breakdown of the Gaddafi regime (end of 2013) when the occurrence of dorcas gazelle was observed to increase. The different responses of each species to the year of survey likely relate to differences in levels of persecution (i.e., addax are larger and would be expected to be more valued for their meat) or allee effects (Kramer, Dennis, Liebholt, & Drake, 2009; Stephens & Sutherland, 1999) resulting from small and isolated populations. Emigration could also lead to occurrence changes, although this factor is likely minimized due to the length, areal extent and conservative methodology used to denote species occurrence.

In contrast to dorcas gazelle models, few variables had strong effects on predicting addax occurrence. This is a result of the sparse number of sightings across the survey region/study period, muting parameter responses of other variables and reducing the explanatory power of our top model. The inclusion of additional data layers could help to improve fit (e.g., modified soil adjusted vegetation index (Qi, Chehbouni, Huete, Kerr, & Sorooshian, 1994), fine-scale estimates of vegetation productivity), but are unlikely to circumvent the recognized limitations of the occurrence dataset.

Dorcas gazelle were observed in higher abundance than addax throughout the survey period, resulting in models with greater explanatory power. Several factors including NDVI, surface roughness, human disturbance (P2) and season of survey were observed to have strong parameter effects on species occurrence. The response of NDVI likely indicates that the species is more dependent on vegetation quantity than addax, leading to niche partitioning between the two species across the Sahelo-Saharan biome and observed in our predictive models (P1). Dorcas gazelle are known to be habitat generalists (Chammem, Selmi, Noura, & Khorchani, 2008), feeding on a variety of plants across flat-gravel plains (Mallon & Kingswood, 2001), dry wadis (Baharav & Mendelssohn, 1976) and subdesert steppes (Dupuy, 1967). This generalist strategy could explain why we observed a U-shaped response to the parameter surface roughness, tracking flushes in vegetation across a range of habitats. Alternatively, the species' acknowledged sensitivity to disturbance caused by human activities (Chammem, Selmi, Noura, & Khorchani, 2008) could account for why we observed an increase in occurrence probability across areas with high surface roughness, with animals potentially being forced into these areas. Including interactive terms, such as the season or year of survey, with surface roughness into our models could help further evaluate whether this observed response is a result of seasonal habitat changes or localized disturbances that may have occurred throughout portions of our study period, but not others.

Our predictive model highlights differences in habitat selection among addax and dorcas gazelle (P1), with addax occurring in remote, difficult-to-access and very dry fringe habitats to the north-east of the Termit Massif. These areas have intermediate levels of surface roughness and have historically provided refuge for addax from predators and locally based subsistence hunters. More recently and especially as oil exploration activities have increased throughout the region, these areas are no longer free of permanent human settlement (Duncan

et al., 2014). Addax move more slowly than other species of antelope (Krausman & Casey, 2007), making them easy targets for modern hunters outfitted with vehicles and armed with automatic weapons (Actman, 2016). Dorcas gazelle habitat, however, was located more to the south/south-west of the Massif. These areas offer better vegetation production across flatter, less topographically diverse areas than drier areas to the north, but incur increased use by domestic grazers and local pastoralists. As such, growing conservation concern exists for this species as well, even though populations are larger/more stable than addax (IUCN, 2015).

Predictive models performed remarkably well, especially considering the relatively coarse scale of the two remotely sensed variables included in models, exhibiting high predictive power and accuracy when tested with independent data. This was an encouraging result which could be applied to other regions with similar habitat characteristics, such as the Ténéré and Majâbat al Koubra in Niger and Mauritania where addax have been observed in the past. Additional survey data from these regions could further evaluate our result and aid in prioritizing survey effort. A key question, however, is whether or not predicted areas represent prime habitat for either species. Addax, for example, are severely restricted in comparison with their former habitat range. Thus, predicted habitat could represent fringe areas rather than core areas, but most certainly represents a subset of habitats in which the species formerly persisted. Climate forecasts also predict that the severity and frequency of drought will increase across Sahelian regions in the coming decades (United Nations Environment Programme (UNEP), 2011; Payne & Bro-Jorgensen, 2016), reducing the area of suitable habitat available and increasing the vulnerability of wildlife to anthropogenic disturbance.

Coefficients related to the season in which field surveys were conducted changed non-significantly for addax. For dorcas gazelle, however, the probability of occurrence was highest during the cold season. During cold season periods, dorcas gazelle move northwards to exploit seasonal grazing, providing support for alterations in habitat use that have been suggested by other researchers (Baharav & Mendelssohn, 1976; Ward & Saltz, 1994). Predictive models created from NDVI data illustrate only small shifts in the areal extent of predicted occurrence throughout the region (Appendix S5). Interesting, however, is the increased density of occurrence that is observed across the predicted range during wet and cold season periods. Information on the movement patterns of these animals would help determine the extent of movements between seasonal ranges, especially considering the patchiness of habitat that relates to the localized variability of rainfall throughout the region, and provide a measure of the degree of interaction with human disturbances when vegetation conditions deteriorate.

The occurrences of *S. acutiflora* and *C. monacantha* were both observed to be important locally collected parameters in models for addax and dorcas gazelle (P3). *S. acutiflora* is a perennial grass, often observed to be eaten by addax and dorcas gazelle during periods of rapid growth with greening. The positive response to this variable provides empirical support to expectations from field observations. *C. monacantha*, however, is very salty and unlikely to be eaten regularly by either species, although addax do eat it when there are no other

options. While speculative, the animals' response to this resource is more likely related to indirect secondary effects, such as other plants (e.g., *Cistanche phelypaea*) found in association with *C. monacantha* or the shelter that the plant provides from persistent winds. *C. phelypaea* is a parasitic plant that extracts water and nutrients from the roots of neighbouring plants, resulting in a large root mass full of moisture. Addax may exploit this valuable water source during portions of the year, although the actual proportion of use is unknown (Rabeil/Wacher, pers. observ.).

We did not incorporate the detectability of either species into our sampling design. Many authors (e.g., Gu & Swihart, 2004; Kéry, 2010; Kéry & Schmidt, 2008; MacKenzie, 2006; MacKenzie et al., 2002, 2006; Royle & Dorazio, 2008) have stressed the importance of accounting for detection probability in models of species occurrence, emphasizing that disregarding detectability has the potential to underestimate species' distributions, bias covariate relationships towards zero and incorporate factors into predictive models that also affect the difficulty with which a species is observed. We have assumed detectability to be near 1, a reasonable assumption given the landscape and the size of each animal. Incorporating this component into future surveys, however, could help improve the strength of parameter relationships and provide an important framework for separating potential confounding relationships, such as the relationship of species occurrence/detectability in areas of high surface roughness. Future field surveys, where the distance and angle to the animal are collected, could aid in estimating undercounting bias and be included in predictive models of habitat suitability.

For species occurring across expansive open areas, such as addax and dorcas gazelle, combined ground and aerial survey offer perhaps the best method to enumerate, monitor and assess the conservation status of threatened species (Wacher, Potgieter, Hassan, Dogringar, & Rabeil, 2015). Although expensive and often suffering from an unknown level of under-counting bias (Mallon & Kingswood, 2001), aerial surveys can be combined with other non-invasive methods (i.e., track counts (Keeping & Pelletier, 2014)) to better estimate the status and distribution of rare Saharan ungulates. Our results from ground surveys highlight a strong and consistent decline in addax across our study period and provide detailed information on the effect of individual parameters on species occurrence. Further surveys can help monitor population changes, but urgent conservation action is required if these species are to persist into the future.

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BIOSKETCH

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SUPPORTING INFORMATION

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