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Modelling habitat suitability of reintroduced scimitar-horned oryx (*Oryx dammah*) in Sidi Toui National Park, Tunisia

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Abstract

Reintroducing endangered species into their restored habitats is a significant aspect of conservation biology. The scimitar-horned oryx (*Oryx dammah*), one of the most critically endangered antelopes worldwide, was reintroduced into several protected areas in Tunisia. Understanding their habitat requirements within micro-level ecosystems is crucial for developing effective management plans to aid in species recovery. Using information-theoretic and multimodel inference (MMI) techniques, we evaluated the impact of habitat and management characteristics on the distribution of the scimitar-horned oryx in Tunisia's Sidi Toui National Park during different seasons, from June 2020 – May 2022. Our analyses, using regression coefficients and selection probabilities, revealed that factors influencing habitat suitability varied seasonally for the scimitar-horned oryx. However, the presence of grasses emerged as the most consistent indicator of their occurrence throughout the year. The strong fit of models to the data was confirmed by Receiver Operating Characteristic (ROC) plots, which indicated an Area Under the Curve (AUC) > 0.9. The study has significant implications for developing practical habitat management plans for the scimitar-horned oryx in Sidi Toui National Park

1. INTRODUCTION

Reintroduction, an increasingly common strategy in conservation and management, refers to releasing a species into a previously native area after eradication due to human activities or natural disasters (IUCN/SSC 2013). Reintroduction efforts are aimed at restoring local biodiversity and ensure the long-term survival of previously eradicated species in their native habitats (IUCN/SSC 2013; Berger-Tal et al., 2019). However, reintroductions are uncertain endeavors that might not yield viable populations, even when preceded by extensive research (Godefroid et al., 2011; Ewen et al., 2014). Large herbivore reintroductions have had varying degrees of success, with only 4 of 17 bighorn sheep reintroductions in Utah being successful (Shannon et al., 2008), while 60% of elk reintroduction projects in eastern North America produced viable populations (Popp et al., 2014). More generally, a multi-method analysis based on broad, conservative criteria indicated that only 11% of reintroduction projects were successful (Beck et al., 1994).

Habitat quality in the release area is key to the success or failure of a reintroduction program (Griffith et al., 1989; Osborne & Seddon, 2012). Evaluating habitat quality and the way in which habitat variables affect reintroduced species is essential to reintroduction success (Miller et al., 1999; Stoinski et al., 2003). Generally, habitat assessments for reintroductions involve identifying locations with conditions that seem to match where the species is (or has historically been) known to exist (Armstrong & Reynolds, 2012). Various modeling approaches have been employed to understand the relationships between species and their habitats, aiming to identify potential areas suitable for reintroduction and identify the key environmental factors affecting species distribution (Guisan & Zimmermann, 2000; Phillips et al., 2006; Elith & Leathwick, 2009). Ecologists currently acknowledge that the process of habitat selection is inherently sensitive to scale, recognizing that characteristics of habitats can be studied at various spatial scales. On a broad scale, macro-level terrestrial habitats encompass continents, while at the micro-level, the ecosystem is the fine-scaled local habitat an animal directly occupies as part of its daily activities (Morris, 1987; Kotler & Brown, 1988; Barnes et al., 1998; Traba et al., 2015).

The scimitar-horned oryx, *Oryx dammah* (Cretzschmar, 1826), hereafter referred to as oryx, is a large antelope that is adapted to arid environments (Newby, 1978, 1980; Morrow et al., 2013). Oryx have a flexible foraging strategy (Newby, 1975a; Wakefield, 1992), but prefer grasses (Poaceae) (Mungall & Sheffield, 1994). During the rainy season and colder months, oryx primarily rely on temporary pastures formed by the emergence of annuals, including grasses, as well as young green shoots from perennial shrubs (e.g., Fabaceae (legumes), Nyctaginaceae (four-o'clock flowers), Amarantaceae (amaranths); Gillet, 1965; Newby, 1974a, 1988; Dragesco-Joffé, 1993). However, during the hot season, the oryx's diet can shift towards perennial grasses (Gillet ,1965; Newby, 1974a, 1988; Dragesco-Joffé, 1993), fallen pods of umbrella thorn acacias (Fabaceae: *Vachellia* (formerly *Acacia*) *tortilis*), foliage from shrubs, and a few herbs (Malbrant, 1952; Gillet, 1965; Newby, 1974a, 1988; Dragesco-Joffé, 1993).

Historically, oryx undertook extensive seasonal migrations (Newby, 1978; Harris et al., 2009). Population declines have been attributed to factors including overhunting, habitat degradation and fragmentation, and growing competition with livestock (Lavauden, 1926b; Kacem et al., 1994; Dixon et al., 1991). Oryx were officially declared extinct in the wild in 1999 (Hilton-Taylor, 2000), with the last known sightings occurring in the late 1980s (Newby, 1988). They have been successfully reintroduced into several small fenced, protected areas (100 ha–100 km^2) including, North Ferlo (Senegal), Souss-Massa National Park (Morocco), Bou Hedma National Park (Tunisia), Oued Dekouk Nature Reserve (Tunisia) (Kacem et al., 1994; Beudels et al., 2005), and into Sidi Toui National Park (STNP, Tunisia) in 1999 (Molcanova, 2006). Our study assesses the effectiveness of reintroduction efforts for oryx in STNP by modelling habitat preferences at the micro-level scale, considering their seasonal and spatial variations characteristic's. When reintroduced into an extensive park (93,000 km2, Ouadi Rimé-Ouadi Achim Wildlife Reserve, Chad), the average home range of oryx exceeded 1000 km^2 (Mertes et al., 2019), which is a much larger area than STNP can provide. However, ascertaining specific environmental and ecological factors that characterize their habitat preferences at the micro-level ecosystem scale is crucial to understanding the qualities needed to identify and protect viable habitat patches, as well as to improve the quality of degraded habitats. Given the extreme environmental conditions proximate to the Sahara Desert in southern Tunisia, we hypothesize that oryx would choose different habitat patch characteristics at different times of the year. Specifically, we expect that grasses and forbs will be the main determinants influencing their occurrence. Furthermore, we predict a preference for areas with water accessibility and man-made shade structures during the dry season.

2. MATERIALS AND METHODS

2.1. Study area

Sidi Toui National Park, created in 1991, is a small, protected area in south Tunisia (11.24° E, 32.70° N) spanning 63.15 km^2 of undulating semidesert steppes (Fig. 1). The park contains a hill, Djebel Sidi Toui (culminating at 172 m asl), surrounded by an extensive plain composed of small dunes, sebkhas, and dry sandy wadis, designed to protect a cluster of 14 ancient religious sites (Marabouts) (Souissi, 2008). The region's climate is hot desert (BWh, Köppen-Geiger classification) (Geiger, 1954). STNP is dominated by steppe-like vegetation, including grasses (e.g., *Cenchrus ciliaris*, *Stipa retorta*, and *Stipa lagascae*), forbs (e.g., *Atractylis serratuloides*, *Diplotaxis harra*, and *Medicago minima*), and shrubs (e.g., *Argyrolobium uniflorum*, *Helianthemum sessiliflorum*, and *Ziziphus lotus*) (Tarhouni et al., 2017). The vertebrate fauna is distinct, with various Saharan protected mammals (i.e., *Felis silvestris lybica* (African wild cat), *Vulpes zerda* (Fennec

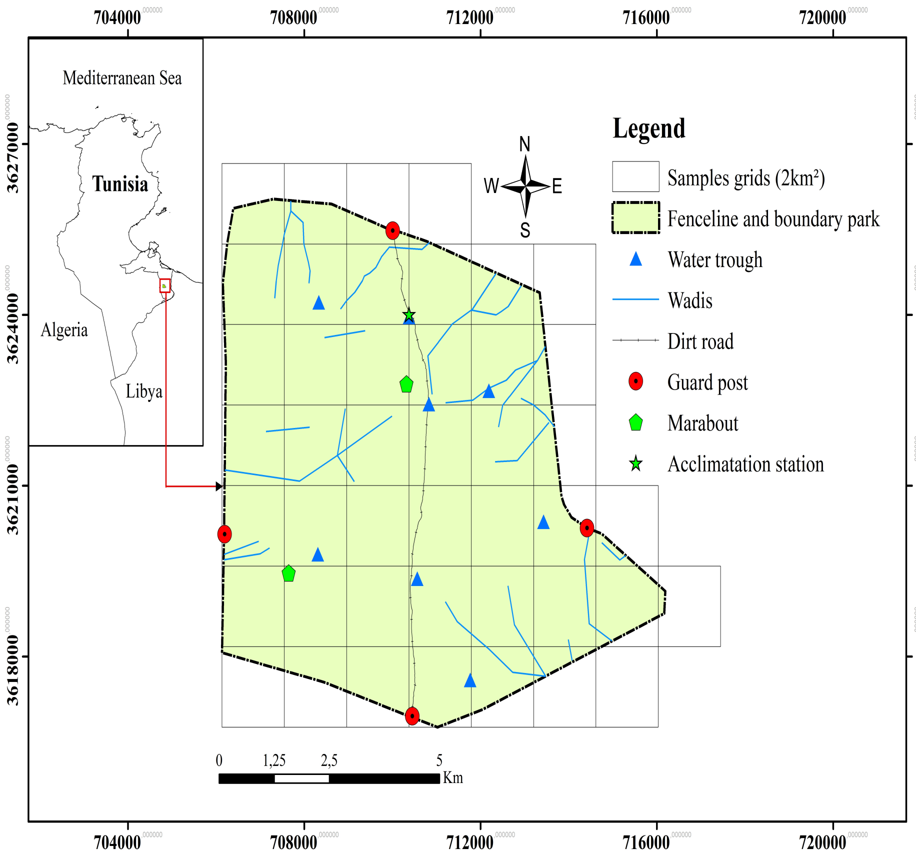

Fig. 1. Localization, delimitation, and infrastructure map of STNP.

sox), *Canis anthus* (African golden wolf), *Vulpes vulpes* (Red fox) and Sahelo-Saharan bovids (i.e., *Oryx dammah* (oryx), *Gazella dorcas* (Dorcas gazelle)). In addition, STNP contains a wealth of avian fauna that includes non-migratory species (i.e., *Alectoris barbara* (Barbary partridge), *Pterocles alchata* (pin-tailed sandgrouse), *Alauda arvensis* (Eurasian skylark), *Corvus corax* (common raven), and *Cursorius cursor* (cream-colored courser), as well as numerous migrants due to the park's location along the Mediterranean and trans-Saharan migration paths. Finally, there are some rare and protected reptiles (i.e., *Chamaeleo chamaeleon* (common chameleon), *Uromastyx acanthinura* (North African spiny-tailed lizard), and various snakes).

2.2. Field design and methods

Data were collected from June 2020 from May 2022 and blocked by season. Seasons were defined as: spring (March–May), summer (June–August), fall (September–November) and winter (December–February). Because 2 km^2 corresponds well with the home range of antelope having a similar morphology to our study species (Krishna et al., 2008; Ben et al., 2013; Fructueux et al., 2020; Ehlers et al., 2020; Kumar et al., 2020), the study area was divided into 40-2 km2 sample units (grids) distributed over a regular grid layer on the GIS platform using ArcGIS (version 10.8). The study area was visited for five days each month with each sampling unit being visited either in the morning or the afternoon. During surveys, each grid was explored by four researchers (ML, KD, AZ, & MJ) who walked in different directions and using binoculars (Leica 10 × 50) searched extensively for oryx, recording whether they were grazing, drinking or resting and GPS coordinates when we found animals (Garmin 60Cx). For analysis, we considered a species to be present in a given sampling site if at least one individual was observed.

2.3. Variable selection

Within each grid, we also recorded variables on the quality and suitability of the habitat that might influence the presence and behavior of oryx (i.e., composition and cover of vegetation, carnivore presence through identified tracks and fresh fecal scats, and the presence of man-made structures: passenger-vehicle accessible dirt roads, man-made water troughs, buildings, or shade shelters).

2.3.1. Habitat quality and suitability

Using the point-quadrat method (Daget & Poissonet, 1971), we recorded the subdominant categorical composition and cover of vegetation (n = 3 variables: shrubs (SC), forbs (FC), and grasses (GC)) in each sampling site during each season of the study period. In each sampling site, we randomly located 5–20 m transects. Along each transect, we systematically lowered sampling pins at 20-cm intervals and assessed intercepts made by plants, providing 100 total points per transect. We recorded each time contact was made with a plant species or ground cover class. To determine the cover of each plant species, we summed the intercept measurements for all individuals of that species along the transect line and converted the sum into a percentage to represent total cover. To calculate the total cover for each vegetation category, we added the cover percentages for all plant species within those categories (Tarhouni et al., 2017). For analysis, we averaged the total cover for each plant species and for each vegetation category across the 5 transects in each sampling site.

Within each sampling unit, we also estimated the area covered by wadis (WAD). Wadi lengths, measured using a topography and cartography map of Tunisia (1978), were multiplied by average wadi widths, as determined during surveys. Additionally, we assessed the predation risk (PRE) posed by the African golden wolf (*Canis anthus*), which was the only predator we encountered, by recording signs of its presence within each sampling unit during each season. Specifically, we counted the number of fresh fecal scats, a commonly used method to monitor the abundance of carnivores (Forsyth et al., 2014). Based on the number of fecal pellets observed, we classified predator impact as "class 1" (<10 wolf fecal pellets), "class 2" (10 to < 20 wolf fecal pellets), and "class 3" (≥ 20 wolf fecal pellets).

2.3.2. Man-made structures

Man-made structures (n = 4 variables) included guardhouses and marabouts (DPM), main dirt road and used by visitors (DR), fences (DFE), and constructed water troughs (WT) (Figure 1). We recorded the distance from each grid center to the closest guardhouse post or marabout (DPM) that could potentially hinder the movement of oryx (i.e., park entrances: Magroun, Mhijra, Madi, and Hawach; acclimatization station: Zriba; and major marabouts frequently visited by pilgrims: Rotila and Torki). We utilized the park infrastructure map to measure the percent cover of main dirt road utilized by visitors (DR). The collected GPS coordinates of human infrastructure and the center of sampling sites were imported into ArcGIS® (Version 10.8, Environmental Systems Research Institute Inc., 2023) to calculate the Euclidean distance between each sampling site's center and the nearest category of man-made infrastructure. Similarly, we calculated the distance from the center of each grid to the nearest fence (DFE). Because in hot environments like southern Tunisia, ungulates rely heavily on water sources and shade for maintaining water balance, we also recorded GPS coordinates for artificial water troughs (WT). A total of eight water troughs are distributed across STNP. To assess the distance to artificial water troughs, we assigned "1" if the distance between the grid center and the nearest water point was ≤ 1.414 km (representing the side of the grid (√2 km)) and a value of "0" if the nearest water point was > 1.414 km.

2.4. Statistical data analysis

2.4.1. Modelling effects of predictors on occurrence

We employed information-theoretic and multimodel inference (MMI) techniques on presence-absence data to predict the factors influencing the distribution of oryx in different seasons. To examine the relationship between the probability of occurrence of the oryx and nine explanatory variables (i.e., SC, FC, GC, WAD, PRE, DPM, DR, WT, and DFE), we ran generalized linear models (GLM) and applied binary logistic regression using logit link functions. To avoid autocorrelation and multicolinearity, we used Spearman's rho correlation coefficient to test for pairwise correlation among our nine predictor variables. We retained predictors with a correlation < 0.7 (Wisz & Guisan, 2009) and used the Akaike Information Criterion (AIC Burnham & Anderson, 2002) to compare alternative models. For a given model,

$$AIC = -2\log(L) + 2K$$

where L is the likelihood of the model given the data, and K is the number of parameters in the model. We used AICc to correct for small samples, as n/k < 40 (n sampling sites = 40 and k variables = 9) (Burnham & Anderson, 2002). We fitted a set of competing models using multi-model inference (Burnham & Anderson, 2002). AICc was calculated for each model in the dataset, and we considered the model with the lowest AICc value (AICcmin) as the best, and indicating the most parsimonious fit. To rank the candidate models, we calculated the AICc differences (Δi) relative to AICcmin. Larger Δi values indicate weaker models, with Δi < 2 indicating no significant difference between the models (Burnham & Anderson, 2002).

2.4.2. Significance of predictors

We assessed the relative importance of predictors in determining the habitat suitability for oryx through two approaches: (1) the predictor selection probability, which represents the likelihood of a predictor being included in the top models if the analysis were repeated with a different dataset (Whittingham et al. 2006), and (2) the standardized regression coefficients, which indicate the magnitude of each predictor's contribution to variation in the habitat suitability index.

2.4.3. Model Assessment

We assessed the level of agreement between the best logistic regression model in each season and the explanatory variables with two approaches. First, we used the strength of McFadden's pseudo-R^2 correlation. Higher R^2 values indicate a better fit, and values > 0.40 indicate a very accurate model with strong predictive capabilities. Second, we used the AUC (area under the curve) of the receiver operating characteristic (ROC) to evaluate the performance of the predictive model (Fielding & Bell, 1997; Lobo et al., 2008). Models with AUC values > 0.7 are useful, but values > 0.85 indicate reliable models (Swets, 1988; Fielding & Bell, 1997; Wiley et al., 2003; Glover & Vaughn, 2010).
The statistical analyses were all performed with RStudio (Version 4.3.2, October 2023). We used the "MuMIn" package (version 1.47.5, March 2023) for information-theoretic and multimodel inference.

3. RESULTS

3.1. Modelling the suitable habitat in different seasons

During our two-year investigation, oryx occurred in 16 of the 40 sampling units, indicating a seasonal occupancy rate of 40%. When comparing the binary logistic regression models based on AICc for oryx across different seasons, no single model fit the data (ΔAICc < 2, Table 1). The results of multi-model inference based on model averaging indicate that different variables were selected as determinants of oryx habitat suitability in different seasons. However, grasses emerged as the primary factor influencing oryx habitat selection across all seasons.
During the dry season, the most parsimonious models (Δi < 2) for oryx included grasses (GC) and water troughs (WT) as significant predictors (Table 1), displaying a high probability of selection (≥ 0.90). The remaining variables, specifically fence (DFE), shrubs (SC), and predator presence (PRE), exhibited low selection probabilities (<0.56). Guardhouse post and marabout (DPM) had a low probability of selection in 2020, receiving moderate support with a selection probability of 0.69 and a negative coefficient (-1.63) in 2021. Dirt road (DR) was excluded from all the best models for both years. The variables in the best model for both years were ranked, with WT having the highest coefficient value, followed by GC (Table 2). In the fall, the best models for 2020 and 2021 exhibited significant differences (Table 1), with notable variations in coefficients. In 2020, grasses (GC) and forbs (FC) had strong effects (selection probabilities = 0.86 and 0.88, respectively), while in 2021, with grasses, we note the importance of the selection probability of shrubs (SC) and guardhouse posts and marabout (DPM), which were respectively 0.97 and 0.82. The coefficient for forbs was 0.40. When we ranked their regression coefficients, FC > GC in 2020 and GC > DPM > SC in 2021 (Table 2). During winter, the presence of wadis with grasses emerged as a significant predictor, with selection probabilities of 0.87 in 2020 and 0.81 in 2021. During winter 2021–2022, forbs (FC) also showed a high selection probability (0.83). During the spring of two years, the two most parsimonious models of habitat suitability for oryx included grasses and forbs. Predator (PRE) had a moderate selection probability (0.61) and a relatively important coefficient (1.79) in the best models of 2021. Dirt road (DR) had the highest coefficient (2.56) in 2021, but due to its low selection probability (0.24), it was not adopted. The covariates ranked according to the importance of their coefficients are GC > PRE > FC in spring 2021 and GC > FC in spring 2022.

3.2. Model evaluation

All the habitat suitability models derived from binary logistic regression fit the data well and have high predictive power (Table 3), with McFadden's pseudo-$R^2 > 0.4$ and excellent performance (AUC > 0.9).

Table 1. Information-theoretic statistics of seasonal habitat suitability models for oryx in STNP. The best model is in **bold**. For each predictor included in the best model, we present AICc, AICc differences (ΔAICc), model Akaike weight (Wt), and selection probability. Predictors are shrubs (SC), forbs (FC), grasses (GC), wadi (WAD), distance to guardhouse or marabout (DPM), distance to fence (DFE), dirt road (DR), Predator (PRE), and water troughs (WT).

Predictors										AICc	ΔAICc	Wt
Summer 2020												
AICc best			**GC**						**WT**	**30.83**	**0.00**	**0.13**
		FC	GC						WT	32.51	1.68	0.06
	SC		GC						WT	32.54	1.71	0.05
			GC		DPM				WT	32.75	1.92	0.05
Selection probability	0.21	0.27	0.90		0.22				0.90			
Summer 2021												
AICc best			**GC**		**DPM**			**PRE**	**WT**	**26.95**	**0.00**	**0.10**
			GC		DPM				WT	27.73	0.78	0.07
			GC						WT	28.73	1.78	0.04
			GC		DPM	DFE		PRE	WT	28.89	1.94	0.04
	SC		GC		DPM			PRE	WT	28.92	1.97	0.04
Selection probability	0.20		0.94		0.69	0.19		0.46	0.94			
Fall 2020												
AICc best		**FC**	**GC**							**28.85**	**0.00**	**0.12**
		FC	GC			DFE				30.15	1.30	0.06
		FC	GC				DR			30.47	1.62	0.06
Selection probability		0.88	0.86			0.30	0.22					
Fall 2021												
AICc best	**SC**		**GC**		**DPM**					**29.22**	**0.00**	**0.13**
	SC	FC	GC		DPM					30.04	0.82	0.09
	SC		GC		DPM			PRE		31.10	1.88	0.05
Selection probability	0.97	0.40	0.95		0.82			0.25				
Winter 2020-2021												
AICc best		**FC**	**GC**	**WAD**						**41.13**	**0.00**	**0.09**
			GC	WAD						41.61	0.48	0.07
		FC	GC	WAD				PRE		42.30	1.17	0.05
			GC	WAD	DPM					43.04	1.91	0.04
Selection probability		0.51	0.84	0.87	0.17			0.22				
Winter 2021-2022												
AICc best		**FC**	**GC**	**WAD**						**36.95**	**0.00**	**0.15**
		FC	GC	WAD			DR			38.56	1.61	0.07
	SC	FC	GC	WAD						38.86	1.92	0.06
		FC	GC	WAD					WT	38.89	1.94	0.06
Selection probability	0.22	0.83	0.79	0.81			0.24		0.19			
Spring 2021												
AICc best		**FC**	**GC**					**PRE**		**27.38**	**0.00**	**0.07**
		FC	GC							28.11	0.72	0.05
		FC	GC		DFE			PRE		28.83	1.44	0.04
			GC					PRE		28.88	1.50	0.03
	SC	FC	GC					PRE		29.19	1.81	0.03
Selection probability	0.22	0.75	0.94		0.28			0.61				
Spring 2022												
AICc best		**FC**	**GC**							**36.47**	**0.00**	**0.14**
		FC	GC					PRE		38.24	1.77	0.06
Selection probability		**0.78**	**0.82**					**0.24**				

Table 2: The coefficients and standard errors (SE) calculated from MMI for the AICc ≥ 95% certainty average models for predicting oryx habitat suitability in STNP for different seasons.

Predictors	Intercept	SC	FC	GC	WAD	DPM	DFE	DR	PRE	WT
					Summer 2020					
Estimate	-2.61	-0.04	-0.47	1.80	-0.02	-0.13	0.04	-0.41	0.08	3.77
SE	6.69	0.12	1.30	0.88	0.07	0.40	0.28	2.81	0.36	1.31
					Summer 2021					
Estimate	-9.85	0.05	0.79	3.04	0.01	-1.63	0.17	-2.20	1.40	5.03
SE	10.87	0.18	2.30	1.54	0.07	1.86	0.68	5.71	2.25	2.31
					Fall 2020					
Estimate	-13.28	0.04	4.40	3.67	0.00	0.04	0.19	1.36	-0.10	0.05
SE	9.69	0.15	1.80	2.04	0.04	0.38	0.45	4.24	0.55	0.55
					Fall 2021					
Estimate	-77.35	1.22	0.76	4.34	0.02	1.48	0.04	-0.15	-0.32	0.04
SE	32.80	0.52	1.43	2.10	0.07	1.12	0.30	2.93	0.91	0.64
					Winter 2020/2021					
	-5.51	0.00	0.56	2.51	0.78	-0.11	-0.02	0.52	-0.31	0.09
	4.55	0.07	0.65	1.39	0.37	0.35	0.21	2.55	0.69	0.51
					Winter 2021/2022					
Estimate	-11.40	0.06	3.85	2.45	0.31	-0.09	0.01	1.71	-0.01	0.26
SE	10.69	0.17	1.70	1.50	0.19	0.36	0.24	4.47	0.36	0.76
					Spring 2021					
Estimate	-18.06	0.07	1.35	3.04	-0.01	0.02	-0.26	2.56	1.79	-0.07
SE	14.90	0.20	1.09	1.62	0.06	0.55	0.61	6.58	1.87	0.72
					Spring 2022					
Estimate	-9.97	0.02	2.49	4.37	0.00	-0.01	-0.07	0.97	0.16	0.05
SE	7.06	0.11	1.44	1.81	0.03	0.25	0.30	3.39	0.41	0.49

Table 3: Model goodness of fit, showing pseudo-R^2 (McFadden) and area under the ROC curve (AUC) for the best habitat suitability models for oryx for different seasons in the STNP.

Season	R^2	AUC
Summer 2020	0.62	0.96
Summer 2021	0.80	0.99
Fall 2020	0.64	0.96
Fall 2021	0.70	0.97
Winter 2020/2021	0.46	0.91
Winter 2021/2022	0.55	0.93
Spring 2021	0.77	0.98
Spring 2022	0.53	0.94

4. DISCUSSION

The information-theoretic and multimodel inference indicated that, at the micro-level ecosystem scale, vegetation emerged as the most influential habitat factor affecting the occurrence of oryx in STNP during all seasons. Certainly, the abundance of vegetation, which serves as a significant indicator of food biodiversity and nutritional quality of diets, plays a crucial role in establishing sustainable food systems for herbivore species (Lachat et al., 2018).

Additionally, food high in quality and quantity is a primary determinant for resource partitioning among ungulates in savannah and arid environments (Cromsigt & Olff, 2006; Henley et al., 2007).

Our research confirmed earlier findings that oryx are primarily grazers and prefer a diet of grasses (Gillet 1965, 1966a, 1966b; Newby, 1974a, 1975b, 1988; Dragesco-Joffé, 1993; Robinson & Weckerly, 2010; Wache, 1988; Wakefield, 1996a; Spalton, 1999). Oryx can also adopt a flexible strategy in its search for food. Across all seasons, grasses in STNP were the best indicator of oryx presence. Forbs had a comparatively lesser effect but still played a significant role in their spatial occupancy over five seasons. Additionally, shrubs had an explanatory effect on spatial occupancy during one specific season. The dietary importance of grasses could stem from their chemical composition and nutritional value, as indicated by their mineral concentrations, crude protein, metabolizable energy, and digestible fiber contents (Buxton & Redfearn, 1997; Terré et al., 2013; Gamoun, 2014; Louhaichi et al., 2021). Moreover, grasses have low stomatal conductance and efficient CO_2 uptake, which contributes to their water utilization capabilities. Their capacity to extract water from the soil (Jaballah et al., 2008) coupled with their tall stature facilitates the capture of dew and fog, which increases their appeal as a food source in arid lands, particularly during the dry season (Gillet, 1965, 1966a, 1966b; Newby, 1974a, 1975b, 1988; Dragesco-Joffé, 1993; Gilbert, 2008; Robinson & Weckerly, 2010). Oryx can survive long periods without drinking and rely on meeting their water needs from available vegetation (Gillet, 1965, 1966a, 1966b; Newby, 1974a, 1975b; Wacher, 1988). Severe droughts change the nutritional value of plants and restrict the growth of annual species, leading to food scarcity (Schut et al., 2009; Tarhouni et al., 2017). Forbs, of secondary importance to grasses for oryx, were ranked higher than grasses in two seasons that were preceded by heavy rainfall (fall 2020: ca. 27 mm in September–October 2020 and spring 2022: 25 mm in October–November 2021). Beside their nutritional value (high protein content), selection of forbs by oryx can be attributed to increases in their abundance and species diversity, especially since they have the fastest growth rates among plant growth forms globally (Codron et al., 2007; Bråthen et al., 2021). In arid regions, the quality of food, characterized by crude protein and water content, reaches its peak immediately following rainfall (Rutherford, 1980; Le Houérou, 1995; Spalton, 1999). In response to rainfall, oryx swiftly migrate to areas where recent rain has fallen, allowing them access to high-quality forage from emerging annual plants and young green shoots (Gillet, 1965, 1966a, 1966b; Newby, 1974a, 1975b, 1988; Dragesco-Joffé, 1993).

The occurrence of oryx on a micro-level ecosystem scale was influenced by several other factors, including wadis, predation, and some man-made structures, particularly troughs of water and distance from guardhouse posts and marabouts. However, their effect was either limited to a short duration (one or two seasons) or ranked lower compared to other factors. Wadis were important predictors of oryx occurrence, specifically during two consecutive winters, likely owing to wadis being a source of food and shelter as well as a potential protective barrier against cold winter winds. The positive relationship we observed between predators (African golden wolves, Canis anthus) and oryx indicates that they do not actively avoid predators. African golden wolves, a mesocarnivore whose weight generally varies from 7–14 kg, are expected to specialize on small prey (Estes 2012), while large carnivores (> 20 kg) should prefer large prey that equal or exceed their own mass (Carbone et al., 2007a). Future investigations of oryx vigilance behaviour in relation to predators should indicate whether the predator-size relationship affects ungulate distribution at STNP. Among man-made structures, water availability from artificial troughs emerged as the exclusive influential factor determining oryx presence during two consecutive summers. Despite possessing the ability to thrive in arid environments, including physiological adaptations to endure extended periods without drinking (Gillet 1965, 1966a, 1966b; Dolan, 1966; Newby, 1974a, 1975b; Kingdon et al., 2013), oryx made occasional visits to watering points, especially during the summer. Under severe heat and drought conditions (i.e., temperatures ≥ 40°C), their endurance in the absence of water is limited (Ghobrial, 1974). Moreover, the provision of water might not be the exclusive factor contributing to their shift towards water sources. The installation of umbrellas near water points provided shade, which can be important for oryx (Dragesco-Joffé, 1993). Similarly, distance from guardhouse posts and marabouts had a significantly positive effect on oryx presence solely during the fall season, likely due to the large influx of pilgrims (ca. 2000 visitors) in October (Souissi, 2008). Additionally, other man-made structures (i.e., dirt road and fences) did not have a discernible effect on the distribution of oryx in STNP, although dirt road are generally recognized as influencing ungulate space use, with some species avoiding roads while others are attracted to roads when water runoff results in greener vegetation along the roadside (Trombulak & Frissell, 2000; Fahrig & Rytwinski, 2009; Leblond et al., 2013; Muposhi et al., 2016; Fuda et al., 2018; Mkonyi et al., 2018; Cavada et al., 2019; Tsalyuk et al., 2019). Ungulates that avoid roads can reduce their likelihood of collisions with vehicles (Jones et al., 2022). However, at STNP, oryx distributions might not be affected by roads because vehicle use in the park is limited (pers. obs.). Likewise, ungulates might avoid fences due to human encroachment along fencelines, which can alter their survival, movement, and behaviour (Rich et al., 2016; Sheidler et al., 2015), as well as increase their risk of injury (Visscher et al., 2016). Ungulates that do use areas near fences (e.g., bushbuck) are avoiding areas of unsuitable vegetation rather than showing a preference for the fence line (Reece et al., 2023).

5. CONCLUSIONS

In the confined space of STNP, the spatial distribution of oryx was primarily affected by the presence of grasses throughout the year, but during the summer, the presence of water exerted an additional strong influence. We demonstrate that the micro-level ecosystem scale can be a valuable indicator of the local distribution of oryx and elucidate the conditions under which oryx distribution in other parks could be reliably predicted. The factors we determined to be important to reintroduced oryx seasonally can be used to help develop effective management plans for arid region ecosystem conservation and the effects of reintroduced species on local flora and fauna.

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