Title: Daily and seasonal activity patterns of the dorcas gazelle, scimitar-horned oryx, north-African ostrich and canids in an arid habitat

Running title: Activity patterns of DG, SHO, NAO and canids

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Abstract

North Africa's megafauna has developed behavioural adaptations to reduce energetic and fitness costs under harsh aridland conditions. Animal behaviour and activity patterns are difficult to study in the wild, but remote camera traps provide a solution to collecting data without the presence of a researcher influencing outcomes. Here, we report results from a study comprising over 20,382 camera-trap days during a 34-month period in Dghoumes National Park, Tunisia. We aimed to evaluate temporal activity patterns, their overlap and explore opportunities for niche partitioning. Our focal species were the reintroduced scimitar-horned oryx, north-African ostrich, dorcas gazelles, and extant regional top-order predators, African wolf and red fox. We found differences in activity patterns between seasons across the focal species, with the most noticeable change being an increase in dawn activity from 1% to 33% between winter and summer for the red fox. Consequently, higher summer temperatures limit opportunities for temporal niche partitioning and push focal species towards dawn-time activity peaks resulting in higher intra-guild overlap values at dawn. Arid antelopes have physiological adaptations that enable them to better exploit ecological resources in hotter time periods than the carnivores, and this reduces inter-guild overlap during summer days.

Keywords: conservation, Tunisia, antelope, predator, protected area, Dghoumes national park, camera trapping

Introduction

The activity pattern of a species is the result of compromises made in response to the various biotic (competition, predation or cooperation) and abiotic (temperature, photoperiod or humidity) factors that alter throughout the day and across the year (Hut et al., 2012; Castillo-Ruiz et al., 2012). The challenging conditions of North Africa's aridlands have led to physiological, anatomical and behavioural adaptations of its endemic mega-fauna (Ghobrial, 1970; Seri et al., 2018). Behavioural adaptations are especially important in arid habitats where activity in high temperatures can extract a high energetic or fitness cost (Owen-smith, 2006). Tunisia's arid lands are a prime example of such habitats.

The Sahelo-Sahara's megafauna has suffered catastrophic declines and much is locally extinct in Tunisia and globally threatened (Durant et al., 2014). The dorcas gazelle (*Gazella dorcas*) is still wild occurring but has suffered from over-hunting and consequently listed as endangered in the Mediterranean region (Jdeidi et al., 2010). While the species was common in central and southern Tunisia in 1887, Gharaibeh (1997) documents its gradual decline across the country until it became rare in 1935; the species is now present at probably unviable numbers in the wild (personal data).

The scimitar-horned oryx (*Oryx dammah*) is a large-bodied antelope that stands approximately 1.2m high and can weigh over 150kg. It features prominently in local culture particularly in the south of the country. It became extinct in the wild in the late 20th century but had previously disappeared from Tunisia in 1906 (Kacem et al., 1994).

The north-African ostrich (*Struthio camelus camelus*) was of high cultural significance in Tunisia and is depicted in historic drawings, mosaics and engraved on eggshells (Streidter, 1984) as far back as 13,000 B.C. It has been the subject of long-standing trade primarily for its feathers for decoration, bones for jewellery and meat for food (Kinzelbach, 1997). It suffered substantial declines in Tunisia due to over-hunting through the 19th century until it became extinct in 1888 (Seurat, 1943).

Following the extinction of the Barbary lion (*Panthera leo leo*) and the leopard (*Panthera pardus*) (Haltenorth, 1985), the African wolf (*Canis lupaster*) and the red fox (*Vulpes vulpes*) are now the top-order predators in Tunisia's aridlands. Whilst both canids predate primarily on rodents, the African wolf also includes wild and domesticated ungulates in their diet (Eddine et al., 2017; Karssene et al., 2019a).

Previous studies report that diurnal activity for the scimitar-horned oryx is limited by higher temperatures (Wacher, 1986). The species is primarily active at dusk and dawn (Gillet, 1971), but Gordon and Gill (1993) also recorded nocturnal activity. Under Sahelian climate, the Dorcas gazelle has shown a primary activity peak in the middle of the day in December, January and February, but it switches to a bimodal pattern with two peaks at dawn and dusk in April (Abáigar et al., 2018). An ex-situ observation of captive ostriches (*Struthio camelus*) in the Negev desert shows a 12h activity period with activity exclusively taking place between dawn and dusk (Degen et al., 1989). For predators, activity patterns of the African wolf and the red fox have been studied under a colder climate in the Atlas Mountains between autumn and winter. The African wolf exhibited a unimodal pattern with an activity peak at dawn while the red fox exhibited activity peaks at both dawn and dusk (Gil-Sanchez et al., 2021).

Tunisia's strategy to restore the integrity and ecological function of its aridland ecosystems is reliant on reintroduction programmes and habitat-scale conservation projects in key protected areas. Dghoumes National park (DNP) is one of Tunisia's arid protected areas where its natural habitat has been restored before reintroductions for dorcas gazelle, scimitar-horned oryx and North-African ostrich took place in 2002, 2007, and 2013, respectively (Woodfine et al., 2009). These reintroduced species coexist with a re-establishing community of indigenous wildlife.

Inhabiting the fringes of the Sahara Desert, the indigenous fauna in DNP must optimize resource partitioning especially between competing sympatric herbivores (Ostfeld & Keesing, 2000; Traba et al.,

2016) and carnivores (Karssene et al., 2019b) to cope with low resource availability, predation risk and harsh climatic conditions (Illius & O'Connor, 2000; Kittle et al., 2008).

In line with the global conservation efforts and the continuing post-release monitoring of Sahelo-Saharan wildlife, here we present data on the seasonal variation of activity patterns and temporal niche partitioning of the emblematic dorcas gazelle, scimitar-horned oryx and north-African ostrich populations, as well as the key predators, the African wolf and red fox in situ using data from a 34-month camera-trap dataset. Due to the high daytime temperatures at the study site, we hypothesized that all species would engage in predominately nocturnal activity. This preference should be more apparent during the summer when temperatures are higher, exhibiting a marked change in behaviour between seasons. We also hypothesized that overlap between the focal species' activity patterns would be higher in the summer as activity would be compressed within the cooler times of day and at night. In this study we provide basic ecological data on key protected species and insights into their behavioural responses to seasonality, competition and predation risk.

Materials and methods

Study site

We conducted the camera-trap survey between April 2018 and February 2021 in DNP (34.04°N; 8.54°E; figure 1). DNP is located 11 km from Dghoumes village in the governorate of Tozeur and covers an area of 8,000 hectares with an upper-arid climate. DNP's northern area is characterized by a low mountain range and bordered on the south by the largest salt lake of the Maghreb, the Chott Ejjrid. The park is fenced along the edge of the Chott and the Chareb plain, but open along the mountain range.

The mountain range was originally considered a natural barrier, but it is now used as extended habitat by ungulates and predators, with individuals occasionally exiting the park through the mountains. Lack of connectivity to other protected areas or suitable habitat, restricts dispersal of large herbivores from DNP. Since 1997, DNP has been under conservation management with efforts focused on habitat restoration and the reintroduction of the dorcas gazelle, the scimitar-horned oryx and the north-African ostrich.

Camera-trap survey

Camera traps were distributed across the study site according to a grid design developed in QGIS (QGIS Geographic Information System, 2018). Initially, thirty cameras were placed at approximately 1km from each other along two rows to cover mountain and plain habitat. Each camera was placed as close as possible to the centre of the grid cell. To maximise detection rates, we aimed cameras at visible trails. Cameras were attached to rocks at knee height (~60 cm) to capture medium to large-bodied animals (>1kg) (Lyra-Jorge et al., 2010). All camera traps were set to take a series of three photos at the highest image quality when triggered. Intervals between triggers were set at a maximum of 60 seconds. Following the same placement criteria, camera-traps were moved twice during the study to explore more locations within the study site (table 1).

The cameras were set on 19 April 2018. The cameras were initially checked 24h after setup and approximately once per month after that to reduce disturbance at the sampling site and ensure correct functioning and positioning of devices. During each device check, the memory cards were removed and replaced with empty ones. The memory card contents were later downloaded. To reduce potential bias resulting from the novelty effect (Kalan et al., 2019) e.g. newly introduced elements could be attractive or a deterrent for some species, we eliminated the first 73 days of data and only include data starting from the 1st of July 2018.

In the present study, we used the conventional Tunisian seasons defined as: winter as December, January and February; spring as March, April and May; summer as June, July and August; and autumn as September, October and November (Bargaoui et al., 2014). We also defined the dawn period as one hour before and one hour after official sunrise and dusk as one hour before and one hour after official sunset. The diurnal period is defined as one hour after sunrise to one hour before sunset. The nocturnal period is defined as one hour after sunset to one hour before sunrise (Ross et al., 2013).

Data analysis

Data were manually compiled in a database summarising each capture event by the camera ID/location, the time, date and temperature as recorded by the device, the observed species identification and the number of visible animals in each event (i.e. each cluster of photos showing a single or multiple animals). In the case of a repeated capture of the same individual e.g. a dorcas gazelle grazing in front of the camera-trap for an extended period of time, a new record was created after each 30-minute period to account for the species activity during that time of day. The data were then exported to a .csv format for further analysis in R (R core team, 2021)

Aimed at trails, motion-triggered camera traps only detect animals when active. For the following analysis, detection of an animal was assumed as indicative of its activity and variation in temporal detection frequency was considered a reflection of the activity pattern of the focal species (Rowcliffe at al., 2014).

The camera traps were set to record a full 24-hour period. To tackle the difficulty of applying traditional statistical methods to wrapped distributions (Zar, 1999), we chose to use trigonometric functions to estimate Kernel densities and display activity patterns. Kernel densities of species' activity patterns were calculated using R package "Activity" (Rowcliffe et al., 2014). We obtained the 95% confidence intervals through 1000 bootstrap samples.

Ridout and Linkie (2009) overlap index Δ was used through the "Overlap" R package to calculate true overlap between the fitted kernel density curves of the different species pairs (Meredith & Ridout, 2014). The Mardia-Watson-Wheeler test was used to test for homogeneity on two samples using the R package "Circular" (Lund et al., 2017).

Results

A total of 10,546 animal capture events were recorded over a sampling effort of 20,382 camera days. Dorcas gazelle appeared most frequently (n=2712) followed by African wolf (n=2336), scimitar-horned oryx (n=2166), and red fox (n=1626). The north-African ostrich accounted for n=731 captures (figure 2; full capture data for the detected species in table 2).

We calculated the average hourly temperatures for all seasons using the data recorded by the cameras. The winter temperatures were approximately 20°C lower than the summer ones, with autumn and spring temperatures falling in between. Values on average highest and lowest temperatures during the study period are detailed in table 3.

The daily activity patterns of the focal species were different across seasons (figure 3). Activity patterns in autumn and spring were comparable for most of the focal species. Dorcas gazelle showed a peak of activity exhibiting 28.5% and 25.6% of its daily activity at dawn in autumn (figure 3.a.iv) and spring (figure 3.a.iii) respectively. Overall activity is principally diurnal exceeding 40% in both seasons. Autumnal activity for the scimitar-horned oryx revealed crepuscular activity pattern, accounting for 44% of total daily activity. Nocturnal activity accounted for 30% of total activity while 26% was exhibited during the day (figure 3.b.iv). Oryx's activity at dusk decreased in the spring (figure 3.b.iii). North-African ostrich activity patterns were predominantly diurnal and showed the highest peak at dawn in both autumn (figure 3.c.iv) and spring (figure 3.c.iii). Diurnal activity of predators was limited in both seasons, however, the wolf exhibited crepuscular activity with approximately 50% of its activity at dusk and dawn (figure 3.d.iii; iv), but the red fox exhibited peak activity at night (figure 3.e.iii; iv).

Both summer and winter yielded evidence of a change in activity patterns across the focal species. In winter, dorcas gazelle exhibited 42% of its activity during the day, 35% equally divided between dawn and dusk and 23% during the night (figure 3.a.ii). Scimitar-horned oryx exhibited a similar level of activity across the day and night, accounting for approximately 34% and 32% of total activity, but had reduced activity at dawn (15%) and dusk (19%) (figure 3.b.ii). The North-African ostrich's activity patterns were predominantly diurnal (68%) but was still active at dawn (15%) and dusk (15%). However, activity almost completely ceased at night (2%) (figure 3.c.ii). The red fox showed a strong preference for nocturnal activity (61%; figure 3.e.ii), but this was not emulated by the African wolf (20%), which exhibited peak activity levels at dawn (23%) and dusk (31%; figure 3.d.ii). In comparison, the red fox had very low activity levels at dawn (1%), but this increased for dusk (18%).

During the summer, all five focal species exhibited a primary peak in activity at dawn accounting for approximately a third of their daily activity (27% for the Dorcas gazelle, 34% for the scimitar horned oryx, 34% for the north African ostrich, 31% for the African wolf and 33% for the red fox). All species decreased their day-time activity levels except dorcas gazelle that was slightly more active (43% of its daily activity; figure 3.a.i). For the north-African ostrich, the dusk activity almost doubled from winter and represented 27% of its total daily activity (figure 3.c.i). The greatest shift was exhibited by the red fox which increased its dawn activity levels from 1% in winter to 33% in summer (figure 3.e.i). During the summer, dorcas gazelle and scimitar-horned oryx also exhibited a high activity rate during the hottest hours of the day which coincided with the hours where predators were inactive (figure 3.a.i; b.i; d.i; e.i).

The overlap values were generally high across all species (table 4). The most segregated species (red foxes and north-African ostriches) shared 38% of their temporal niche in the autumn and spring whilst the most similar (dorcas gazelles and scimitar-horned oryx) shared more than 80% of their activity time year-round. Overlap values were slightly higher in the summer especially between ecologically similar species i.e. between scimitar-horned oryx and gazelle and between the canids. The overlap decreased during the summer between the scimitar-horned oryx and the canids and between the dorcas gazelle and all focal species with the exception of scimitar-horned oryx, indicating a partitioning of activity. Additionally, overlap increased from 84% in the winter to 86% in the summer and from 76% to 81% between the African wolf and the red fox.

Discussion

Designing camera-trap monitoring protocols to target mammal communities presents a challenge. This mainly arises from a differential use of habitat between carnivores and herbivores (de Matos Dias et al., 2018). In this study we used a systematic design and did not target specific habitat structures (dens, trees or marking sites, etc.), we also did not use any attractants or baits that would increase the detection probability of one guild over another (Holinda et al., 2020). Changing the placement of cameras is common in camera-trap studies of daily activity patterns to increase the sampled area within the study site (Kays et al., 2009; Rowcliffe et al., 2014; Cravaggi et al., 2018). The impact of the sampling design and effort on detection probabilities of different species is a potential source of bias for camera trapping studies. However, Cusack et al. (2015) concluded that large sampling efforts with >1,400 camera days reduces the impact of sampling design biases on detection probabilities of species across the community.

Across seasons, our results show an increase in dawn activity during the summer compared to the winter. The focal species responded to seasonal change either by reducing overall day and night-time activity while maintaining a peak at dawn or in the case of the red fox by creating a dawn-time peak that was exclusive to the summer months.

The higher temperatures and the absence of precipitation during the summer months give way to a reduction in the primary production of arid habitats making trophic resources rarer and increasing foraging costs (Williams et al., 2001). This impacts herbivores and carnivores equally; consequently, arid lands cause physiological stress for the whole community during the hotter months. Our temperature data indicate that dawn temperatures in the summer are very similar to night temperatures. Dawn potentially decreases predation risk for herbivores in addition to keeping a lower metabolic stress with its tolerable temperatures (Owen-smith & Goodall, 2014). For predators, we postulate that dawn activity represents a trade-off between higher foraging efficiency and greater detectability by prey. We suggest that as African wolves and the red foxes are habitat generalists, both species are at a physiological disadvantage in arid environments that dissuades them from hunting in the hottest hours of the day. Consequently, both predator species prefer overlapping activity at dawn during which, despite having the higher probability of being detected by prey and potential competition, they should have the highest foraging efficiency as most prey species are simultaneously active (Foster et al., 2013).

Niche partitioning is crucial to the maintenance of diverse communities regardless of habitat quality or resource abundance. Resources are intrinsically finite and are distributed through competition over the present species (Patterson et al., 2003). This observation is particularly true in arid habitats, in which resources are even scarcer (Safriel et al., 2005). Under arid climates, as exemplified by DNP, the high variation in temperatures limits the availability of tolerable time slots possibly reducing the opportunities for niche partitioning on the temporal axis.

Our results demonstrate high overlap values between the activity patterns of the focal species, particularly those belonging to the same guild e.g. 0.8 to 0.86 for scimitar-horned oryx/dorcas gazelle and 0.7 to 0.81 for African wolf/red fox. These overlap values were at their maximum in the hot summer season probably due the cost-benefit trade-offs. Limited availability and slow regeneration of trophic resources especially in arid ecosystems should decrease the efficacy of temporal niche segregation at reducing competitive exclusion and enabling the coexistence of species with dietary overlap (Shoener, 1986). This mainly stems from the fact that a resource that is consumed by a competitor is made unavailable for those who are active later in the day. In such cases, spatial and trophic niche partitioning are thought to be the dominant mechanism in shaping the realised niche of the competing species

(Anderwald et al., 2015). In DNP, Cooke et al. (2016) have demonstrated a spatial niche segregation for the scimitar-horned oryx and dorcas gazelle, the former preferring the wadis while the latter favours open plain habitat. Such segregation enables both species to reduce competition while exploiting the most suitable times of the day to reduce metabolic stress and predation risk.

Inter-guild temporal niche overlap between canids and ungulates is less prominent during the summer. The physiological adaptations of the arid-specialist ungulates i.e. greater metabolic water efficiency (Ghobrial, 1970) enables them to exploit the hottest times of the day with the benefit of reduced predation risk. The observation of a secondary activity peak during the hot mid-days for dorcas gazelle and scimitar-horned oryx confirms their high heat tolerance.

Studying the daily activity patterns and their seasonal variation in free-ranging animal communities with high conservation value is of considerable benefit in planning successful reintroductions. It enhances our understanding of wild animals' behaviour and their ability to adapt to a novel environment in a notoriously understudied region (Durant et al., 2014) and helps to monitor how reintroduced species adapt to new living conditions (Abáigar et al., 2018). Camera-trap monitoring is still being deployed in Tunisia's national parks and promises to answer many questions about North African ecosystems and biodiversity.

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Data availability statement: The data that support the findings of this study are available from the corresponding author upon reasonable request.

Conflict of interest: None to declare

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Table 1 Data for the three camera-trap grids set in Dghoumes national park

Grid name	Start date	End date	Stations	Camera days	Camera models	Number of cameras per model	Area of minimum convex polygon around the grid
A	01/07/2018	22/08/2019	30	10316	• Bushnell trophy cam Aggressors • Bushnell Trophy cam HD • Moultrie cam	• 10 • 19 • 1	1,765.36 ha
B	23/08/2019	26/10/2020	24	8632	• Bushnell trophy cam Aggressors • Bushnell Trophy cam HD	• 8 • 16	1,872.12 ha
C	27/10/2020	26/02/2021	13	1434	• Bushnell trophy cam Aggressors • Bushnell Trophy cam HD	• 10 • 3	288.48 ha

Table 2 Total number of camera-trap captures and camera days per season from a 34 month study in Dghoumes National Park

Season	Winter	Spring	Summer	Autumn
Camera days	5667	4245	4926	5544
Dorcas gazelle (*Gazella dorcas*)	848	593	560	711
Scimitar-horned oryx (*Oryx dammah*)	788	418	464	496
African Wolf (*Canis lupaster*)	803	473	446	614
Red fox (*Vulpes vulpes*)	595	321	359	351
North-African ostrich (*Struthio camelus camelus*)	292	210	85	144
Cape hare (*Lepus capensis*)	228	138	77	168
Wild Cat (*Felis silvestris*)	80	46	37	63
Wild boar (*Sus scrofa*)	23	31	22	9
Crested porcupine (*Hystrix cristata*)	8	7	7	13
Striped hyaena (*Hyaena hyaena*)	10	1	0	3
Aoudad (*Ammotragus lervia*)	1	1	1	0
Libyan striped weasel (*Ictonyx libyca*)	0	0	0	1

Table 3 Temperatures in °C measured by camera traps during the sampling period in Dghoumes National Park

	Dawn		Day		Dusk		Night	
	Average highest tempera ture	Average lowest tempera ture	Average highest tempera ture	Average lowest tempera ture	Average highest tempera ture	Average lowest tempera ture	Average highest tempera ture	Average lowest tempera ture
Autum	24	16.6	36.7	26	26.2	20.2	19.6	16
Winter	9.3	3.8	25.9	14.5	18.7	11.4	10.6	4.7
Spring	15.3	20.7	35.6	24	27	20.1	18.8	14.6
Summer	29.9	24	48	34.8	39	30.1	29.1	24

Table 4 Seasonal delta overlap values calculated from kernel density estimates between focal species. Significant differences (p<0.05) in Mardia–Watson–Wheeler test are indicated by an asterisk after the values.

Autumn	Dorcas gazelle	Scimitar-horned oryx	North-African ostrich	African wolf
Scimitar-horned oryx	0.82*			
North-African ostrich	0.76*	0.7*		
African wolf	0.8*	0.8*	0.64*	
Red fox	0.56*	0.68*	0.38*	0.7

Winter	Dorcas gazelle	Scimitar-horned oryx	North-African ostrich	African wolf
Scimitar-horned oryx	0.84*			
North-African ostrich	0.71*	0.62*		
African wolf	0.81*	0.83	0.57*	
Red fox	0.68*	0.78*	0.41*	0.76*

Spring	Dorcas gazelle	Scimitar-horned oryx	North-African ostrich	African wolf
Scimitar-horned oryx	0.8*			
North-African ostrich	0.71*	0.55*		
African wolf	0.8*	0.82	0.57*	
Red fox	0.56*	0.76*	0.38*	0.72*

Summer	Dorcas gazelle	Scimitar-horned oryx	North-African ostrich	African wolf
Scimitar-horned oryx	0.86			
North-African ostrich	0.65	0.64		
African wolf	0.72*	0.67*	0.61*	
Red fox	0.63*	0.72*	0.49*	0.81*

Figure 1 Map of Dghoumes national park's location, its main topographic features and camera-trap grid placements; Dghoumes national park is filled in black on the country's map

Figure 2 Camera trap photos of: **a.** dorcas gazelle (*Gazella dorcas*); **b.** scimitar horned oryx (*Oryx dammah*); **c.** north-African ostrich (*Struthio camelus camelus*); **d.** African wolf (*Canis lupaster*); e. red fox (*Vulpes vulpes*) in Dghoumes national park

Figure 3 Seasonal patterns of daily activity of five focal species: **a.** dorcas gazelle (*Gazella dorcas*); **b.** scimitar horned oryx (*Oryx dammah*); **c.** North-African ostrich (*Struthio camelus camelus*); **d.** African wolf (*Canis lupaster*); e. red fox (*Vulpes vulpes*) in Dghoumes National Park. Kernel density activity estimates on y-axis with 95% confidence intervals in dotted grey lines. Tick marks on the x-axis show times of independent observations used to estimate the activity pattern. Average sunrise and sunset times for each season in black dashed vertical lines

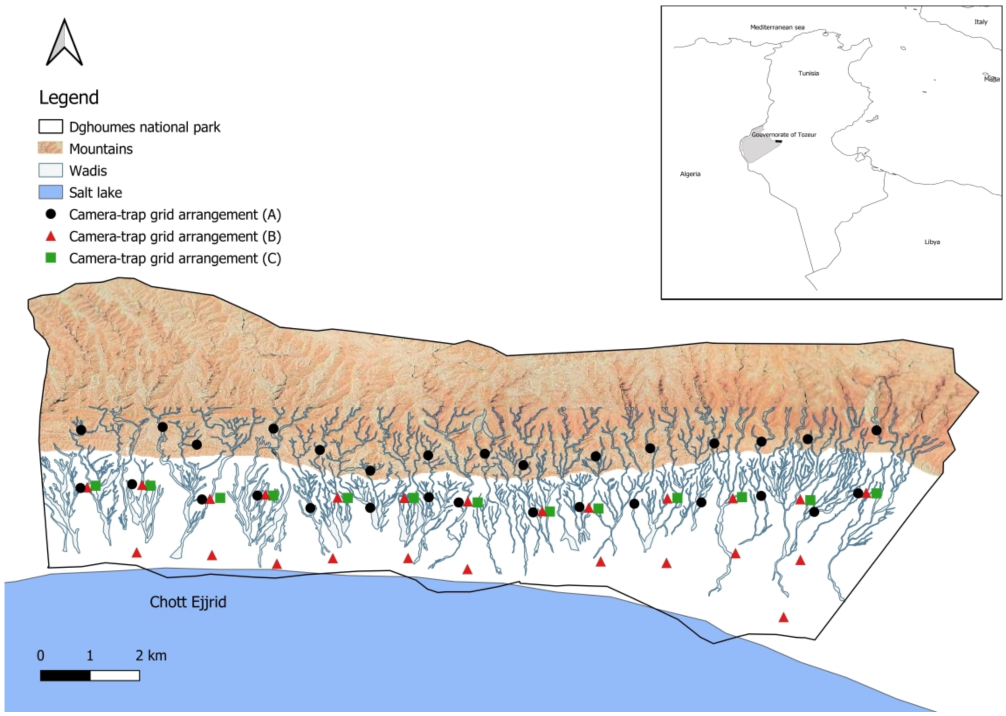
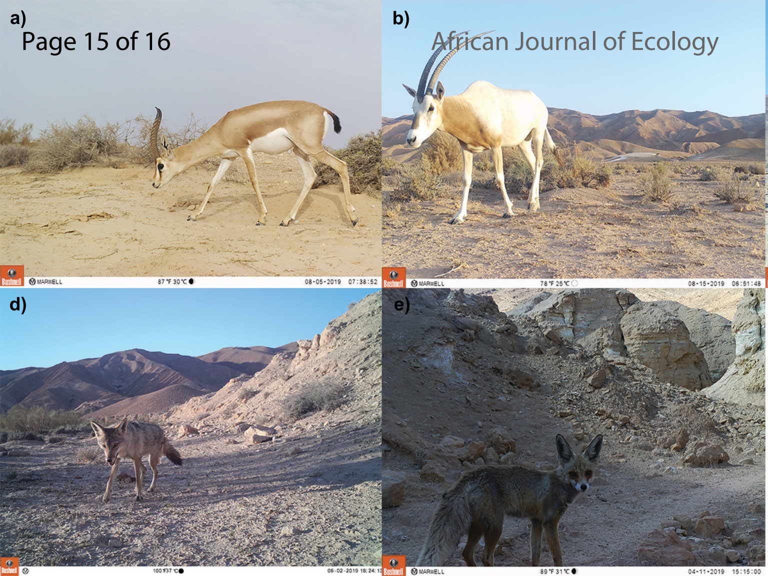
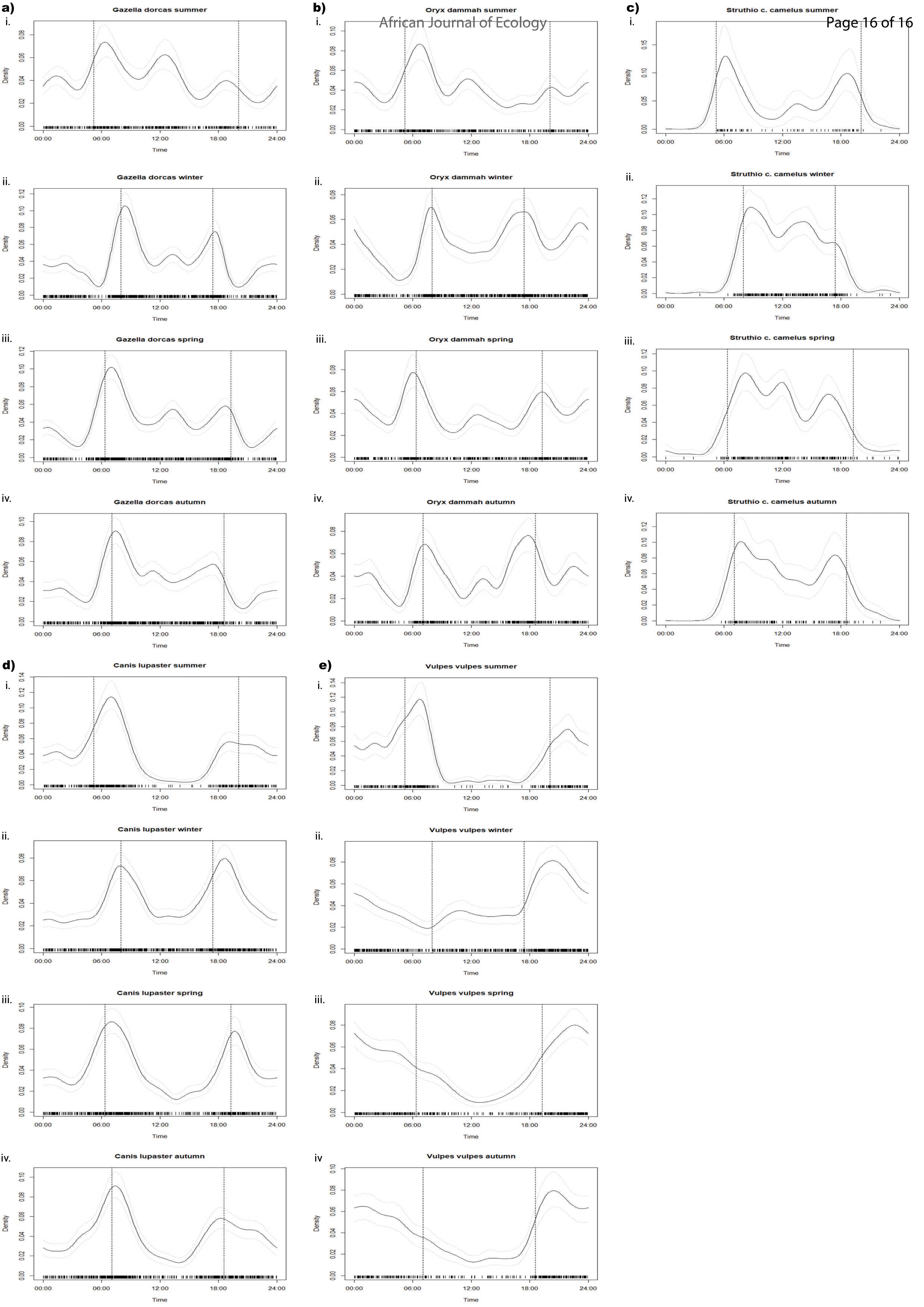


Figure 1 Map of Dghoumes national park's location, its main topographic features and camera-trap grid placements; Dghoumes national park is filled in black on the country's map

296x209mm (600 x 600 DPI)


a)
b)
c)
d)
e)
Bushnell
MARWELL
87 °F 30 °C
08-05-2019 07:38:52
78 °F 25 °C
08-15-2019 06:51:48
88 °F 31 °C
04-13-2019 09:17:52
89 °F 31 °C
04-11-2019 15:15:00


a)
i.
Gazella dorcas summer
ii.
Gazella dorcas winter
iii.
Gazella dorcas spring
iv.
Gazella dorcas autumn
b)
i.
Oryx dammah summer
ii.
Oryx dammah winter
iii.
Oryx dammah spring
iv.
Oryx dammah autumn
c)
i.
Struthio c. camelus summer
ii.
Struthio c. camelus winter
iii.
Struthio c. camelus spring
iv.
Struthio c. camelus autumn
d)
i.
Canis lupaster summer
ii.
Canis lupaster winter
iii.
Canis lupaster spring
iv.
Canis lupaster autumn
e)
i.
Vulpes vulpes summer
ii.
Vulpes vulpes winter
iii.
Vulpes vulpes spring
iv
Vulpes vulpes autumn
Density
Time
00:00
06:00
12:00
18:00
24:00