

## Coexistence between camels and wild animals

Mohsen Chammem<sup>1\*</sup>, Touhami Khorchani<sup>1</sup>, Slaheddine Selmi<sup>2</sup>, Said Nouira<sup>3</sup>

<sup>1</sup>Laboratory of Animal Husbandry and Wildlife, Arid Land Institute, Tunisia;

<sup>2</sup>Department of Life Sciences, Faculty of Sciences of Gabès, Tunisia;

<sup>3</sup>Department of Biology, Faculty of Sciences of Tunis, Tunisia.

### Abstract

Livestock, especially small ruminants and camels, have been implicated for negatively affecting the abundance and distribution of other large wild animals in desert areas. We tested whether the occurrence of two emblematic species, the *Dorcas gazelle* (*Gazella dorcas*) and *Houbara bustard* (*Chlamydotis undulata undulata*), in south-eastern Tunisia was affected by camel abundance. Data were collected during March and April 2004. The study area was divided into 32 400 km<sup>2</sup> sample units (20 km x 20 km) distributed over a regular grid. Within each unit, five sampling sites were randomly placed 3 km apart along a line transect. Each sampling site was visited once for a single 30-minute survey session. During these monitoring periods, we collected data on *Houbara bustards* and *dorcas gazelle* presences. We also recorded the number of sheep, goats and camels. Areas occupied by these two wild species were characterized by a significantly higher number of camels than unoccupied areas. The occurrence probability of these species was positively correlated with the number of camels. These results may be explained by the fact that the two wild species share similar habitat requirements with camels. The three species coexist in open areas and seem to avoid urbanised and agricultural areas. Camels may not compete with the other two wild species because camels generally consume poor-quality plants that are generally unpalatable and indigestible for these two species.

Key words: Camels, *Dorcas gazelle*, *Houbara bustard*, Tunisia, coexistence.

---

\* Corresponding author: Email: mohsen.chammem@ira.agrinet.tn

### 1. Introduction

Species coexistence, particularly between livestock and wild species, has become an increasingly important issue (Slatkin, 1974; Putman, 1996; Prins, 2000). There are numerous mechanisms that may explain coexistence of species occurring in natural communities such as traditional niche partitioning and fluctuation-dependent mechanisms such as the “storage effect” and “relative nonlinearity” (Chesson, 2000). For example, Colwell and Fuentes (1975) and Diamond (1978) suggest that coexistence can occur between species that share niche components throughout resources partitioning. However, it should be noted that, at any spatial scale, coexistence between species requires two conditions: when at least one of the competing species is generalist (it can use different

types of resources) or when the shared resource shows a heterogeneous distribution (Rosenzweig, 1981). In addition, the size of the resource patch may enhance or decrease the potential for coexistence (Kouki and Hanski, 1995; Horgan, 2005). Coexistence can occur if there is considerable variation between species in their ability to find food (Davidson, 1998) or if there is little overlap in their foraging ranges and different preferences for food resources (Belovsky, 1986; Wiens, 1989; De Boer and Prins, 1990; Putman, 1996).

The southern region of Tunisia has a pastoral history dating back several millennia (Le Houérou, 1969, 1993, 1995; Pignatti, 1983; Gomez-Campo, 1985; Abaab et al., 2000; Bourbouze, 2000). In this region, the grazing of domestic camels,

goats and sheep represents a great potential resource for the Tunisian economy. Of the diverse wild animals inhabiting this region, Houbara bustard (*Chlamydotis undulata undulata*) and Dorcas gazelle (*Gazella dorcas*), are considered the most important native species and of high conservation concern. Houbara bustard is a Palearctic species inhabiting steppe and semi-desert areas with open and scattered vegetations (Johnsgard, 1991). This bird is known to be omnivorous and opportunistic, its diet consisting of plants, arthropods and small vertebrates, probably reflecting seasonal and local variations in resource abundance (Johnsgard, 1991; Tigar, 1995; Khan, 1996; Tigar and Osborne, 2000). With regard to Dorcas gazelle, it is considered as an extreme habitat generalist since it inhabits a great variety of dry habitats (Lavauden, 1920, 1926; Heim de Balsac, 1936; Dupuy, 1967; Baharav and Mendelssohn, 1976; Mallon and Kingswood, 2001; Osborn and Helmy, 1980; Kacem et al., 1994), and feeds on a great variety of desert plants (Baharav, 1982; Loggers et al., 1992). These two wild species were very common in the central and southern Tunisia (Lavauden, 1920; Lavauden, 1926; Joleaud, 1929; Schomber and Kock, 1961, Chammem et al., 2003) until the last decades when they had suffering a dramatic decline (East, 1992; Chammem et al., 2003, 2008). Presently, only a few small populations persist in isolated arid areas near the southern border between Gafsa (34.42° N, 8.78° E) and Gabès (33.87° N, 10.09° E) (Kacem et al., 1994, Chammem et al., 2003). The key reason for this decline may be attributed to overhunting, habitat degradation and alteration due to human activities, and overgrazing by domestic animals. In fact, intensified pastoralism activities as a consequence of the settling formerly nomadic populations have led to changes in animal herding management practices and to local over-stocking and over-grazing (Dregne, 1986; Mainguet,

1994; Bencherifa, 1996; Swearingen and Bencherifa, 1996; Ouled Belgacem and Sghaier, 2000). These changes can indirectly affect wild animal populations by changing vegetation structure and limiting access to suitable habitat (Le Cuziat et al., 2005).

According to Prins (1992), Fleischner (1994), Noss (1994), and Voeten (1999), the impacts livestock grazing on native wildlife should be taken into account for the establishment of conservation programs. However, little is known about the interaction between native wildlife and livestock and there is a widespread opinion that livestock appeared among factors contributing to the decline of native wildlife.

It is important to note difference between goats/sheep and camels' livestock in foraging strategies and diet selection, particularly in harsh grazing conditions (Schwartz, 1988; Engelhardt et al., 1989, 1992). If there is similarity between goats/sheep and Houbara bustards and gazelles in their preference for annual plants and green foods, as there is between small ungulate (Mongolian gazelle) and sheep/goats (Campos-Arceiz, 2004), there is a possibility of competition for food between them if food supply is limited (Wiens, 1977; Belovsky, 1984; De Boer and Prins, 1990; Voeten and Prins, 1999). This seems to be the case for camels. Camels are able to feed on very fibrous and low quality plants that are generally unpalatable and indigestible for small herbivores such as gazelles and Houbara bustard (Heller et al., 1986; Tandon et al., 1988; Lechner-Doll and Engelhardt, 1989). Moreover, grazing regime of camels has been reported to provide a rational utilisation of desert vegetation because camels' way of feeding does not cause significant damages on desert vegetation. Mobility of camel herds and taking only small portions of each plant should be also considered. (Gauthier-Pilters, 1961; Gauthier-Pilters and Dagg, 1981), which

may further reduce negative competitive effects of this species on Houbrara and gazelles, hence we expect that there is no compete between camels and wild animals.

In the present paper we investigated coexistence between livestock and wild animals using data on the occurrence of Dorcas gazelle and Houbara bustard and a set of variables particularly number of camels, sheep and goats as well as some other habitat variables that could affect the distribution of these wild species. The major aim of this work was to investigate coexistence between camels and wild species in the El-Ouara region in south-eastern Tunisia. We hypothesized that camels herds did not affect the abundance of these wild species and they use different food plants.

## 2. Material and methods

### 2.1. Study areas

Our work was carried out in an area situated along the Libyan border in south-eastern Tunisia, from N32.00° to N33.2°, and from E10.26° to E11.58° (Fig. 1). The

area is characterized by flat to gently undulating topography with a sandy to gravel texture and with flat saline depressions (Sebkha and chott) (Floret and Pontanier 1982). The climate is arid and hot, with annual rainfall less than 200 mm and average annual temperature exceeding 21°C (Floret and Pontanier 1982). The vegetation is generally dominated by patches of short perennial grasses and dwarf shrubs (chamaephytes), with some scattered shrubs, such as *Stipagrostis pungens*, *Anthyllis sericea*, *Gymnocarpos decander*, *Hammada schmittiana*, *Hammada scoparia*, *Traganum nudatum*, *Limoniastrum guyonianum* *Retama raetam* and *Ziziphus lotus* (Le Houérou 1959). Urban and agricultural developments border the study area, and are mainly concentrated around the road joining Ben Guerdane in the north to Tataouine in the west and Dhehibat in the south (Fig. 1). This area is increasingly used as a permanent grazing area for camels, as well as for goats and sheep.

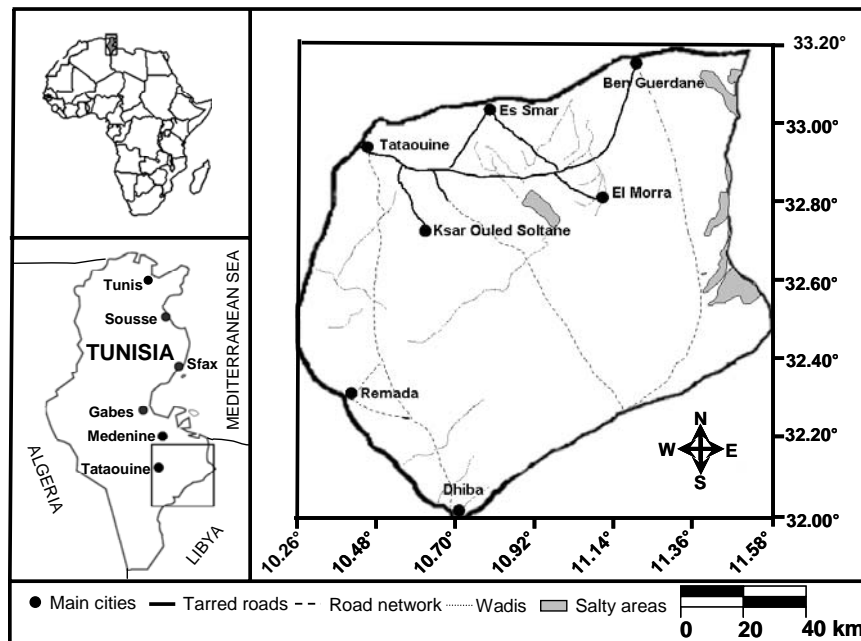


Figure 1. Localisation of the study area.

## 2.2. Animal surveys

Data used in this work were collected during March and April 2004. The study area was firstly divided arbitrarily into 32 400 km<sup>2</sup> sample units (20 km x 20 km) distributed over a regular grid which are hereafter considered as sites. Within each site, five sampling stations were randomly selected along a line transect, separated from one another by 3 km. Each sampling station was visited once for a 30 min survey session. All monitoring was conducted by the same four observers who collected data on Houbara and Dorcas gazelle early in the morning or at the end of the afternoon when these species are most active and therefore their occurrence is more easily detected. During these monitoring periods, the observers walked in different directions and searched for Houbaras and gazelles using long-distance binoculars. Because it is very difficult to make direct observations of these very vigilant, shy and cryptic species, the observers concentrated their effort on searching for signs of Dorcas gazelle and Houbara bustard that are easily recognized, such as tracks (Launay et al., 1997; Yang et al., 2003). We considered target species as present in a given site when at least one individual was observed, or when tracks or faeces were found in at least one survey station.

## 2.3. Human and habitat survey data

During each survey session, the observers recorded the number of small ruminants, that is sheep and goats (hereafter called SRUM), and the number of camels (SCAM) in the surroundings. For each sampled square, we calculated the average value of these variables. The data obtained were then added to those extracted from official maps and were used to monitor the distribution of the Dorcas gazelle and Houbara bustard. For each sample unit, we used a 1/1 000 000

scale vegetation map (Le Hou rou and Le Floc'h, 2001) to measure the proportional area covered by each of the main vegetation types in the study region: shrubs (SHRU), desert woody plants (WOOD) and halophytes (HALO). We also used the 1/100 000 scale maps of Medenine and Tataouine governorates (Cartes Agricoles, 2002) to measure the percentage cover of each of the main geomorphologic units identified in the region: plains (PLAI), sandy areas (SAND) and salty areas (SALT). The latter maps were also used to measure a set of variables describing human pressure within each sample unit: the percentage cover of urbanized areas (URBA) and the percentage cover of agricultural lands (AGRI). Proportional data were arcsine transformed to match normality when the normality assumption was not met (Sokal and Rohlf, 1995).

## 2.4. Data analysis

Given that original human and habitat variables were probably correlated, two separate principal component analyses (PCA) were used to summarize each dataset (proportions arcsinus transformed) of dataset into a few independent factors.

To investigate the effect of the original variables on Houbara and gazelle occurrence in the study area we used multivariate GLM (MANOVA) in the SAS statistical package (SAS institute, 1996). This allowed us to check for possible correlations between variables and then to test for differences between occupied and unoccupied sites (sampled squares). Moreover, the association between the presence of each species (Houbara and gazelle) and independent human and habitat descriptors (as PCA components) was investigated using logistic regression (GENMOD) procedure in SAS statistical package (SAS Institute, 1996). This procedure

allowed us to determine which descriptors affect Dorcas gazelle and Houbara bustard distributions. Through these analyses, we hoped to identify and understand correlations between these species and domestic animals, most notably camels.

### 3. Results

The first PCA summarized the four studied human variables into two independent factors accounting for 67.50% of the variance in the original dataset. The first factor (HUM1) represents an axis of increasing human

land use intensity as it was positively correlated with URBA and AGRI and decreasing camel abundance as it was negatively correlated with SCAM. The second factor (HUM2) represents an axis of increasing small ruminant abundance as it was positively correlated with SRUM (Table 1). The second PCA summarized the original habitat variables into two independent factors, accounting for 62.26% of the original variance. The first factor (HAB1) is positively correlated with SALT and HALO, while the second factor (HAB2) is positively correlated with SAND and WOOD but negatively correlated with PLAI (Table 1).

**Table1.** Variables describing human land use and habitat characteristics in south eastern Tunisia and their correlation with components extracted by the two principal components analysis.

Variable	HUM1	HUM2	HAB1	HAB2
<i>Human variables:</i>				
URBA	0.671**	0.179	-	-
AGRI	0.761**	-0.3517	-	-
SCAM	-0.772**	0.002	-	-
SRUM	0.158	0.945**	-	-
<i>Habitat variables:</i>				
PLAI	-	-	-0.235	0.736**
SAND	-	-	-0.255	0.763**
SALT	-	-	0.743**	-0.182
SHRU	-	-	-0.879**	-0.204
WOOD	-	-	0.014	0.488*
HALO	-	-	0.922**	-0.032
Eigenvalue	1.6518	1.0481	2.2967	1.4391
Variance explained (%)	41.30	26.20	38.38	23.99
Cumulative variance (%)	41.30	67.50	38.28	62.26

\* $P < 0.01$ , \*\*  $P < 0.0001$

The human and habitat variables derived from the PCAs of the original variables were not correlated (Table 2). Thus, these descriptors were considered to be independent explanatory variables and were entered into a logistic regression model to assess their significance in predicting the probabilities of occurrence of Dorcas gazelle and Houbara bustards.

With regard to Dorcas gazelle, Houbara bustard and camels, we found that they occurred respectively in 13, 11 and 10 of the 32 sample units, corresponding with occupancy rates of 40.6%, 34.4% and 31.3%, respectively. Camels were present in 9 of the 13 sample units occupied by Dorcas gazelle (69.2%) and 8 of the 11 sample units occupied by Houbara bustards, (72.7%).

**Table 2.** Pearson correlation coefficient ( $r$ ) and their probability ( $P$ ) between human and habitat descriptors derived from the principal components of the original human and habitat variables.

		HUM1	HUM2
HAB1	$r$	-0.172	-0.224
	$P$	0.3470	0.2169
HAB2	$r$	0.250	-0.119
	$P$	0.1671	0.5143

The two focal wildlife species showed crepuscular to nocturnal activities. However, grazing activities of camels, sheep and goat took place generally at day with avoidance of heat periods. Consequently, no evidence to find domestic livestock, Houbara bustard and Dorcas gazelle grazing together.

The MANOVA results showed an overall significant difference between occupied and unoccupied sample units in relation to human use for Dorcas gazelle (Wilks'  $\lambda = 0.2626$ ,  $F_{4,27} = 18.95$ ,  $P < 0.0001$ ) as well as for Houbara bustard (Wilks'  $\lambda = 0.606$ ,  $F_{4,27} = 4.39$ ,  $P = 0.0073$ ).

However, the comparison of habitat variables within occupied and unoccupied sites, showed significant difference only for Dorcas gazelle (Wilks'  $\lambda = 0.443$ ,  $F_{6,25} = 5.24$ ,  $P = 0.0013$ ). Regarding the original variables, number of camels (SCAM) was the only variable associated with each of the two focal wildlife species. Thus, areas occupied by these two species were characterised by a significantly higher number of camels than unoccupied areas (Tables 3 and 4), suggesting that Dorcas gazelle and Houbara bustard share the same habitat as camels.

**Table 3.** Comparison of human and habitat variables between areas occupied and unoccupied by Dorcas gazelle.

	Occupied area (n = 13)		Unoccupied area (n = 19)		F	P
	Mean	SE	Mean	SE		
<i>Human variables</i>						
URB	0	0	1.30	0.54	3.97	0.0554
AGRI	1.86	1.12	56.99	6.67	35.02	< 0.0001
SRUM	266.15	124.20	142.10	67.75	0.05	0.8289
SCAM	81	22.75	2.37	2.37	29.18	< 0.0001
<i>Habitat variables</i>						
PLAI	47.51	8.94	8.63	2.65	18.31	0.0002
SAND	18.77	7.20	23.16	5.16	0.18	0.6718
SALT	3.83	2.39	6.82	1.99	0.91	0.3488
SHRU	80.25	7.02	87.44	3.29	0.51	0.4813
WOOD	1.24	0.89	2.93	1.46	0.78	0.3840
HALO	18.50	7.18	9.27	3.10	1.82	0.1873

**Table 4.** Comparison of human and habitat variables between areas occupied and unoccupied by Houbara bustard.

	Occupied area (n = 11)		Unoccupied areas (n = 21)		F	P
	Mean	SE	Mean	SE		
Human variables						
URB	0.10	0.06	1.12	0.50	2.16	0.1519
AGRI	20.86	11.42	41.79	7.13	2.61	0.2136
SRUM	95.46	41.72	243.33	94.44	0.85	0.3643
SCAM	75.00	23.92	13.00	9.72	17.89	0.0002
Habitat variables						
PLAI	35.04	10.06	18.86	5.68	2.16	0.1517
SAND	22.46	8.46	20.81	4.74	0.06	0.8159
SALT	6.48	2.98	5.15	1.78	0.17	0.6830
SHRU	74.32	7.82	89.86	2.81	4.62	0.0398
WOOD	2.73	1.92	2.00	1.05	0.13	0.7160
HALO	22.95	8.1	7.82	2.73	4.57	0.0407

The logistic regression analyses showed that only the first factor extracted from the principal component analysis of the human variables (HUM1) was negatively related to both the probability of occurrence of Dorcas gazelle and of Houbara bustards (Tables 5 and 6). Since this human descriptor was negatively related to the number of camels (Table 1)

these findings indicate that Dorcas gazelle and Houbara bustards tend to inhabit the same areas as those used by camels. These results are consistent with those of the MANOVA and suggest that the distributions of these wild species in our study area are not negatively affected by camels but in fact co-occur with them.

**Table 5.** Results of logistic regression of Dorcas gazelle occurrence probability as a function of human and habitat descriptors derived from the principal components of the original human and habitat variables.

Effect	Df	Estimate ± SE	$\chi^2$	P
Intercept	1	0.406 ± 0.047	75.39	< 0.0001
HUM1	1	-0.389 ± 0.050	60.90	< 0.0001
HUM2	1	0.059 ± 0.049	1.42	0.2338
HAB1	1	-0.036 ± 0.050	0.54	0.4616
HAB2	1	-0.083 ± 0.050	2.82	0.0933

**Table 6.** Results of logistic regression of Houbara bustard occurrence probability as a function of human and habitat descriptors derived from the principal components of the original human and habitat variables.

Effect	Df	Estimate ± SE	$\chi^2$	P
Intercept	1	0.312 ± 0.066	22.03	< 0.0001
HUM1	1	- 0.191 ± 0.055	1.99	0.0005
HUM2	1	0.024 ± 0.068	0.13	0.7185
HAB1	1	0.048 ± 0.046	1.08	0.2990
HAB2	1	-0.012 ± 0.058	0.04	0.8367

#### 4. Discussion

The results of the present study demonstrated the coexistence of wild animals' species with domestic camels in southern Tunisia pasture. We found that areas occupied by these two wild species were characterised by significantly higher numbers of camels than unoccupied areas, and that the occurrence probabilities of these species were positively correlated with the number of camels. These results were in line with our initial prediction and may be explained by the fact that Dorcas gazelle and Houbara bustard and camels use different food plants while sharing the same habitats which are represented mainly by flat and open steppes, sebkhas, dry wadis, plateaus and mountain piedmont. Such habitats were characterised by their openness and remoteness with low levels of disturbance caused by urbanisation and agricultural activities. Furthermore, shared food resources are probably abundant during spring, when surveys were carried out, after the rainy season from October to April (Le Hou  rou, 1982, 1984; Le Hou  rou et al., 1988; Floret and Pontanier, 1982; Neffati, 1994) and this may also have facilitated the coexistence of these species. Temporal segregation, as reported in the interaction between livestock and vicunas (Koford, 1957), may also explain the co-occurrence of camels and the focal wildlife species. In order to minimise the risk of being hunted, Houbara bustard and Dorcas gazelle also may become crepuscular or active at night, particularly in areas where they face persecution such as in southern Tunisia (Cramp and Simmons, 1980; Combreau and Launay, 1996; Launay et al., 1997; CMS, 2006; Chammem et al., 2008).

Camels generally consume poor-quality plants that are generally unpalatable and indigestible for the two

focal species of wildlife (Heller et al., 1986; Tandon, Bissa and Khanna, 1988; Lechner-Doll and Engelhardt, 1989). Furthermore, as camel grazing may promote rational utilisation of desert vegetation (Gauthier-Pilters, 1961; Gauthier-Pilters and Dagg, 1981), this also may reduce possible negative effects on gazelles and houbara. According to McNaughton (1979), Prins & Olf (1998); Olf and Ritchie (1998) and Woolnough and du Toit (2001), rational forage use arises as large grazing animals feed on grass and improve its quality, thereby 'facilitating' food for other smaller species. Moreover, it has been argued that camels' feeding behaviour does not cause significant damages to desert vegetation. Camels disperse widely during grazing (Knoess, 1977; Sohail, 1983; Stiles, 1988) and move constantly taking only small portions from any plant, whatever the quality or density of the pasture (Gauthier-Pilters, 1961; Gauthier-Pilters and Dagg, 1981). The existing system of seasonally rotation of camels among different kind of pastures would increase the possibility of coincidental co-occurrence. On the other hand Dorcas gazelle and Houbara bustards also use a wide range of habitat conditions (Lavauden, 1920, 1926; Heim de Balsac, 1936; Dupuy, 1967; Baharav and Mendelsohn, 1976; Osborn and Helmy, 1980; Kacem et al., 1994; Mallon and Kingswood, 2001; Goriup, 1983; Alekseev, 1985; Launay et al., 1997; Osborne et al., 1997; Chammem et al., 2003). At times of increasing competition for resources we suspect therefore that poor habitats also will be used, especially if animals move between habitats in an 'ideal free' manner (Fretwell and Lucas, 1970; Rozenzweig, 1991). Moreover, to avoid interspecific competition for food, most gazelles and houbara in pasture habitat feed and move alone, or in small groups. These wild species are therefore



able to select food items in the high quality localities found on the study areas. They also adopt a time minimizing feeding strategy in response to release from possible interference competition for resources (Lawes and Nanni, 1992). Moreover, as Houbara bustard, are omnivorous and exhibit opportunistic foraging behaviour (Ali and Ripley, 1980; Coles and Collar, 1980; Gallagher and Woodcock, 1980; Goriup, 1983; Mian and Surahio, 1983; Mian, 1984; Alekseev, 1985; Surahio, 1985; Morris, 1991; Tigar, 1995), dietary separation may be achieved as animal prey become more important as a source of food. During this study ingestion of animal prey likely coincided with the breeding season, as animals prey contain more energy for breeding success (Tigar and Osborne, 2000). In addition, a mutually beneficial interaction probably exists between camels and Houbara bustard which can use camel-parasites like ticks as a food resource. More work is required to determine the foraging strategies and dominant foods selected by these species during all seasons. Camel herds also seem to be used by both Dorcas gazelle and Houbara bustards to assist awareness of predator approaches, such as the Golden jackal (*Canis aureus*) and red fox (*Vulpes vulpes*).

It should be noted also that our results showed no significant relationship between small ruminants i.e. sheep and goats, and the focal wildlife species. This could be due to the presence of small ruminants across the entire study area, but also to the traditional and ecologically sound system of small ruminant breeding applied in this Saharan region. This system is based on seasonal movements and nomadism, which may not strongly affect habitat quality for wild animals, as it does not lead to overgrazing or disturbance (Le Houérou, 1993; Abaab et al., 2000; Bourbouze, 2000). Therefore in the

absence of disturbance events or positive interactions with Dorcas gazelle and Houbara bustards, these small ruminant flocks may co-occur randomly in the same areas with these wild animals.

The coexistence of Dorcas gazelle, Houbara bustards and domestic livestock particularly camels, suggests that despite differing resource availabilities over space and time, the species differentiate themselves ecologically. However, the possibility of mitigate competition, notably during drought, cannot be excluded. Manipulative experiments to critically determine if camels affect the abundance of the two wild species could be undertaken by removing camels from some sampling units. The impact of camels on Dorcas gazelle, Houbara bustard and other flagship species living in a pastoral context as in our study or elsewhere would depend also upon the nature and intensity of the domestic breeding system adopted in that area.

The present results were restricted to one area and one period namely spring and may not reflect the situation in other areas and other seasons. Hence, further studies should use several areas over all seasons to quantify any correlational evidence for the coexistence patterns. Furthermore, finer-scale investigation of vigilance behaviour of these two wildlife species in relation to camel presence/absence should provide more insight into coexistence, as should other mechanisms that may operate in natural communities such as storage effects and relative nonlinearity effects (Roxburgh et al., 2004).

## 5. Acknowledgements

We are indebted to M. Abid, H. Tir and S. Sekrafi, who provided invaluable fieldwork. We thank F. Abdelli and A. Barmat for their help in the use of official maps for data collection. We are also grateful to M. Hammadi and two

anonymous reviewers for commenting on an earlier version of the paper.

## References

- Abaab A., Bedrani S., Bourbouze A., Chiche J., 2000. Les politiques agricoles et la dynamique des systèmes agropastoraux au maghreb. Options Méditerranéennes. (Série B) 14, 11-23.
- Alekseev A.F., 1985. The houbara Bustard in the north-west Kyzylkum (USSR). Bustard Studies 3, 87-91.
- Ali S., Ripley S.D., 1980. Handbook of the birds of India and Pakistan. Vol. II. Oxford University Press, Oxford. 2nd eds. 185-198.
- Baharav D., 1982. Desert habitat partitioning by the dorcas gazelle. J. Arid Environ. 5, 323-335.
- Baharav D., Mendelssohn H., 1976. Distribution and movement of the dorcas gazelle in the southern Negev. Israel. J. Zool. 25, 215-216.
- Belovsky G.E., 1984. Moose and snowshoe hare competition and a mechanistic explanation from foraging theory. Oecologia 61, 150-159.
- Belovsky G.E., 1986. Generalist herbivore foraging and its role in competitive interactions. Am. Zool. 26, 51-59.
- Bencherifa A., 1996. Is sedentarization of pastoral nomads causing desertification? The case of the Beni Guil in eastern Morocco. The North African Environment at Risk (eds. W.D. Swearingen & A. Bencherifa), 117-131. Westview Press, Boulder.
- Bourbouze A., 2000. Pastoralisme du Maghreb: La révolution silencieuse. Fourrages 161, 3-21.
- Campos-Arceiz A., Takatsuki S., Lhagvasuren B., 2004. Food overlap between Mangolian gazelles and livestock in Omnogoni southern Mongolia. Ecol. Res. 19, 455-460.
- Chammem M., Khorchani T., Boukhris M., Combreau O., Chniti L., Hammadi M., 2003. L'outarde houbara *Chlamydotis undulata undulata* en Tunisie : statut actuel et distribution géographique. Alauda, 71, 41-47.
- Chammem M., Hingrat Y., Jarray M., Le Nuz E., Orhant N., Abid M., Touiti Y., Karem A., Khorchani T., 2008. Statut et distribution des sites de parade et de site de nidification de l'outarde houbara (*Chlamydotis undulata*) dans la région de Jbil -Tunisie. Proc. des journées scientifiques de l'INGREF, Hammamet 11,12 et 13 novembre 2008. La Biodiversité dans les aires protégées. 144-155.
- Chesson P., 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31, 343-366
- CMS, 2006. Sahelo-Saharan Antelopes. Status and Perspectives. IRScNB-CMS. 2006.
- Combreau O., Launay F., 1996. Activity rhythms of houbara bustards (*Chlamydotis undulata macqueniei*) in relation to some abiotic factors. Journal of Arid Environments, 33, 463-472.
- Coles C.L., Collar N.J., 1980. Symposium papers. 'The Great Bustard. Sofia 1978'; 'The houbara bustard. Athens 1979'. Sydenham Printers, Poole.
- Colwell R.K., Fuentes E.R., 1975. Experimental studies of the niche. Annual Review of Ecology and Systematics 6, 281-310.
- Cramp S. Simmons K.E.L., 1980. A hand book of the birds of Europe, the Middle East and North Africa. Oxford University Press, Oxford.
- Davidson D.W., 1998. Resource discovery versus resource domination in ants: a functional mechanism for breaking the tradeoff. Ecol. Entomol. 23, 484-490.
- De Boer W.F., Prins H.H.T., 1990. Large herbivores that strive mightily but eat and drink as friends. Oecologia 82, 264-274.
- Diamond J.M., 1978. Niche shifts and the rediscovery of interspecific competition. American Scientist 66, 322-331.
- Dregne H.E., 1986. Desertification of arid lands. Physics of desertification (eds. F. El-Baz & M.H.A. Hassan), pp. no pagination. Martinus Nijhoff, Dordrecht.
- Dupuy A., 1967. Répartition actuelle des espèces menacées de l'Algérie. Bull. Soc. Sci. Nat. Phys. Maroc 47, 355-386.
- East R., 1992. Conservation status of antelopes in North Africa. Species 18, 35-36.
- Engelhardt W.V., Rutagwenda T., Lechner-Doll M., Kaske M., 1989. Comparative aspects of ruminants and camels grazing on a thornbush savannah pasture. Proc. of a combined advisory group meeting and a research coordination meeting. International atomic energy agency vienne,
- Engelhardt W.V., Abbas A.M., Moussa H.M., Lechner-Doll M., 1992. Comparative digestive physiology of the forestomach in camelids. Proc. of 1st Camel conference. 263-270.
- Fleischner T.L., 1994. Ecological. Conservation Biology, 8, 629-644. costs of livestock grazing in western North America
- Floret C., Pontanier R., 1982. L'aridité en Tunisie présaharienne. Paris, France: ORSTOM.
- Fretwell, S.D., Lucas, H.L., 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheoretica, 19, 16-36.
- Gallagher M., Woodcock M. W., 1980. The birds of Oman. Quartet Books, London. UK.

- Gauthier-Pilters H., 1961. Observations sur l'écologie du dromadaire dans le Sahara nord-occidental. *Mammalia* 25, 195-280.
- Gauthier-Pilters H., Dagg A.I., 1981. The camel: Its evolution, ecology, behavior and relationships to man. Chicago, USA: University of Chicago Press.
- Gomez-Campo C., 1985. The conservation of Mediterranean plants: principles and problems. In: Gomez-Campos, C. (Eds.). *Plant Conservation in the Mediterranean Area*. Dr W. Junk Publishers. Dordrecht, The Netherlands.
- Goriup P.D., 1983. The Houbara Bustard in Morocco ICBP, Al-Areen.
- Heim de Balsac H., 1936. Biogéographie des mammifères et des oiseaux de l'Afrique du nord. *Bulletin Biologique France/ Belgique* 21, 1-446.
- Heller R., Lechner M., Engelhardt W.V., 1986. Forestomach mobility in the camel (*Camelus dromedarius*). *Comp. Biochem. Phys.*, 84A, 285-288.
- Horgan F.G., 2005. Aggregated distribution of resources creates competition refuges for rainforest dung beetles. *Ecography* 28: 603-618.
- Johnsgard, P. A., 1991. Bustards, Hemipodes and Sandgrouse Birds of dry places. Oxford university press. 106-125.
- Joleaud L., 1929. Etudes de la géographie zoologique de la Berberie. *Bulletin de la Société Zoologique de France*. 59, 438-457.
- Kacem S.B.H., Muller H.P., Wiesner H., 1994. Gestion de la faune sauvage et des parcs nationaux en Tunisie: Réintroduction, gestion et aménagement. Tunis: Direction Générale des Forêts, and Eschborn: Deutsche Gesellschaft für Technische Zusammenarbeit. Tunis. 305 pp.
- Khan W.A., 1996. Food and feeding behaviour of houbara bustard (*Chlamydotis undulata macqueenii*). Houbara Foundation International of Pakistan, Rajanpur District (Dera Ghazi Khan Division).
- Knoess K.H., 1977. Le chameau producteur de viande et du lait. *Rev. Mond. Zoot.* 22, 39-44.;
- Koford C.B., 1957. The vicuna and the Puna. *Ecological Monographs*, 27, 153-219.
- Kouki J., Hanski I., 1995. Population aggregation facilitates coexistence of many competing carrion fly species. *Oikos* 72, 223-227.
- Launay F., Roshier D., Loughland R., Aspinall, S.J., 1997. Habitat use by houbara bustard (*Chlamydotis undulata macqueenii*) in arid shrubland in the United Arab Emirates. *J. Arid Environ.*, 35, 111-121.
- Lavauden L., 1920. La chasse et la faune cynégétique en Tunisie. Tunis, Tunisia: Imprimerie Centrale.
- Lavauden L., 1926. Les vertébrés du Sahara: Eléments de zoologie saharienne. Tunis, Tunisia: Imprimerie Centrale.
- Lawes M.J., Nanni R.F., 1993. The density, habitat use and social organization of Dorcas Gazelles (*Gazella dorcas*) in Makhtesh Ramon, Negev Desert. *J. Arid Environ.*, 24, 177-196.
- Le Cuziat J., Lacroix F., Roche P., Vidal E., Médail F., Orhant N., Béranger P.M., 2005. Landscape and human influences on the distribution of the endangered North African houbara bustard (*Chlamydotis undulata undulata*) in Eastern Morocco. *Anim. Conserv.*, 8, 143-152.
- Lechner-Doll M., Engelhardt W.V., 1989. Particle size and passage from the forestomach in camels (*Camelus dromedaries*) Compared to cattle and sheep fed a similar diet. *J. Anim. Physiol. An. N.*, 61, 120-128.
- Le Houérou H.N., 1959. Recherches écologiques et floristiques sur la végétation de la Tunisie méridionale. 1ère partie: Les milieux naturels, la végétation. Alger, Algeria: Institut de Recherches Sahariennes.
- Le Houérou H.N., 1969. La végétation de la Tunisie steppique (avec références aux végétations analogues d'Algérie, de Libye et du Maroc). *Annales de l'institut de la Recherche Agronomique de Tunisie* 42, 1-624.
- Le Houérou H.N., 1982. Prediction of rang production from weather records in Africa. *Proceedings. Technical Conference on Climate in Africa*. WMO. Genrva, pp. 286-298.
- Le Houérou, H.N., 1984. Rain use efficiency: a unifying concept in arid land ecology. *J. Arid Environ.*, 7, 213-247.
- Le Houérou H.N., Bingham R.E., Skerbek W., 1988. Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. *J. Arid Environ.*, 15, 1-18.
- Le Houérou H.N., 1993. Grazing lands of the mediterranean basin. In: Coupland RT, eds. *Ecosystems of the world*. Vol. 8B. Amsterdam: Elsevier.
- Le Houérou H.N., 1995. Bioclimatologie et biogéographie des steppes arides du nord de l'Afrique: Diversité biologique, développement durable et désertisation. 1st eds. CIHEAM, Montpellier.
- Le Houérou H.N., Le Floc'h E., 2001. La végétation potentielle de la Tunisie aride et désertique (Notice détaillée de la carte 1/1

- 000 000). *Revue des Régions Arides* 12, 5–64.
- Loggers C., Thévenot M., Aulagnier S., 1992. Status and distribution of Moroccan wild ungulates. *Biol. Conserv.* 59, 9–18.
- Mallon D.P., Kingswood, S.C., 2001. Antelopes. Part 4: North Africa, the Middle East and Asia. Global survey and regional action plans. SSC Antelope specialist group. Gland, Switzerland: IUCN.
- Mainguet M., 1994. Desertification: natural background and human mismanagement, 2nd eds. Springer-Verlag, Berlin
- McNaughton S.J., 1979. Grazing as an optimisation process: grass-ungulate relationships in the Serengeti. *Am. Nat.*, 113, 691-703.
- Mian A., Surahio M. I., 1983. 'Biology of the houbara (*Chlamydotis undulate macqueenii*) with reference to western Baluchistan'. *J. Bombay Nat. Hist. Soc.* 80: 111-118.;
- Mian A., 1984. Houbara in Baluchistan: 1983-84 population status, Rep. No. 3. W.W.F. PAKISTAN, Lahore.
- Morris R.P., 1991. A literature review of the houbara *Chlamydotis undulata*. NARC internal report. 65p.
- Neffati M., 1994. Caractérisation morpho-biologique de certaines espèces végétales nord-Africaines. Implications pour l'amélioration pastorale. Universty of Ghent, Dissertation, 264 pp.
- Noss R.F. 1994. Cows and conservation biology. *Conserv. Biol.* 8, 613-616.
- Osborn D.J., Helmy I., 1980. The contemporary land mammals of Egypt (including Sinai). *Fieldiana Zool. New Ser.* 5, 1-579.
- Osborne P.E., Launay F., Gliddon D., 1997. Wintering habitat use by Houbara Bustards *Chlamydotis undulata* in Abu Dhabi and implications for management. *Biol. Conserv.*, 81, 51-56.
- Oloff H., Ritchie M.E., 1998. Effects of herbivores on grassland plant diversity. *Trends Ecol. Evol.* 13, 261-265.
- Ouled belgacem A., Sghaier M., 2000. Impact de la sédentarisation des nomades sur l'équilibre écologique et socio-économique en zone saharienne de Tunisie : cas d'El-Faouar. Séminaire International MEDENPOP 2000 : Population rurale et environnement en contexte bioclimatique méditerranéen (eds. IRA IRD CNT), IRA IRD CNT, Jerba.
- Pignatti S., 1983. Human impact on the Mediterranean Basin. In: Holzner, W. (Eds.) man's Impact on vegetation. Dr. W. Junk Publishers, the Hague, the Netehrlands;
- Prins H.H.T., 1992. The pastoral road to extinction: competition between wildlife and traditional pastoralism in East Africa. *Environ. Conserv.*, 19, 117-123.
- Prins H.H.T., Oloff H., 1998. Species-richness of African grazer assemblages: towards a functional explanation. Dynamics of tropical communities (eds D.M. Newbery, H.H.Y. Prins & N. D. Brown), pp. 449-490. The british Ecological Society, London. UK.;
- Prins H.H.T., 2000. Competition between wildlife and livestock in Africa. In: Wildlife conservation by sustainable use: 51-80. Prins, H. H. T., Grootenhuis, J.G. & Dolan, T.T (eds.): Boston, MA: Kluwer Academic Publishers.
- Putman R.P., 1996. Competition and Resource Partitioning in temperate Ungulate Assemblies. Chapman & Hall, London.;
- Rosenzweig M.L., 1981. Habitat selection and population interrelation: The search for a mechanism. *Am. Nat.*, 137 (suppl.): S5-S28.
- Roxburgh S.H., Katriona S., Wilson, B., 2004. The intermediate disturbance hypothesis: Patch dynamics and mechanisms of species coexistence. *Ecology*, 85(2), 2004, 359-371.
- SAS Institute, 1996. SAS/STAT user's guide, version 6.12. Cary, NC: SAS Institute Inc.
- Schomber H.W., Kock D., 1961. Wild life protection and hunting in Tunisia. *Africa Wildlife* 15, 137-150.
- Schwartz H.J., 1988. Verbesserte Nutzung natürlicher Weiden in den trockenzone Afrikas durch Beatz mit gemischten Herden. In: Beispiele deutscher Agrarforschung in den Tropen und Subtropen (eds.: J. H. Weniger), I. C.T., Berlin, 33-34.;
- Slatkin M., 1974. Competition and regional coexistence. *Ecology* 55, 128-134;
- Sohail M.A., 1983. The role of Arabian camel in animal production. *World review of Animal Production*. XIX, 3, 37-40.
- Sokal R.R., Rohlf F.J., 1995. Biometry: the principles and practice of statistics in biological research. 3rd eds. New York, USA: W.H. Freeman and Company.
- Stiles D.N., 1988. Le dromadaire contre l'avancé du désert. *La Recherche*, 19, 948-952.
- Surahio M.I., 1985). 'Ecology and distribution of Houbara bustard in Sind'. *Bustard Studies* 3, 55-58.
- Swearingen W.D., Bencherifa A., 1996. The North African Environment at Risk. Reprint 1998 eds. Westview Press, Boulder.
- Tandon S.N., Bissa U.K., Khanna, N.D., 1988. Camel meat: present status and future prospects. *Annals of Arid Zones* 27, 23-28.
- Tigar B.J., 1995. A review of the diet of the houbara bustard, Rep. No. 35. National Avian Research Center, Abu Dhabi.

- Tigar B.J., Osborne P.E., 2000. Invertebrate diet of the Houbara Bustard *Chlamydotis [undulata] macqueenii* in Abu Dhabi from calibrated faecal analysis. *Ibis*, 142, 466-475.
- Voeten M.M., 1999. Living with wildlife: coexistence of wildlife and livestock in an East African savanna system; PhD Thesis. Wageningen University, Wageningen, the Netherlands.
- Voeten M.M., Prins H.H.T., 1999. Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. *Oecologia* 120, 287-294.
- Wiens J.A., 1977. On competition and variable environments. *Am Sci.* 65, 590-597.
- Wiens J.A., 1989. Spatial Scaling in Ecology. *Funct. Ecol.*, 3, 385-397.
- Woolnough A.P., Du Toit J.T., 2001. Vertical zonation of browse quality in tree canopies exposed to size-structured guild of African browsing ungulates. *Oecologia*, 129, 585-590.
- Yang W., Qiao J., Combreau O., Gao X., Zhong, W. 2003. Breeding Habitat Selection by the Houbara Bustard *Chlamydotis [undulata] macqueenii* in Mori, Xinjiang, China. *Zoological Studies*, 42, 470-475.