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Differences in space use and habitat selection between captive-bred and wild-born houbara bustards in Saudi Arabia: results from a long-term reintroduction program

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Abstract

In light of widespread declines of houbara bustard *Chlamydotis macqueenii* populations across its extant range, captive breeding has emerged as a viable option for regenerating viable populations of houbaras in addition to limiting hunting pressure, habitat management and amelioration of predation pressure. Although reintroductions of captive-bred houbaras have been carried out in many regions in recent years, information on differences in ranging behavior and habitat selection between captive-bred and wild-born houbaras is lacking. In this study, we utilized radiotelemetry data spanning 13 years to assess differences in home range use and habitat selection by houbara bustards in the Mahazat as-Sayd reserve in Saudi Arabia. The mean (±standard error of the estimate) annual home range size, estimated using the Kernel density method, was 307.76 ± 15.91 km^2, and did not differ significantly between genders. Annual home ranges of wild-born houbaras were however larger than those of their captive-born counterparts (wild-born: 423.77 ± 62.66 km^2, captive-bred: 299.31 ± 16.39 km^2). Rainy season home ranges were the largest (279.29 ± 27.75 km^2) followed by winter home ranges (245.79 ± 19.19 km^2) and summer home ranges (110.51 ± 8.91 km^2) indicating larger-scale movements of houbaras when forage was available. Seasonal home ranges did not differ significantly between wild-born or captive-bred houbaras. Analysis of habitat selection patterns using the distance-based method revealed consistent patterns of habitat preferences across years and seasons and between genders, ages and whether the bird was captive-bred or wild-born. Results indicate that scrub forms the most preferred habitat for houbaras, and should be conserved for the population welfare of the houbara in Saudi Arabia.

Introduction

Houbara bustards, *Chlamydotis macqueenii* (Gray, J.E. 1832), have suffered range-wide declines in recent years (Bailey, Samour & Bailey, 1998; Tourenq *et al*., 2004, 2005). Recently, most studies investigating local declines have indicated the role of excessive hunting, and to a lesser extent, predator-related mortality in exacerbating population losses in houbaras (SaintJalme *et al*., 1996; Bailey *et al*., 1998; Combreau, Launay & Lawrence, 2001; Tourenq *et al*., 2004, 2005). Apart from the houbara's intrinsic value as a charismatic species emblematic of desert environments, the houbara's importance in a large portion of its extant habitat is due to its traditional role as the premier quarry for falconers (Goriup, 1989; Islam *et al*., 2007*a*,*b*,*d*,*e*; Islam, Basheer & Shobrak, 2007*c*). In addition to ameliorating hunting pressure, curbing habitat destruction and predation, captive breeding may be an important option for regenerating sustainable houbara populations (United Arab Emirates (UAE): Ramadan-Jaradi & Ramadan-Jaradi, 1989; Saudi Arabia: Gelinaud, Combreau & Seddon, 1997).

Globally, and in addition to the closely related *C. undulata*, houbara bustards are thought to occupy six distinct geographical regions. Resident and migratory birds occur in the Middle East (Turkey, Jordan, Iraq, Kuwait, Bahrain, Oman, Qatar, Saudi Arabia, UAE, Syria, Yemen), in Russia (including in the Asian region), Iran, Pakistan, India, Afghanistan, Uzbekistan, Tajikistan, from western Kazakhstan to Turkmenistan, and on the Mongolian plateau and in the Gobi desert of Mongolia and western China (Ali & Ripley, 1987; Goriup, 1997; BirdLife-International, 2011). In particular, populations of *C. macqueenii* have been reduced through overexploitation and habitat loss to a single nomadic population utilizing the Harrat al-Harrah protected area (PA) in the far north of Saudi Arabia and may no longer be viable in the long term (Seddon *et al*., 1995; SaintJalme *et al*., 1996; van-

Heezik & Seddon, 1999). In light of the decline in houbara populations in Saudi Arabia, the reestablishment of a viable resident breeding population of houbaras is desired to restore its status as the flagship species, to contribute to regional and international efforts for houbara conservation, and as a precondition for future possible sustainable use (Abu-Zinada, Goriup & Nader, 1989; Seddon & van-Heezik, 1993; Saint-Jalme *et al*., 1996). However, it might be noted that regulated falconry focused on the winter influx of migrant birds continues in the Kingdom.

In recognition of reported declines in houbara densities in Saudi Arabia, the Minister of Foreign Affairs, His Royal Highness Prince Saud Al Faisal established a captive breeding center near the city of Taif in the Emirate of Makkah (the National Wildlife Research Center; NWRC), and the National Commission for Wildlife Conservation and Development (now the Saudi Wildlife Authority) in Riyadh to oversee all species conservation efforts in Saudi Arabia (Seddon & van-Heezik, 1993; Seddon *et al*., 1995). Started in 1991, the houbara reintroduction program at the Mahazat as-Sayd PA provides an invaluable opportunity to conduct research in the ecology, behavior, trapping, captive breeding (Combreau & Smith, 1998), space and habitat use of houbaras at multiple scales (Islam, 2008). The program also aims to establish and manage a network of suitable habitat and initiate collaborative research and conservation programs in the Gulf Cooperation Council (Islam *et al*., 2010).

One possible way to inform habitat management decisions in such programs is to compare the habitat use and survival between captive-bred and wild-born individuals of a reintroduced population. This study uses data spanning 13 years of continuous monitoring of reintroduced and captive-born houbara bustards at the Mahazat as-Sayd PA in Saudi Arabia to investigate differences in home range use and habitat selection between captive-bred and wild-born houbara bustards. Specifically, we estimated home range sizes and investigated factors influencing variations in annual and seasonal home range sizes among genders, ages and between wild-born and captive-bred birds. Secondly, we tested for differences in annual and seasonal habitat selection by houbaras of different genders, ages and by whether they were captive-bred or wild-born.

Study area

The Mahazat as-Sayd PA (Fig. 1) was selected for the houbara bustard reintroduction in Saudi Arabia in 1990 (Child & Grainger, 1990). Mahazat was initially established as a special nature reserve in 1988 to reintroduce oryx, gazelle and houbaras. The PA is about 175 km north-west of Taif and south of Al-Muwayh. It is a fenced facility with a few rock outcrops, moderately to well vegetated with *Acacia tortilis*, *Indigofera* and *Salsola cyclophylla* as dominant shrub/trees and with a sandy, gravelly or alluvial clays substrate. The PA admeasures *c*. 2244 km^2 of fairly level plain at *c*. 900–1100 m above mean sea level. Mahazat has historically attracted winter migrant houbaras and anecdotal accounts suggest breeding may have occurred here in the past. Mahazat forms the main site for reintroductions and has been coupled with Saja Umm Ar-Rimth near Mahazat and at At-Taysiyah PA near the Iraq border. In combination with Mahazat, the two satellite sites will be used to encourage houbara dispersal and genetic mixing (Islam *et al*., 2010).

Material and methods

Field data collection

Captive breeding at the NWRC, Taif was initiated in 1986–1989 with birds sourced from Pakistan and Iran (*c*. 90 and 40 birds, respectively). Subsequently, 1005 birds were moved to

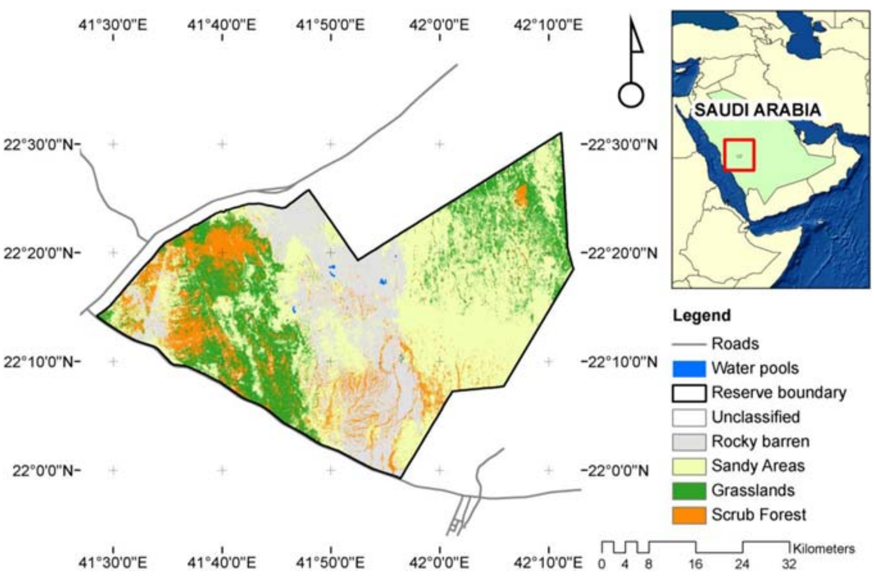

Figure 1 Location of the Mahazat as-Sayd protected area, Saudi Arabia.

the enclosures at Mahazat as-Sayd in 1990 for prerelease acclimation. Of the total stock at Mahazat, 35 died during relocation and 970 were released into the wild from 1991 to 2010. Nearly all released houbara bustards were fitted with radio transmitters and released for regular monitoring of movements and mortality. It should be noted here that whereas the taxonomic classification of the two species is an ongoing debate, we follow Sangster (1996; Sangster *et al.* 1999) and Knox *et al.*'s (2002) classification that suggests houbaras in Mahazat as-Sayd study come from the *C. macqueenii* stock. This also follows Gaucher *et al.* (1996) that houbaras in Saudi Arabia and neighboring countries are most likely *C. macqueenii*. All juveniles houbara bustards released in Mahazat were captive-bred at NWRC in Taif. We define 'juveniles' as birds aged a year or less, 'sub-adults' as birds from 1 to 2 years old and 'adults' as all birds 3 years or older. All reintroductions were done in accordance with the International Union for Conservation of Nature (IUCN) guidelines for reintroductions (IUCN, 1998). Prior to release, birds were kept in long tunnels in prerelease electrified predator exclosures measuring around a 4 km^2 area to acclimate them to the wild. During this period, human contact with birds was minimized except for one person who would provide water and food to the birds every second day. The birds were soft-released after keeping them for 2–3 weeks in the tunnels. Water and food were provided near the tunnels for up to 2 weeks after the release. Each bird was fitted with an identifying metal tag and a radio transmitter and was monitored using either a four-element Yagi antenna attached to a four-wheel drive vehicle or a two-element directional antenna (Telonics, Inc., Mesa, AZ, USA) attached to each wing strut of a Maule-6 aircraft (Maule Air Inc., Moultrie, GA, USA). Ground-based monitoring was conducted 6 days a week and aerial telemetry was carried out 12 days in a month. All locations recorded by aircraft were reconfirmed via direct observation by ground crews using vehicle-mounted very high-frequency receivers. Nest locations were also monitored for successful/unsuccessful nesting attempts and hatchlings were captured and banded opportunistically. We term a bird 'captive raised' when the bird was either relocated to the reserve or was hatched in captivity (inside predator exclosures). We term a bird 'wild born' when it was hatched in the wild (in the general reserve, outside predator exclosures) by parents that were either captive-bred or wild-born. In all, we recorded more than 44 000 individual locations since 1991.

Statistical analysis: space use

We monitored 546 radio-tagged houbara bustards from October 1992 to December 2006. We used these data to investigate factors influencing annual and seasonal home range sizes. To analyze annual home ranges, we used radio locations collected from March 1 of year 1 to the last day of February of year 2. The annual period thus spanned the rainy season (1 March – 31 May), summer (1 June – 30 September) and winter (1 October – 28 February) seasons. Annual home ranges were estimated for birds that had $\geq$30 radiolocations spanning at least 3 months in each season. Data from 1992 were dropped from all analysis because of insufficient sample sizes. We estimated annual home ranges using the 95% Kernel density method (Worton, 1989; Seaman & Powell, 1996) using the least cost cross-validation procedure in ArcView® Animal Movement Analyst (Hooge & Eichenlaub, 2000). To analyze seasonal home ranges, we selected all birds that had $\geq$20 radiolocations within a season and estimated home ranges in a fashion similar to annual home ranges. Rainfall data for the region was extracted from the Global Combined Precipitation Dataset (GPCP V2.2, sourced from: http://www.esrl.noaa.gov/psd/data/gridded/data.gpcp.html).

As home range estimates were heavily right-skewed, we log-transformed estimates of home range size prior to all analyses, and analyzed annual and seasonal home ranges separately. We first tested separately for the effect on annual home range size of gender, age, year of study, rainfall and a variable describing whether a bird was wild-born or captive-raised. In all comparisons, as multiple observations of the same bird could be temporally autocorrelated, we fitted generalized linear mixed models (Zuur *et al.*, 2009) with Gaussian-distributed random errors to partition variation attributable to individual birds. Then, to test for the combined effect of all variables, we tested simultaneously for all main and two-way interaction effects (Slade, Russell & Doonan, 1997; Moyer, McCown & Oli, 2007; Singh *et al.*, 2011). We removed nonsignificant (α = 0.05) interaction terms sequentially such that the least significant interaction term was removed at each step. We sequentially refit models until only significant interaction effects and all main effects remained in the model (Slade *et al.*, 1997; Moyer *et al.*, 2007; Singh *et al.*, 2011). Significant interaction effects were further explored using least squares means (i.e. estimated marginal means) multiple comparison procedures. Seasonal home ranges were analyzed in a similar fashion. All data were analyzed using the SAS software, version 9.2 (SAS Institute Inc., Cary, NC, USA).

Statistical analysis: habitat selection

Spatial data on land cover, water pools and major roads were sourced from the National Wildlife Conservation Foundation's geographical information system database. Locations of water pools were available as global positioning system locations, and were largely ephemeral. They were included in all analysis as they supported substantial scrub vegetation in the immediate vicinity and were likely an important forage source for houbaras. The land cover map was derived from SPOT4 satellite imagery from the year 2009 and described four major land cover classes. These were: rocky barren (477.03 km^2; 21.25%), sandy areas (1038.67 km^2; 46.28%), grassland (439.54 km^2; 19.58%) and scrub forest (289.26 km^2; 12.89%). Water pools in the region are mostly ephemeral in nature, and are only full immediately following rainfall and dry out rapidly. However, good vegetation growth in the vicinity of water pool supports a diversity of insects and reptiles and is likely a good source for food for houbaras.

Habitat selection was conducted using distance-based method techniques (Conner, Smith & Burger, 2003, 2005). We chose the distance-based method over composition-based methods (Aebischer, Robertson & Kenward, 1993) because two important habitat features (water pools: points, roads: line) would not be adequately represented in compositional analysis, which requires area-based estimates of available habitat (Aebischer *et al.*, 1993; Conner *et al.*, 2003, 2005). In short, distance-based habitat selection analysis analyzes the ratios of distances from habitat features to observed locations (i.e. radiolocations) to those of random locations to test the hypothesis that available habitat is used more or less than what would be expected by chance alone (Conner *et al.*, 2003). Also, when compared with composition-based techniques, distance-based technique are more robust with respect to habitat misclassifications and radiolocation error (Conner *et al.*, 2003).

Preliminary home range analysis revealed that home ranges of a majority of houbaras exceeded the boundaries of the study area (total home range of all birds pooled across all years = 5374 km^2, exceeds reserve area by 3129 km^2). We therefore limited analysis of habitat selection to the third-order scale (i.e. selection of habitat within the home range; Johnson, 1980). Analysis of habitat selection therefore refers only to the habitat available within the reserve boundaries. To determine the optimal density of random locations, we generated random points across the study area at progressively increasing densities (from 10 point km^{-2} to 1/10 km^2) and determined where the variance of the distance of random locations to habitats stabilized. Results indicated that random locations generated at a density of 1 point km^{-2} was adequate to represent the 'available' habitat (Fig. 2).

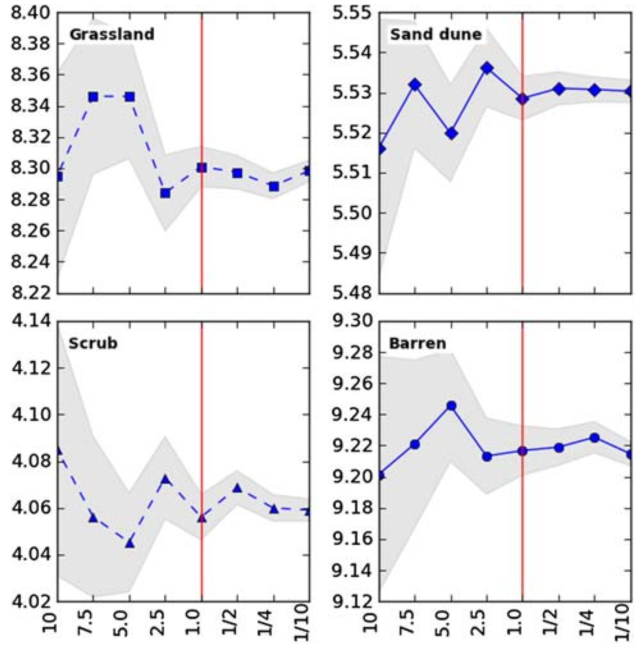

Figure 2 Determining optimal density of random locations to characterize available habitat for distance-based habitat selection analysis. Density of randomly generated locations on *x*-axis (in points km^{-2}), variance of *log*(distance to habitat) on the *y*-axis. The shaded area indicates the standard deviation of the variance about the mean (solid line). Results indicate that the variance of the distance of random locations to habitat stabilizes after 1 point km^{-2}. Note: *y*-axis in log scale.

Results

Space use

Annual home ranges

Data were adequate for estimating annual home ranges for 442 birds. The mean (±standard error of the estimate) size of annual home ranges varied from 482.02 ± 58.45 km^2 in 2002–2003 to 163.91 ± 24.32 km^2 in 1999–2000, with an overall mean of 307.76 ± 15.91 km^2 (Table 1). When the effect of each factor was tested separately, we found that home ranges of houbaras varied significantly across years ($F_{11,313}$ = 5.90, P < 0.0001, Fig. 3). Annual home ranges of female birds did not differ significantly ($t_{1,324}$ = 0.93, P = 0.335) from male birds. Home ranges of birds of different age classes were also different, but only weakly so ($F_{2,322}$ = 2.99, P = 0.0515). Multiple comparisons of estimated marginal means of home range estimates showed that adults had significantly larger home ranges than juveniles (t_{322} = 2.42, P = 0.016, Table 1), and home ranges of subadults were larger than those of juveniles (t_{322} = 2.18, P = 0.030, Table 1). Home ranges of adults and subadults did not differ significantly (t_{322} = 0.07, P = 0.954, Table 1). Wild-born houbaras had larger annual home ranges than captive-bred birds, but the effect was only marginally significant ($t_{1,323}$ = 3.35, P = 0.0681).

When the effects of year, gender, age and the factor describing whether a bird was wild-born or captive-raised were evaluated simultaneously, we found that the effect of year ($F_{11,310}$ = 6.94, P < 0.0001) and age ($F_{2,310}$ = 8.84, P = 0.0002) were strongly significant. The effects of gender was not significant ($F_{1,310}$ = 0.64, P = 0.424) and the factor describing whether a bird was wild-born or captive-bred was marginally significant ($F_{2,310}$ = 3.69, P = 0.056). None of the interaction effects were significant.

Seasonal home ranges

Mean rainy season, summer and winter home range sizes were 279.29 ± 27.75, 110.51 ± 8.91 and 245.79 ± 19.19 km^2, respectively (Table 2, Fig. 4). Preliminary tests revealed that home ranges differed significantly between seasons ($F_{2,617}$ = 26.63, P < 0.0001). We therefore split the dataset across seasons and analyzed the data for each season separately.

Rainy season home range

Tests of single-factor effects revealed that rainy season home ranges differed significantly among years ($F_{7,116}$ = 5.37, P < 0.0001). Bonferroni-adjusted least squares means comparisons revealed that rainy season home ranges of 1995–1995, 1996–1997, 1997–1998, 2000–2001, 2001–2002 and 2004–2005 were larger than those in 1998–1999 (all P < 0.01). Rainy season home ranges differed marginally between genders

Table 1 Estimates of annual home range sizes of houbara bustards at the Mahazat as-Sayd protected area, Saudi Arabia, 1993–2005

	n	Mean (km^2)	SE
By year			
1993–1994	3	292.37	21.66
1994–1995	12	211.89	43.30
1995–1996	22	322.27	51.63
1996–1997	27	256.64	29.93
1997–1998	35	211.03	33.09
1998–1999	32	217.22	33.03
1999–2000	43	163.91	24.32
2000–2001	51	173.08	16.15
2001–2002	68	323.44	41.41
2002–2003	55	482.02	58.45
2003–2004	52	430.63	64.38
2004–2005	42	416.18	70.56
By age			
Juvenile	28	174.17	20.25
Subadult	75	281.29	29.02
Adult	339	324.64	19.52
By gender			
Female	230	326.59	24.59
Male	212	287.33	19.66
Wild-born?			
Yes	30	423.77	62.66
No	412	299.31	16.39
Overall	442	307.76	15.91

Mean home range sizes (in km^2) estimated using the 95% Kernel density method are presented by year, age, gender and whether the bird was captive-bred or wild-born. The number of home ranges (*n*) used to estimate the means and the standard error of the estimate (SE) are also presented.

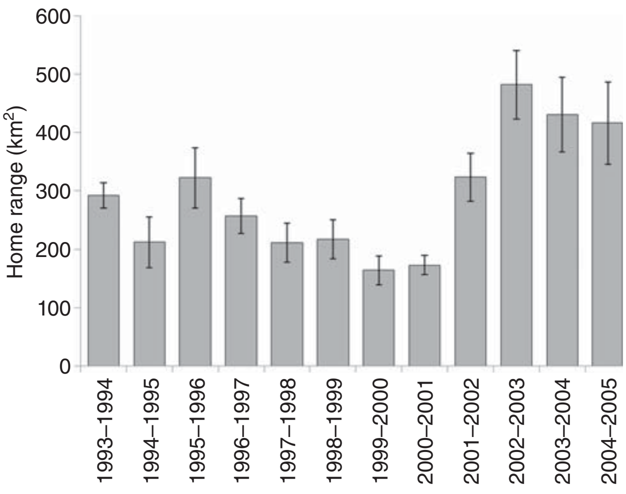

Figure 3 Size of houbara annual home ranges (km^2; mean ± standard error) for each year of the study at the Mahazat as-Sayd protected area, Saudi Arabia. Home ranges are 95% Kernel density estimates using least costs cross-validation.

($F_{1,123}$ = 3.14, P = 0.079), wherein female birds had slightly larger home ranges than male birds (Table 2). Rainy season home ranges did not differ significantly between birds of different ages or whether they were captive-born or wild (all $P > 0.05$).

When the effect of all factors was evaluated simultaneously, rainy season home range size varied significantly across years ($F_{7,112}$ = 6.59, $P < 0.0001$) and the pattern of variation was similar to the annual home ranges. The interaction term between age and gender was significant ($F_{1,112}$ = 5.83, P = 0.0174). Least squares means comparisons revealed that the difference was only significant between adult and subadult males wherein adult males had larger rainy season home ranges than subadult males (t_{112} = 3.53, P = 0.0006, Table 2). Rainy season home ranges did not differ between wild-born or captive houbaras ($F_{1,112}$ = 0.50, P = 0.480). The effect of mean rainfall was significant ($F_{1,112}$ = 14.86, P = 0.0002), wherein houbaras had generally larger home ranges in years with higher rainfall.

Summer home range

Tests of single-factor effects revealed that summer home ranges differed significantly among years ($F_{10,162}$ = 4.30, $P <$ 0.0001). Bonferroni-adjusted least squares means comparisons revealed that summer home ranges of houbaras in 2001–2002 were larger than those in 1999–2000, 2000–2001, 2002–2003 and 2003–2004, and summer home ranges in 2002–2003 were larger than those in 1995–1996 and 1996–1997 (all $P < 0.05$). Summer home ranges differed between genders ($F_{1,172}$ = 4.99, P = 0.0267) wherein female birds had larger home ranges than male birds (Table 2). Summer home ranges did not differ significantly between birds of different ages or whether they were captive-born or wild (all $P > 0.05$).

When the effect of all factors was evaluated simultaneously, summer home range size varied significantly across years ($F_{10,159}$ = 4.08, $P < 0.0001$) and the pattern of variation was similar to that of annual home ranges. The interaction term between gender and whether a bird was captive-bred or wild-born was significant ($F_{1,159}$ = 5.38, P = 0.0217). Least squares means comparisons revealed that the difference was only significant between female and male wild-born houbaras wherein male birds had larger summer home ranges than female birds (t_{159} = 2.74, P = 0.0411, Table 2). Summer home ranges did not differ between houbaras of different ages and the effect of mean summer rainfall was not significant (both $P > 0.05$).

Winter home range

Tests of single-factor effects revealed that winter home ranges differed significantly among years ($F_{10,157}$ = 7.05, $P < 0.0001$). Bonferroni-adjusted least squares means comparisons revealed that winter home ranges of houbaras in 2004–2005 were smaller than those in 1995–1996, 1996–1997, 1998–1999, 2000–2001 and 2003–2004. Winter home ranges of houbaras were also significantly larger in 2003–2004 than those in 1997–1998, 1999–2000 and 2004–2005 (all $P < 0.001$). Winter home ranges did not differ between houbaras of different genders or

Table 2 Estimates of seasonal (rainy season, summer, winter) home range sizes of houbara bustards at the Mahazat as-Sayd protected area, Saudi Arabia, 1993–2005

	Rainy season (March–May)			Summer (June–September)			Winter (October–February)		
	n	Mean	SE	*n*	Mean	SE	*n*	Mean	SE
By year									
1993–1994	–[a]	–	–	3	60.77	19.56	2	43.49	8.34
1994–1995	–	–	–	11	48.15	7.92	6	145.31	28.21
1995–1996	12	241.27	48.69	17	149.52	37.48	21	297.00	54.05
1996–1997	14	482.51	177.19	21	127.09	24.37	29	256.53	37.93
1997–1998	20	267.52	56.90	24	94.44	13.26	32	131.08	30.53
1998–1999	19	89.25	45.75	21	143.31	32.61	23	140.53	26.95
1999–2000	40	176.31	43.63	40	81.11	18.02	40	113.67	14.12
2000–2001	35	204.24	31.29	40	63.28	6.71	41	243.59	32.66
2001–2002	42	311.70	72.63	57	144.90	18.83	15	140.39	32.32
2002–2003	–	–	–	20	55.69	12.91	–	–	–
2003–2004	–	–	–	18	206.24	87.96	43	563.07	81.87
2004–2005	19	639.42	125.14	–	–	–	12	164.70	99.85
By age									
Juvenile	–	–	–	15	70.34	16.43	22	168.64	29.53
Subadult	34	274.77	48.73	70	89.73	13.46	53	214.10	29.36
Adult	167	280.21	31.95	187	121.52	11.80	189	263.66	25.19
By gender									
Female	122	310.31	37.41	149	98.06	9.71	149	253.50	26.88
Male	79	231.39	40.30	123	125.60	15.75	115	235.81	27.06
Wild-born?									
Yes	4	637.13	261.67	15	176.61	84.10	10	501.91	141.17
No	197	272.03	27.70	257	106.66	8.08	254	235.71	18.95
Overall	201	279.29	27.75	272	110.51	8.91	264	245.79	19.19

[a]Sample sizes were inadequate to estimate home range sizes.
Mean home range sizes (in km^2) estimated using the 95% Kernel density method are presented by year, age, gender and whether the bird was captive-bred or wild-bred. The number of home ranges (*n*) used to estimate the means and the standard error of the estimate (SE) are also given.

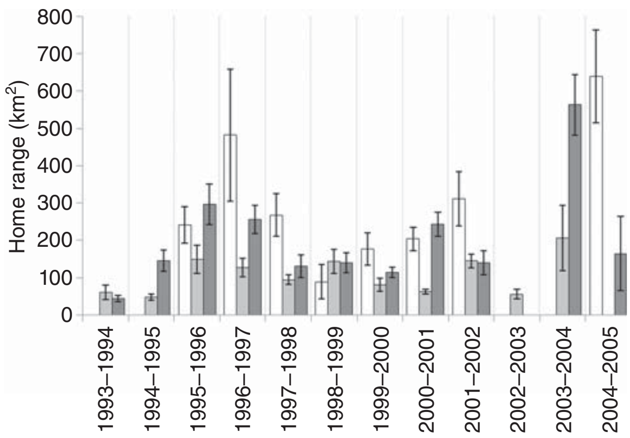

Figure 4 Size of houbara home ranges stratified by season (in km^2; mean ± standard error; open bars: rainy season, light grey bars: summer, dark grey bars: winter) for each year of the study at the Mahazat as-Sayd protected area, Saudi Arabia. Home ranges are 95% Kernel density estimates using least cost cross-validation.

ages (all $P > 0.05$), but were significantly larger for wild-born houbaras than captive-bred ones ($t_{167} = 2.40$, $P < 0.017$).

When the effect of all factors was evaluated simultaneously, only year explained any significant variation in home range sizes ($F_{10,154} = 6.21$, $P < 0.0001$). Winter home ranges did not differ significantly between houbaras of different ages, genders or whether they were wild-born and the effect of mean winter rainfall was not significant (all $P > 0.1$).

Habitat selection

Multivariate analysis of variance results of habitat selection indicated that strong habitat selection occurred ($F_{6,397} = 28.48$, $P < 0.0001$), and that habitat selection varied across years ($F_{6,386} = 19.65$, $P < 0.0001$), seasons ($F_{6,685} = 38.27$, $P < 0.0001$), between genders ($F_{6,396} = 28.52$, $P < 0.0001$), age classes ($F_{6,395} = 18.42$, $P < 0.0001$), and by whether a bird was captive-bred or wild-born ($F_{6,396} = 11.49$, $P < 0.0001$).

Pooled across years and when stratified by ancestry (captive-bred or wild-born), houbaras preferred scrub habitat over all others. This pattern of selection was evident between genders, age classes and across seasons (Table 3) and years of study (Table 5). Captive-born houbaras preferred habitat near roads, but this preference was not evident for juveniles (Tables 3 and 4). Habitats near roads were not used

Table 3 Habitat selection analysis, overall results and results stratified by gender, age class and whether captive-bred or wild-born and by season

	Overall	Gender		Age class			Wild-born		Season		
		Female	Male	Juvenile	Subadult	Adult	True	False	Summer	Rain	Winter
	(403)	(211)	(192)	(28)	(75)	(300)	(27)	(376)	(264)	(196)	(239)
Road	ns	+++	ns	ns	+++	ns	ns	+++	+++	+++	+++
Water	ns	ns	++	+++	ns	ns	ns	ns	+++	++	+++
Scrub	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++
Grass	ns	+	ns	ns	ns	ns	ns	ns	+++	ns	ns
Sand	+++	+	++	ns	ns	+++	ns	+++	ns	+++	+++
Barren	ns	ns	ns	+++	ns	ns	ns	ns	ns	ns	+++

+++$P < 0.0001$; ++$P < 0.01$; +$P < 0.05$; ns, not significant ($P > 0.1$).
Plus (+) symbols indicate that radiolocations were closer to the given habitat than would be expected by chance alone, 'ns' indicates the differences were not significant ($P > 0.1$). Sample sizes are provided in parentheses.

Table 4 Differences in habitat selection between captive-bred and wild-born houbaras stratified across gender, age class and season

	Gender (captive-bred/wild)		Age class (captive-bred/wild)			Season (captive-bred/wild)		
	Female (203/8)	Male (173/19)	Juvenile (22/6)	Subadult (68/7)	Adult (286/14)	Summer (249/15)	Rain (192/4)	Winter (239)
Road	+++/ns	+++/ns	ns/ns	+++/ns	+++/ns	+++/ns	+++/ns	+++/+
Water	ns/ns	+/ns	+++/+++	ns/ns	ns/ns	++/ns	+/ns	ns/ns
Scrub	+++/ns	+++/+++	+++/+++	+++/+	+++/+	+++/++	+++/ns	+++/+++
Grass	ns/+++	ns/ns	ns/ns	+/ns	ns/ns	+++/ns	ns/ns	ns/ns
Sand	+/ns	+++/ns	ns/ns	ns/ns	+++/ns	ns/ns	+/+	ns/ns
Barren	ns/ns	ns/ns	+++/+++	+/ns	ns/ns	ns/++	ns/ns	+++/+++

Sample sizes are provided in parenthesis. Symbols follow that of Table 3.

Table 5 Differences in habitat selection by houbaras across years.

	Year											
	1993–1994 (5)	1994–1995 (17)	1995–1996 (50)	1996–1997(64)	1997–1998 (76)	1998–1999 (63)	1999–2000 (120)	2000–2001 (115)	2001–2002 (114)	2002–2003 (20)	2003–2004 (61)	2004–2005 (31)
Road	ns	ns	+++	+++	ns	+	+	+++	+++	++	+++	ns
Water	+	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Scrub	++	+++	+++	+++	+	+++	+++	+++	+++	+++	++	+++
Grass	ns	++	+	ns	ns	ns	ns	ns	ns	+++	ns	ns
Sand	ns	ns	ns	ns	ns	ns	ns	ns	ns	++	++	+++
Barren	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	+++	ns

Sample sizes are provided in parenthesis. Symbols follow that of Table 3.

by wild-born houbaras in a significant manner. Habitat near water pools and barren features were preferred by juvenile captive-bred and wild-born houbaras but not by other age classes of either ancestry (Tables 3 and 4). Barren features were the most preferred in the winter season, and to some extent in the summer by wild-born houbaras. Adult male captive-bred houbaras were found to prefer habitat in the vicinity of sand dunes, however, such selection was not evident for wild-born houbaras (Tables 3 and 4). Only subadult female wild-born houbaras seemed to prefer grassland habitat. However, this effect was only pronounced in the summer season (Tables 3 and 4).

The patterns of habitat selection were mostly consistent across years in that scrub habitat was by far the most preferred. Habitat near roads was preferred in the years 1995–1996 and from 1998 to 2004 (Table 5). However, most of the selection for habitat near roads was driven by captive-bred houbaras. Grassland habitat was selected for only in the years 1994–1996 and in 2002–2003. Similarly, selection for habitat in the vicinity of sand dunes was only apparent in the years 2002–2003 (Tables 5 and 6). Most across-year indices of selection were driven by captive-bred houbaras, likely a consequence of smaller sample sizes of wild-born houbaras when stratified by year.

Discussion

In view of the range-wide declines of houbaras in recent years (Bailey *et al.*, 1998; Tourenq *et al.*, 2004, 2005), captive breeding has emerged as an active conservation effort for

Table 6 Differences in habitat selection by houbaras across years stratified by whether the bird was captive-bred or wild-born

	Year (captive-bred/wild)			
	2001–2002 (63/5)	2002–2003 (48/7)	2003–2004 (22/8)	2004–2005 (18/7)
Road	+++/ns	+++/ns	ns/+	ns/ns
Water	ns/ns	ns/+	ns/+	ns/ns
Scrub	+++/ns	++/ns	ns/++	+/+
Grass	ns/ns	+++/+	ns/ns	ns/ns
Sand	ns/ns	+++/ns	+++/ns	+++/+
Barren	ns/ns	ns/ns	+++/ns	+++/ns

Sample sizes are provided in parenthesis. Symbols follow that of Table 3. Sample sizes of wild-born houbaras were inadequate to conduct comparisons in the years previous to 2001–2002.

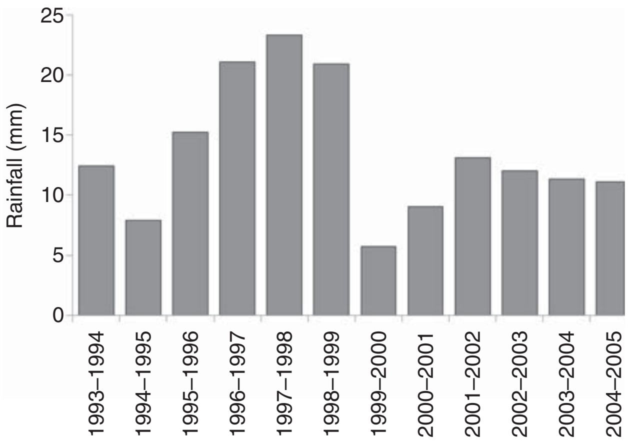

Figure 5 Mean annual rainfall estimates (in mm.) for the Mahazat as-Sayd region extracted from the Global Combined Precipitation Dataset (GPCP V2.2: http://www.esrl.noaa.gov/psd/data/gridded/data.gpcp.html).

regenerating sustainable houbara populations (UAE: Ramadan-Jaradi & Ramadan-Jaradi, 1989; Saudi Arabia: Gelinaud *et al.*, 1997; e.g. Morocco: Bouzendorf & Hingrat, 2006). We used long-term radio-tracking data from the conservation breeding program at the Mahazat as-Sayd PA of Saudi Arabia to investigate factors influencing differences in space use and habitat selection by captive-bred and wild-born houbara bustards.

Pooled across years, the mean annual home range of houbaras in Mahazat as-Sayd was estimated to be 442 ± 15.91 km^2, this is comparative to previously reported estimates (mean = 479 km^2, standard deviation = 194 km^2 for years 1994–1995) in the same region by Combreau, Gelinaud & Smith (2000). However, long-term data revealed that home range sizes varied considerably across years and appeared to display a semi-decadal cyclical pattern. Annual home ranges were the smallest in the years 1999–2001 (~170 km^2) and the largest in 2002–2005 (~650 km^2). This pattern seemed to follow a lagged pattern with mean annual rainfall (Fig. 5). Rainfall has been associated with expanded home ranges in the region (Combreau *et al.*, 2000) and is possibly related to an elevated availability of food in patches away from established home ranges. Houbaras are also observed to move long distances in spring each year just after heavy rain occurs in the area and tend to enlarge their home ranges when food conditions permit (Combreau *et al.*, 2000).

Annual home ranges of male houbaras did not differ significantly from those of female ones. These results are similar to those of Combreau *et al.* (2000) in this region. However, Hingrat *et al.* (2004) found a near eightfold difference between home ranges of male and female houbaras in Morocco (male: 17 km^2, female: 146 km^2). The large difference observed in Morocco was likely due to differences in breeding season ranging behavior between the two genders (Hingrat *et al.*, 2004). Breeding occurs in the post-rainy season in Mahazat (Gelinaud *et al.*, 1997). Differences in home ranges of male and female birds were apparent in this season, but contrary to Hingrat *et al.*'s (2004) findings, home ranges of female ones were much smaller than those of the males (females: 98.06 ± 9.71 km^2, males: 125.60 ± 15.75 km^2 Table 2) likely because of a restriction of movements of female birds around nests (Combreau *et al.*, 2000).

Annual home ranges of wild-born houbaras were found to be larger than their captive-born counterparts, but only marginally so (wild-born: 423.77 ± 62.66 km^2, captive-born: 299.31 ± 16.39 km^2, $P = 0.056$). Although sample sizes were much smaller, the patterns of differences were also apparent in seasonal home ranges in that wild-born houbaras had generally larger home ranges than captive-born birds across all seasons (Table 2). The differences were almost negligible in summer, which may indicate localization of movements around a few wadis and depressions where forage resources are the most easily accessible (Combreau *et al.*, 2000; Islam, 2008). This notion is also supported by the fact that rainfall has a marked bimodal pattern in the study region with the most rainfall occurring in the rainy season, and to a lesser amount, in the winter.

The pattern of habitat selection was also consistent between wild-born and captive-bred houbaras. Houbaras of both groups (wild-born or captive-raised) consistently preferred scrub habitat over all others when stratified across genders, seasons, age classes and years (Tables 4 and 6). Scrub habitat in arid ecosystems harbor an abundance of invertebrate and vertebrate prey and supplies an important source of forage for houbara bustards (Combreau & Smith, 1997; Tigar & Osborne, 2000; Hingrat *et al.*, 2008). The importance of scrub habitat for houbaras has also been indicated across its extant range in the Canary Islands (Carrascal *et al*., 2006), Saudi Arabia (Combreau & Smith, 1997; van-Heezik & Seddon, 1999), Morocco (Le Cuziat *et al*., 2005; Hingrat *et al*., 2007*a*,*b*), UAE (Launay *et al*., 1997; Osborne, Launay & Gliddon, 1997) and China (Yang *et al*., 2002*a*,*b*, 2003). Although habitat near roads were preferred by subadult females, the effect was only significant for captive-bred houbaras. It should also be noted that nonsignificant differences between captive-raised and wild-born birds in habitat selection and home range size comparisons may possibly reflect some amount of parental imprinting of preferences or ranging patterns. However, we do not currently have independent data (in terms of observations from a resident, non captive-bred population) to either support or disprove this hypothesis.

Inasmuch as we did not directly investigate the effects of forage availability on ranging patterns of houbaras, we strongly suspect the study indicates the importance of scrub habitat by influencing houbara habitat selection and ranging patterns across seasons and years. We recommend that in addition to ameliorating direct predation mortality and limiting hunting pressure, a dispersed network of scrub habitat be maintained and preserved across Mahazat as-Sayd to best benefit the long-term population welfare of houbaras. However, it should be noted that our habitat selection analysis only considers habitat available within the reserve. Aggregated across all birds and years, the cumulative area used by radio-tagged houbaras exceeded the reserve by *c*. 3129 km^2. We currently do not have spatially explicit land cover information for these areas. Whereas the land cover patterns around the reserve are similar to those found within the boundaries, and our results reflect what is generally known about houbara habitat preferences from similar regions, there is a distinct possibility our inferences may be biased toward land cover types represented inside the reserve.

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