



Breeding success and juvenile survival in a reintroduced captive-bred population of Asian houbara bustards in the United Arab Emirates

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ABSTRACT: Identifying factors influencing breeding success in endangered species is vital for undertaking appropriate conservation measures. The reintroduced population of the captive-bred Asian houbara bustard *Chlamydotis macqueenii* in reserves of the western United Arab Emirates (UAE) has been closely monitored since releases first began in 2005. Based on 8 yr of monitoring data, we provide novel information on female breeding probability and breeding success within a desert ecosystem. Additionally, we explore factors influencing some breeding parameters. Female breeding probability was on average 0.14 ± 0.31 SD (0.01 ± 0.03 for females less than 1 yr old and 0.23 ± 0.38 for females older than 1 yr). Nest initiation date was influenced by temperature and time. Rainfall during a breeding season increased its length. The estimated nest survival rate for 23 d was 0.52, and was negatively influenced by nest initiation date. Chick survival rate to the age of 6 wk was 0.50 ± 0.39 SD, and survival rate of juveniles in their first year was 0.64 ± 0.02 SE. Our results highlight the ability of captive-bred released houbara in the UAE to breed and of wild born juveniles to survive, 2 vital prerequisites for a successful reintroduction programme. Furthermore, these breeding parameters are similar to the very few that have been reported in other studies of wild resident houbara populations. However, population recruitment rate was low (0.04 individuals per female), resulting mainly from low female breeding probability under harsh weather conditions.

KEY WORDS: *Chlamydotis macqueenii* · Breeding parameters · Captive breeding · Recruitment · Survival · Translocation · RMark

INTRODUCTION

Reintroduction is an important conservation tool to restore populations of endangered species (Seddon et al. 2012, IUCN 2013). The ultimate goal of a reintroduction programme is achieved when translocated animals are able to survive in the long term and reproduce successfully at rates resulting in positive population growth enabling viability (Rout et al. 2009, Schaub et al. 2009). Therefore, for reintroduced populations, knowledge of breeding parameters and key drivers of breeding success are essential to pro-

vide guidance for appropriate conservation strategies (Sutherland 1996). This is especially true when reintroduced individuals are captive-bred, and the knowledge from former wild population is scarce (Parker et al. 2012).

The Asian houbara *Chlamydotis macqueenii* (hereafter 'houbara') is a medium-sized bustard species adapted to arid and semi-arid ecosystems (Hoyo et al. 1996, Van Heezik & Seddon 1999, Riou & Combreau 2014). It is resident in the southern extent of its range (from the Arabian Peninsula to southern Central Asia), but migratory in most of Central Asia and parts

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of Eastern Asia (Goriup 1997). The species is classified as Vulnerable, primarily due to unregulated hunting and habitat loss (Birdlife International 2017). Globally, the current status of wild resident houbara populations is poorly known (BirdLife International 2016), with the latest studies on population trends conducted in the late 1990s (Seddon & van Heezik 1996). More recent studies have examined nest site selection in Iran (Aghanajafizadeh et al. 2012) and reintroduced populations in Saudi Arabia (Islam et al. 2013) and the United Arab Emirates (UAE) (Azar et al. 2016), focusing on survival, densities or habitat selection, but none have examined population breeding parameters. Available data on the breeding parameters of wild populations are also limited, outdated, based on small samples or mainly concern the migrant populations (Table 1).

In the UAE, a resident breeding population formally existed as a part of the Arabian sub-region population (Goriup 1997). Since 2004, the National Avian Research Centre (NARC) has released captive-bred houbaras with the aim of restoring and maintaining a breeding population in a network of protected areas across the UAE (see www.houbarafund.org). By the end of 2016, 13 504 houbara had been released in the UAE, of which 4474 were released in managed protected reserves of Abu Dhabi western area (see Supplement 1 at www.int-res.com/articles/suppl/n035p059_supp.pdf). Ten years of individual monitoring in western Abu Dhabi reserves have highlighted the ability of captive-bred houbara to survive in the long term, with a mean (\pm SD) annual survival of 0.48 ± 0.12 the first year and 0.54 ± 0.08 in the following years (Azar et al. 2016). However, the ability of these individuals to produce viable offspring remains to be assessed.

Here, we provide detailed information about breeding success in a reintroduced captive-bred population of resident houbara in western Abu Dhabi reserves. Specifically, we measured

Table 1. Breeding parameters for resident (r) and migrant (m) Asian houbara *Chlamydotis macqueenii*. Data are presented as means \pm SD where applicable and unless otherwise stated; CI: 95 % confidence intervals. References are 0: Combreau et al. (2002); 1: Qiao et al. (2003); 2: Alekseev (1985); 3: Dementiev & Gladkov (1968); 4: Combreau & Launay (1999); 5: K. A. Parker et al., National Wildlife Research Center, Taif, unpubl.; 6: Rashid (2003); 7: Mendelssohn (1978); 8: Lavee (1988); 9: NARC unpubl. data; 10: Koshkin et al. (2016)

Country	Years	Laying dates	Clutch size	Hatching rate	Predation rate	Apparent nest success	Reference
China (m)	1998–2000	End of April	3.3 ± 1.1 to 4.0 ± 0.8 , Mode = 4 (n = 45)	0.84 ± 0.24		0.59 ± 0.27 nest	0
	1998–2000	End of April	3.3 ± 0.8 to 4.0 ± 0.8 , Mode = 4 (n = 25)	0.80–1.00		Range = 0.23–0.88 Mean female ⁻¹ = 0.51	1
Russia (m)	1965	End of April	Range = 2–4 Mode = 3				2 3
Kazakhstan (m)	1996	Early to mid-April (Syr Darya), 3 nests, 20 April (Balkash)	Range = 2–4 Mode = 3				4
Uzbekistan (m)	2012–2015	Early April to early May	3.2 ± 0.2 (n = 12)	100%	17% nests	88% (First clutches)	10
		Early April	3.2 ± 0.6 Range = 2–5	Mean = 87.5% CI = 83.1–91.8	85% of failed nests	Mean = 51.4% CI = 42.4–60.4	5 6
Pakistan (m)	1987	Early to mid-April	2.50 ± 0.50 (n = 6)				7
	1998–2001	Early April, March–April	2.09 ± 0.06 (n = 23)				8
Israel (r)	1978	Late February to April	Mode = 2, Range = 2–4				9
	1982–1985	April, Early March to end of April	2.8 ± 0.7 (n = 15) Range = 1–4	88.3% n = 43	31% of all nests n = 16	0.47	
Yemen (r)	2002–2010	1–15 April	2.45 ± 0.78 (n = 20)	62.50% n = 24			
	2012	Late January to early June, n = 22	Range = 1–4				

female breeding probability (the proportion of females that attempt to breed each year) and 5 nesting parameters (nest initiation date, clutch size, egg volume, daily nest survival rate and hatching rate), and we estimated chick survival as well as survival of juveniles 1 yr after fledging. Bird breeding performance is driven by a set of individual characteristics (e.g. age and breeding experience) and environmental factors (Barbraud & Weimerskirch 2005, Froy et al. 2013). In desert ecosystems, weather conditions (rainfall and temperature) are key factors affecting reproduction (e.g. timing of breeding, Dunn 2004, Small et al. 2007; female investment, Hargitai et al. 2005) directly, by influencing bird physiology, or indirectly, by regulating food availability (Golabek et al. 2012). Therefore, we examined the influence of female age, breeding experience, rainfall and temperature on nesting parameters. In addition, we modelled the influence of temperature, body condition and transmitter type on the weekly survival probability of juveniles. Finally, we estimated nest productivity, breeding success and population recruitment.

MATERIALS AND METHODS

Study area

The study was carried out from 2008 to 2015 in 4 reserves in western Abu Dhabi Emirate (Fig. 1): Baynunah Mignas (531.13 km²), Berga Sokur (111.71 km²), Tawi (240.88 km²) and Yo Dibsah (215.68 km²), all of which are managed specifically to increase Asian houbara *Chlamydotis macqueenii* survival (Azar et al. 2016). Management activities within the reserves include population reinforcement (see Supplement 1 at www.int-res.com/articles/suppl/n035p059_supp.pdf), fencing to exclude large grazing animals, regular patrolling to prevent poaching and providing supplementary food through the progressive establishment of plantations, representing 0.33% of the reserves in 2015. The dominant species planted are mustards *Brassica* spp., water spinach *Ipomoea aquatica* and moss rose *Portulaca oleracea*, which are maintained through artificial irrigation (Azar et al. 2016). The study area is characterised by a hot desert climate

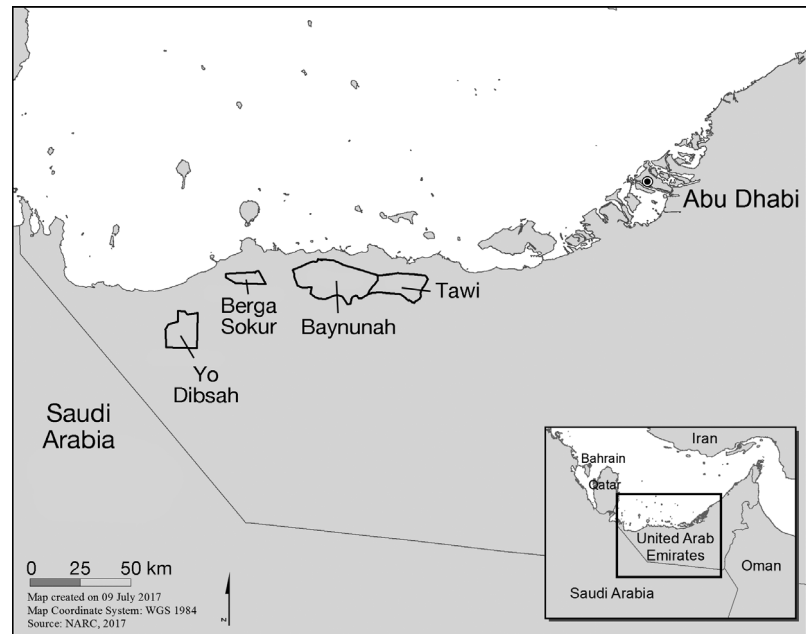


Fig. 1. The 4 main Asian houbara bustard *Chlamydotis macqueenii* reserves in western Abu Dhabi Emirate, United Arab Emirates

corresponding to a Köppen classification of 'BWh' (Kottek et al. 2006), characterised by high humidity and low annual rainfall (<40 mm). Maximum summer temperature is approximately 47°C and minimum winter temperature is approximately 5°C (Bottomley 2008). Habitats in all 4 reserves are similar, each comprised of undulating sand dunes and gravel plains intermixed with flat salty areas (sabkhas) and sparse vegetation scattered between sand dunes. Vegetation is dominated by perennial shrubs, including ham-mada elegance *Haloxylon salicornicum* and *Zygophyllum* spp.

Nest search and female breeding probability

Nests were located primarily by tracking 399 females equipped with transmitters, although some nests of unequipped females were occasionally located during fieldwork or by patrolling rangers. Tracked females were equipped with very high frequency (VHF) radio-transmitters (20 g backpack style; Merlin Systems) or platform transmitter terminal (PTT) satellite transmitters (30 g backpack; Microwave Telemetry), representing, 1.41 and 2.11%, respectively, of the mean body weight of reintroduced adult females (1419.37 ± 148.71 [SD] g, n = 8; NARC unpubl. data). Ground VHF radio-tracking was completed weekly throughout each breeding season, from the time the first displaying male was

observed (generally in December) to fledging of chicks from the last nesting female, and every 2 wk outside the breeding season. Coordinates of PTT-tracked females were checked in a geographic information system (GIS) to identify any location clusters indicating potential nesting sites. These were then confirmed by weekly site visits. All captive-bred released houbara were marked with engraved coloured bands allowing the identification of nesting females not equipped with transmitters. Female breeding probability was estimated from tracked birds for 2 age groups: less than 1 yr old (newly released individuals) or older than 1 yr. Female breeding probability was estimated as the number of females that nested out of the total number of tracked females located weekly during a breeding season. Female breeding experience was categorised as whether a female had a previous nesting attempt (scored as 1) or not (scored as 0).

Nest monitoring

Nests were monitored by regular visits (weekly visits from date of nest discovery and daily visits in the 3 d prior to estimated hatching date) or via camera traps. Camera traps (Reconyx HC600 Hyperfire; RECONYX) were used from 2014 ($n = 46$ nests from 40 females) for accurate determination of hatching rate, nest fate, hatching date and identification of nest predators. A camera trap was deployed within 1 wk following the discovery of a nest, at a distance of 1 m from the nest. Nests monitored by camera traps were visited every 10 d to download pictures and replace batteries; the last visit was scheduled 4 d after the estimated hatching dates (see Supplement 2 at www.int-res.com/articles/suppl/n035p059_supp.pdf).

Nesting parameters

Clutch size was defined as the maximum number of eggs observed in a nest during monitoring. Egg mass (measured with an electronic balance to the nearest 0.1 g), and egg dimensions (measured using a dial or digital calliper to the nearest 0.1 mm), were used to calculate egg volume in mm^3 and estimate its development stage (see Supplement 2). Nest initiation date was defined as the median of estimated egg laying dates of each clutch. Egg laying date was calculated by subtracting the estimated development stage from its measurement date, or in case of known

hatching date (e.g. using camera traps), by subtracting 23 d (mean incubation period; Combreau et al. 2002) from its observed hatching date. Hatching rate was calculated, excluding predated and abandoned nests, as the number of hatched eggs divided by the clutch size.

Offspring monitoring

Houbara chicks fledge at an average age of 8 wk after hatching (Combreau et al. 2002). Because tagging with transmitters would increase their mortality (Combreau et al. 2002), they were not monitored individually, and their survival was estimated from weekly monitoring of brooding VHF-tracked females in 2014. Juveniles were then trapped by hand before fledging (Hardouin et al. 2012) and fitted with GSM-GPS backpack transmitters (30 g Microwave Telemetry, $n = 10$) or VHF backpack radio-transmitters (20 g Merlin Systems, $n = 19$), with transmitters representing <10% of their body mass. Transmitters were attached to juveniles using Teflon harnesses incorporating elastic that could expand as the birds grew (Combreau et al. 2011). VHF-equipped juveniles were monitored weekly from the ground and GSM-GPS transmitters were set to record 1 location every 2 min and to send locations daily.

Weather conditions affecting nest parameters

Houbara females lay eggs on average 2 wk after insemination (Saint Jalme et al. 1994). Therefore, to study how weather conditions influence the timing of nest initiation and breeding parameters, total rainfall and mean maximum temperature 4 wk prior to nest initiation date were used. To analyse effects of temperature during incubation on hatching rate, mean maximum temperature between nest initiation dates and nest hatching or abandonment dates were used. Total rainfall during the nesting period (the period between the first and last nest found each year) was used to study the influence of weather on the length of the breeding season. Weather data were obtained from the Global Land Data Assimilation System in 3-hour increments (Rodell & Beaudoin 2016).

Statistical analysis

Generalised linear mixed models (GLMMs), conducted with the 'lme4' package (Bates et al. 2012) in

R v.2.15.1 (R Development Core Team 2015) were used to model the influence of variables on breeding parameters. The influence of temperature (in quadratic terms) and rainfall on nest initiation date was modelled using binomial error with year as a random effect. The response variable was coded as nest (1)/no nest (0) for all dates between the minimum and maximum nest laying dates of all years. Time was included in the model to account for temporal autocorrelation (Zuur et al. 2009). Similarly, the influence of female age, temperature, rainfall and nest initiation date on egg volume was modelled using Gaussian error, with year and female identity as random effects. The influence of female age, nest initiation date, temperature and rainfall on clutch size was fitted with Poisson error, with female identity and year fitted as random factors. The influence of clutch size, female age and nest initiation date on hatching rate was modelled with a Gaussian error distribution, with hatching rate arcsine transformed prior to analysis (Noriyuki et al. 2012). Using the 'dredge' function in the 'MuMIn' package of R (Barton 2014), we generated subsets of models from global models. Pearson's correlation coefficient was used to measure the relationship between total rainfall during a breeding season and the length of the breeding season.

The influence of female age, nest initiation date, nest age at discovery and females' breeding experience on daily nest survival rates was modelled using a maximum likelihood approach implemented in the program MARK (White & Burnham 1999) and run through the RMark package (Laake 2013). Nest survival (i.e. probability of a nest surviving from initiation to hatching of at least 1 egg) was calculated by raising the estimated daily nest survival rate to the power of the length of the incubation period (23 d).

Chick survival before fledging was defined as the ratio of the number of chicks seen with a tracked female 6 wk after hatching relative to the initial number of hatchlings for that female. After fledging, survival of juveniles was modelled using RMark (White & Burnham 1999) to write Burnham joint live–dead models (Burnham 1993) into MARK (White & Burnham 1999). Encounter histories were constructed into weekly occasions for 1 yr of monitoring, and grouped into tri-monthly time periods. To reduce the number of models, we first selected the best time-varying model for survival and recapture probabilities. The influence of transmitter type, body condition (residuals of mass to tarsus length; Azar et al. 2016), ratio of transmitter mass to body mass and average weekly temperature were tested on the selected time model. We performed goodness-of-fit (GOF) tests for a single

state model by using the program U-CARE (Choquet et al. 2009), as no specific test is available to assess GOF of the general model when combining live telemetry locations and dead recoveries (Duriez et al. 2009). Yearly survival rate was calculated using the delta method in the R package 'msm' (Jackson 2011).

Akaike's information criterion corrected for small sample sizes ($QAIC_c$) was used to rank both GLMM and survival models, and $\Delta QAIC_c$ and Akaike weights (w) were used to assess model likelihood and uncertainty (Burnham & Anderson 2004). Model averaging was used to calculate average parameter estimates based on all models in which the parameter appeared, and the relative importance of each variable (RVI) in the top models ($\Delta QAIC_c < 2$) was calculated by summing the weights of all models containing that variable. Model-averaged parameters were considered strongly supported when their 95% unconditional confidence intervals did not span zero.

Nest productivity (average number of hatchlings per nest) was estimated as the product of nest survival \times hatching rate \times clutch size. Breeding success (average number of juveniles successfully raised to fledging by a nesting female) was estimated as the product of nest productivity \times chick survival. Population recruitment (number of individuals added to the population after 1 yr per female) was estimated as the product of female breeding probability \times breeding success \times juvenile survival.

RESULTS

Between 2008 and 2015, a total of 84 nests from captive-bred released females were found in the western reserves of Abu Dhabi (out of 110 nests found in the UAE as a whole). The number of nests found during 8 successive years was highly variable (mean \pm SD = 10.50 ± 17.71), with the highest number of nests (58%) found in 2014 (Fig. 2). Age of nesting females ranged from 10.82 mo to 7.71 yr (mean \pm SD = 3.43 ± 1.58 yr, $n = 70$). Female breeding probability was on average $0.14 \pm 0.31 \pm$ SD ($n = 8$ yr); 0.01 ± 0.03 for females < 1 yr old and 0.23 ± 0.38 for females older than 1 yr. Median nest initiation date was day-of-the-year 57 (25 February). Nest initiation date was positively influenced by progress of the breeding season, time (RVI = 1, $\beta = 0.001$, 95% CI = 0.0007–0.0014) and negatively with temperature² (RVI = 1, $\beta = -0.04$, 95% CI = -0.05 to -0.02 ; Table 2). Rain did not influence nest initiation date, with RVI = 35% and CI spanning zero. Increase in rainfall during the nesting period caused a statistically significant increase in

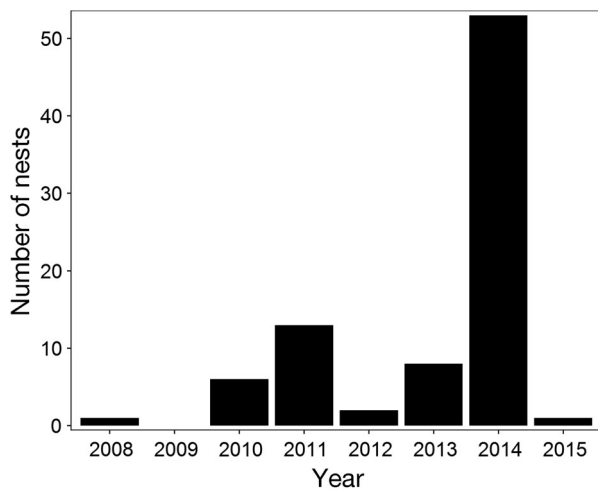


Fig. 2. Number of captive-bred Asian houbara bustard *Chlamydotis macqueenii* nests found each year in western Abu Dhabi Reserves

the length of the breeding season ($r = 0.89$, $n = 5$, $p = 0.04$). A total of 209 eggs were laid, with a mean \pm SD clutch size of 2.49 ± 0.72 eggs ($n = 84$ nests). None of the tested parameters had an influence on clutch size; all displayed an RVI of $<20\%$ and their CI spanned zero (Table 2). Mean \pm SD hatching rate was 0.79 ± 0.25 ($n = 51$) and was not influenced by any of the tested variables (Table 2). All tested variables had an RVI of $<33\%$ and their CI spanned zero. Mean \pm SD egg volume was 46.65 ± 22.86 mm³ ($n = 27$ eggs) and was positively influenced by female age (RVI = 1, $\beta = 0.01$, 95% CI = 0.001–0.02; Table 2).

Nest survival

Nest survival analysis was performed on nests monitored in 2014 only, when the majority of nests were found (Fig. 2), and monitored using camera traps. Nest survival was influenced by nest initiation date (Table 3); nests initiated later in a breeding season had lower daily nest survival rates (RVI = 78%, $\beta = -0.03$, 95% CI = -0.06 to -0.002 ; Fig. 3). Average daily nest survival for nests found in 2014 was 0.972 ± 0.031 SE; therefore, average nest survival for the 23 d of incubation was 0.52. Nest failure was caused mainly by egg predation (66.67%); 60% of nest depredations occurred after the median nest initiation date (1 March), followed by nest abandonment (33.33%); 63%

Table 2. Models of nest initiation date, clutch size, hatching rate, and egg volume of captive-bred Asian houbara bustard *Chlamydotis macqueenii* in western Abu Dhabi reserves, United Arab Emirates, 2008–2015. Only a limited number of relevant models are presented here for clarity. K : number of parameters; AIC_c : Akaike's information criterion adjusted for small sample sizes; ΔAIC_c : change in AIC_c ; w_i : Akaike weight

Model	K	AIC_c	ΔAIC_c	w_i
Egg volume				
Female age + rainfall	5	54.80	0.00	0.55
Female age	4	56.14	1.34	0.28
Clutch size + female age + rainfall	6	58.84	4.04	0.07
Clutch size + female age	5	59.72	4.92	0.05
Hatching rate				
(Null)	3	112.27	0	0.99
Clutch size	4	101.87	10.40	0.01
Female age	4	94.76	17.51	0
Clutch size				
(Null)	1	102.57	0	0.26
Female age	2	103.7	1.13	0.15
Temperature	2	104.23	1.66	0.11
Nest initiation date	2	104.42	1.85	0.10
Rainfall	2	104.48	1.91	0.09
Nest initiation date				
Temperature ² + time	3	279.39	0	0.65
Temperature ² + time + rain	4	280.64	1.25	0.35
Temperature ² + rainfall	3	312.89	33.50	0
Temperature ²	5	297.19	4.64	0

of abandoned nests occurred after the median nest initiation date. Photos from camera traps (46 nests) revealed that red fox *Vulpes vulpes* was the principal nest predator (88% of predated nests). Age of a nesting female had the second highest RVI (25%) but was not statistically significant as its confidence intervals spanned zero ($\beta = -0.01$, 95% CI = -0.05 – 0.03).

Table 3. Candidate models used to analyse nest survival (ϕ) of captive-bred Asian houbara bustard *Chlamydotis macqueenii* in western Abu Dhabi, United Arab Emirates, in 2014. Only a limited number of relevant models are presented here for clarity. K : number of parameters; AIC_c : Akaike's information criterion adjusted for small sample sizes; ΔAIC_c : change in AIC_c ; w_i : Akaike weight; Dev: deviance

Model	K	AIC_c	ΔAIC_c	w_i	Dev
ϕ (Nest initiation date)	2	94.70	0.00	0.50	90.67
ϕ (Nest initiation date + female age)	3	96.44	1.73	0.21	90.38
ϕ (~1)	1	97.15	2.45	0.15	95.14
ϕ (Nest initiation date + female previous breeding attempt)	4	98.59	3.88	0.07	90.49
ϕ (Female age)	2	99.16	4.46	0.05	95.13
ϕ (Female previous breeding attempt)	3	101.18	6.48	0.02	95.12

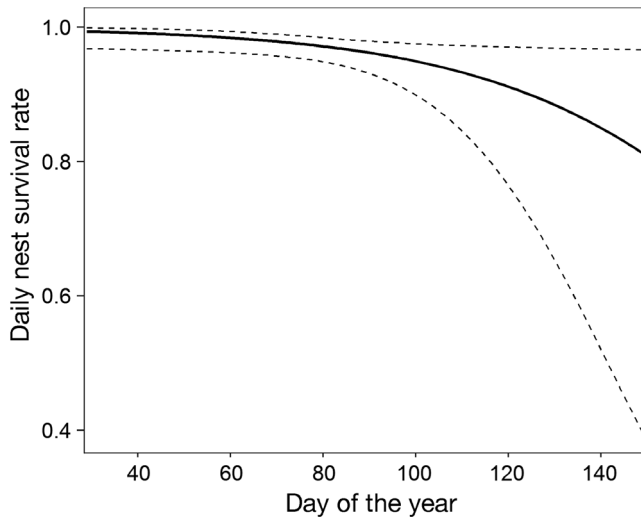


Fig. 3. Daily nest survival rate of captive-bred Asian houbara bustard *Chlamydotis macqueenii* during 2014. Dashed lines represent 95% CI

Offspring survival

Chick survival to the age of 6 wk was 0.50 ± 0.39 SD. The GOF test for juvenile survival 1 yr after fledging was statistically significant for live recaptures ($\chi^2_{53} = 55.16$, $p < 0.01$), revealing overdispersion, while it was not statistically significant for dead recoveries ($\chi^2_5 = 0.94$, $p = 0.96$). An overdispersion was estimated ($\hat{c} = 1.04$), and was used to correct any potential violation of independence between individuals (Cooch & White 2001). The best time-varying model showed that survival varied with time (measured every 3 months) and constant recapture probability ($\Delta\text{QAIC}_c = 5.52$), therefore covariates were tested assuming this model. Averaged models showed no support for any of the tested variables on

Table 4. Candidate models used to analyse variation of weekly survival of juvenile Asian houbara bustard *Chlamydotis macqueenii* hatched in western Abu Dhabi reserves, United Arab Emirates, in 2014, showing only survival (ϕ) and detection (p) probabilities. Only a limited number of relevant models are presented here for clarity. K : number of parameters; AIC_c : Akaike's information criterion adjusted for small sample sizes; ΔAIC_c : change in AIC_c ; w_i : Akaike weight; Dev: deviance

Model		K	AIC_c	ΔAIC_c	w_i	Dev
ϕ (~Time)	$p(\text{model})$	8	824.05	0	0.31	746.49
ϕ (Time + body condition)	$p(\text{model})$	9	825.53	1.48	0.15	807.31
ϕ (Time + trans to body mass)	$p(\text{model})$	9	825.99	1.94	0.12	807.77
ϕ (Time + temperature)	$p(\text{model})$	9	826.10	2.04	0.11	746.49
ϕ (Time + model)	$p(\text{model})$	9	826.11	2.04	0.11	746.50
ϕ (Time+ body condition + trans to body mass)	$p(\text{model})$	10	827.54	3.5	0.05	807.27

survival (RVI < 25% for all the tested variables; Table 4). The mean tri-monthly survival rate was 0.97 ± 0.01 SE, and the 1 yr survival rate (52 wk) was 0.64 ± 0.02 SE. Nest productivity was 1.02 hatchlings nest⁻¹ and breeding success was 0.51 fledging chicks per breeding female. The population recruitment rate was estimated as 0.05 ind. female⁻¹ in the population; 0.006 for females <1 yr and 0.09 for females >1 yr old.

DISCUSSION

Long-term individual monitoring of reintroduced resident houbara *Chlamydotis macqueenii* in western Abu Dhabi reserves provides evidence that captive-bred individuals are able to survive in the long term (Azar et al. 2016). However, population recruitment was generally limited, as a result of low and stochastic female breeding probability.

Breeding parameters of reintroduced houbara in UAE were globally low but similar to the very few reported in other studies of wild resident houbara populations (Table 1). Breeding parameters of resident houbara populations are lower than those of migrant houbaras (Table 1). For example, nest productivity of resident houbara in the UAE and in the Negev Desert were equivalent (1.02 and 0.95 hatchlings nest⁻¹ respectively), but were lower than for migrant houbara in China (1.8 hatchlings nest⁻¹), resulting mainly from smaller clutch size in resident houbara populations (Table 1). Clutch sizes of reintroduced resident houbara in the UAE were similar to those reported from wild populations in areas characterised by hot desert climates (Kottek et al. 2006), i.e. Pakistan, Yemen and the Negev Desert (Table 1). Smaller clutches in a desert ecosystem might be a consequence of lower food availability, either because larger broods will require more food resources, or because smaller clutches allow for rapid replacement of failed nests (Zanette et al. 2006). Conversely, the larger clutches observed in migrant houbara populations might be a product of a time-constrained breeding season, where increasing clutch size can maximise productivity (Combreau et al. 2002). Animal productivity in desert ecosystems, while generally low, is known to be highly variable between years due to the high inter-annual variability of rainfall (Noy-

Meir 1973). This is reflected in our results, with female breeding probability and the number of nests found being low and highly variable between years. Such stochasticity in breeding effort is a common pattern in desert birds, reflecting their plasticity and ability to increase their breeding effort when environmental conditions are favourable (Costa 1995). Furthermore, it is known that reproductive performance improves with age in African houbara bustards *C. undulata*, which reach their peak reproductive performance at the age of 4 yr (Preston et al. 2015) mainly by increasing courtship display rates and egg production (Chantepie et al. 2015). The reintroduced houbara population in western Abu Dhabi is mainly composed of young individuals due to the increasing number of young birds (<12 mo) released each year (see Supplement 1) in conjunction with low survival rates (Azar et al. 2016), which contributes to the low breeding performance of the population. In our study, females older than 1 yr had a higher breeding probability and laid larger eggs. In general, larger egg size results in offspring with larger mass after hatching (Amundsen 1995, Styrsky et al. 1999), which may have a positive effect on their survival (Blomqvist et al. 1997, Risch & Rohwer 2000). However, female age had no effect on clutch size, likely due to a strong influence of harsh environmental conditions on female investment.

Our study population was bred in captivity. The demography of translocated populations, especially those based on captive-bred animals, is known to suffer a substantial release cost, influencing their survival, movements and breeding probability (Sarrazin et al. 1996, Bertolero & Oro 2009, Le Gouar et al. 2012). This cost might be explained by genetic processes, such as outbreeding depression, inbreeding, drift loads and adaptation to captivity (Frankham 2008). However, these processes are unlikely to explain the observed low breeding success of reintroduced females in the UAE, because the captive breeding programme in the UAE follows a strict genetic programme based on maximising genetic diversity and the representation of founders (Lesobre et al. 2010), and breeding parameters were within the range of known parameters obtained from resident wild populations (Table 1). The observed low breeding probability might therefore rather be linked to non-genetic factors, such as bird condition (Champagnon et al. 2012), behaviour (Tavecchia et al. 2009) or external conditions (weather and management practices; Azar et al. 2016). In the absence of data on breeding probability from wild resident houbara in arid environments, the relative influence of these factors cannot be assessed, and further investigations are required.

Weather conditions are known to influence the onset of the breeding season (Wingfield 1984), and in many desert species, rainfall and temperature patterns have been the focus of interest regarding environmental influence on breeding ecology (Zann et al. 1995). Our results showed that rainfall during a breeding season increased its length, potentially as a direct factor inducing a physiological adjustment in females (Dawson 2008), or indirectly through extending favourable environmental conditions that may stimulate more females to breed or re-clutch after a nesting failure. However, rainfall did not stimulate the onset of the houbara breeding season, a result that is in concordance with previously reported findings on captive houbara breeding in outdoor enclosures (Van Heezik et al. 2002, Maloney 2003) and other desert species (Zann et al. 1995, Schaub et al. 2009). Rather, the onset of breeding is generally controlled by an increase in temperature (Wingfield 1984), or by an increase in photoperiod (Lambrechts et al. 1997), which is also associated with progress into the breeding season, these 2 factors acting simultaneously with the seasonal shift from winter to spring. The importance of temperature has been reported for species inhabiting temperate regions (Lack 1950, Slagsvold 1976, Dunn 2004); however, it remains poorly documented in desert species (Barrientos et al. 2007) where early winter temperature is not as cold. Interestingly, in our analysis the increase in temperature was associated with the onset and termination of the breeding season of houbara. However, such a relationship requires further study which should take into account the possible confounding effects of photoperiod.

Nest predation is the main cause of nest failure in many bird species (Muchai & du Plessis 2005). The percentage of predated nests in the UAE (30%) is within the range of reported predation rates for the species (Table 1). Nest survival decreased throughout the breeding season primarily due to increased predation rates, which may result from an increase in the nutritional demand of predators to feed their offspring (Wilson et al. 2007). In addition, most nest abandonment occurred late in the season when heat stress increased with the beginning of summer (Wingfield 1984). A similar time-dependent effect has been reported by Koshkin et al. (2016) in Uzbekistan and by Bacon et al. (2017) in the closely related African houbara.

Surprisingly, nest abandonment was the secondary cause of nest failure, despite apparently low anthropogenic disturbances like herding (Chamberlain & Crick Humphrey 2003), land use or tourism (Beale &

Monaghan 2004). To our knowledge, nest abandonment has not been previously reported as a main cause of nest failure in resident or migratory houbara. However, other potential sources of disturbance require further investigation, such as the maintenance of plantations by workers or research activities. In addition, other causes of nest desertion need to be investigated; for example, houbara densities and sex ratios in the vicinity of plantations which may favour male harassment of nesting females (Rowe et al. 1994), or severe weather conditions (Sherley et al. 2012).

Survival of wild-born juveniles was constant during the first year and was not influenced by any of the tested variables. On average, wild-born juvenile houbara possessed a yearly survival probability higher than that of captive-bred released juveniles (0.48 ± 0.12 SD) in the first year after release (Azar et al. 2016). Higher survival rates in wild-born houbara might result from parental learning (Nicoll et al. 2004), improved foraging abilities (spatial directions, feeding site locations and prey selection; Arnold et al. 2007), effectively coping with the harsh climate, predation avoidance, or the ability to socialize with adults (Brown et al. 2006).

Our results demonstrate that female captive-bred released houbara in the UAE are able to breed; however, population recruitment remains low, probably due to harsh weather conditions in the desert ecosystem. Desert bird populations are generally small with low productivity and their viability relies mostly on adult survival. Due to their low demographic resilience, perturbations such as rapid habitat loss and over-hunting may quickly lead to their extirpation. Reserves in the UAE were created to protect houbara from such anthropogenic disturbances, but their management practices might also influence their demographic parameters. Therefore, a detailed understanding of how management practices may influence (positively or negatively) breeding success is crucial. For example, female breeding probability and nest productivity can be affected by changes in population density (Carrete et al. 2006), sex-ratio and population structure (Fry et al. 1987) caused by population reinforcement, which has already been shown to affect adult houbara survival (Azar et al. 2016). Temporal changes in the quantity and quality of supplementary food resources provided to houbara through the plantations, along with their spatial distribution within reserves may also influence population recruitment (Arcese & Smith 1988, Verhulst 1994, Davies & Deviche 2014). Agricultural practices (the use of fertilisers or pesticides) can also have an impact on breeding (Fluetsch & Sparling 1994). In

addition, nesting success can be influenced by the availability of suitable nesting sites within fenced areas (Kolbe & Janzen 2002). Therefore, further studies aimed at disentangling the effects of weather conditions and reserve management practices are required.

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