



Backpack-mounted satellite transmitters do not affect reproductive performance in a migratory bustard

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Received: 3 April 2019 / Revised: 11 October 2019 / Accepted: 31 October 2019

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Abstract

Backpack-mounted satellite transmitters (PTTs) are used extensively in the study of avian habitat use and of the movements and demography of medium- to large-bodied species, but can affect individuals' performance and fitness. Transparent assessment of potential transmitter effects is important for both ethical accountability and confidence in, or adjustment to, life history parameter estimates. We assessed the influence of transmitters on seven reproductive parameters in Asian houbara *Chlamydotis macqueenii*, comparing 114 nests of 38 females carrying PTTs to 184 nests of untagged birds (non-PTT) over seven breeding seasons (2012–2018) in Uzbekistan. There was no evidence of any influence of PTTs on: lay date (non-PTT $\bar{x} = 91.7$ Julian day ± 12.3 SD; PTT $\bar{x} = 95.1$ Julian day ± 15.7 SD); clutch size (non-PTT $\bar{x} = 3.30 \pm 0.68$ SD; PTT $\bar{x} = 3.25 \pm 0.65$ SD); mean egg weight at laying (non-PTT $\bar{x} = 66.1$ g ± 5.4 SD; PTT $\bar{x} = 66.4$ g ± 5.4 SD); nest success (non-PTT $\bar{x} = 57.08\% \pm 4.3$ SE; PTT $\bar{x} = 58.24\% \pm 4.5$ SE for nests started 2 April); egg hatchability (non-PTT $\bar{x} = 88.3\% \pm 2.2$ SE; PTT $\bar{x} = 88.3\% \pm 2.6$ SE); or chick survival to fledging from broods that had at least one surviving chick (non-PTT $\bar{x} = 63.4\% \pm 4.2$ SE; PTT $\bar{x} = 64.4\% \pm 4.7$ SE). High nesting propensity ($97.3\% \text{ year}^{-1} \pm 1.9\%$ SE) of tagged birds indicated minimal PTT effect on breeding probability. These findings show that harness-mounted transmitters can give unbiased measures of demographic parameters of this species, and are relevant to other large-bodied, cursorial, ground-nesting birds of open habitats, particularly other bustards.

Keywords Asian houbara · *Chlamydotis macqueenii* · Satellite telemetry · PTT · Nesting success · Wildlife tracking

Introduction

The use of tracking devices has substantially advanced our understanding of animal ecology and behaviour (Kays et al. 2015), allowing unprecedented insight into individual behaviour, movement and population processes (McKinnon and Love 2018). However, tracking devices can negatively affect an individual's reproduction, survival and movements, and have rightly been subject to extensive review (Calvo and Furness 1992; Murray and Fuller 2000; Barron et al. 2010;

Costantini and Møller 2013; Bodey et al. 2018; Geen et al. 2019). Such effects vary with study species, transmitter types (GPS/GSM, GPS-loggers, Argos/GPS PTTs, accelerometers, geolocators), attachment method (glue adhesion, tail-mount, leg-ring, necklace, leg-loop, harnesses) and mass of device relative to the animal (see reviews above). Practitioners deploying transmitters clearly want to minimise transmitter effects and often base their methodologies on guidelines, such as the 3% or 5% transmitter relative to body weight 'rule', or use a system that was deemed successful for a similar species. However, recent meta-analyses confirmed that there was no device mass threshold below which effects were not observed (Bodey et al. 2018; Geen et al. 2019). Furthermore, when extrapolating results of one tagging study to another, similar physiognomies of the target species may not always be enough to predict transmitter effects (Thaxter et al. 2016). Rather, extrapolations must be approached critically, considering attachment method (Geen et al. 2019) and also taking account of the animal's behaviour and circumstances, including foraging strategies (Thaxter et al. 2016), seasonal weight changes (Sergio et al. 2015), flight mode (Vandenabeele et al. 2014; Bodey et al. 2018), environment (Bro et al. 1999), and age

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10344-019-1332-0>) contains supplementary material, which is available to authorized users.

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at tagging (Petty et al. 2004). This can indicate combinations of tagging and species characteristics with a high likelihood of negative effects, such as the use of backpack harnesses with tags that exceed 1% of body mass on birds undertaking flapping flight during long-distance migration (Bodey et al. 2018), and therefore requires particular caution when used.

Given the cost and difficulty of tagging and the benefits of monitoring individuals throughout their annual cycle (Marra et al. 2015), the use of backpack-mounted solar-powered GPS platform transmitter terminals (PTTs) is popular, due to device longevity (Mueller et al. 2013; Shephard et al. 2015; Mahood et al. 2016) and the long retention of backpack harnesses (Steenhof et al. 2006). Impacts of backpacks may arise from increased energy expenditure through the additional weight (Barron et al. 2010), loss of aerodynamics (Vandenabeele et al. 2014) or clinical issues related to the harness, such as soft tissue injuries and subsequent infections (Peniche et al. 2011; Michael et al. 2013). If an attachment has an obvious negative effect, the work can quickly be discontinued and the data discounted (Thaxter et al. 2016), but small effects may go unacknowledged or undetected even as they prejudice both the welfare of the tagged animals and the validity of scientific results. Scientific accountability and transparency require such potential effects to be understood, allowing ethical concerns to be assessed and any consequences for parameter estimates quantified (Geen et al. 2019).

Backpack-mounted satellite transmitters have been deployed on a wide range of bustard Otididae species including African houbara *Chlamydotis undulata* (Hardouin et al. 2015), Asian houbara *C. macqueenii* (Combreaux et al. 2011; Madon and Hingrat 2014; Burnside et al. 2017; Dolman et al. 2018), little bustard *Tetrax tetrax* (Marcelino et al. 2018), great Indian bustard *Ardeotis nigriceps* (Habib et al. 2016), kori bustard *A. kori* (Mmassy et al. 2018), great bustard *Otis tarda* (Watzke 2007; Kessler et al. 2013), Bengal florican *Houbaropsis bengalensis* (Mahood et al. 2016; Jha et al. 2018) and Ludwig's bustard *Neotis ludwigii* (Shaw et al. 2014). These species fit a number of the criteria highlighted by Bodey et al. (2018) as increasing risks of negative effects from backpack-mounted transmitters: all have flapping flight, many are migratory and for most the transmitters exceed 1% of body mass. However, to our knowledge, transmitter effects have not been assessed against untagged controls for any species of this family.

Here we test whether carrying a backpack-mounted satellite transmitter affects the reproductive performance of female Asian houbara, a large-bodied terrestrial species that is heavily exploited by hunters and undergoing alarming population declines throughout its range from the Middle East to China, resulting in its IUCN Red List categorisation as Vulnerable (BirdLife International 2018). Sustainable management of the species requires measurement of demographic parameters

(Dolman et al. 2018), for which PTTs represent the only practicable methodology; however, it remains unknown whether undetected negative transmitter-related effects may bias these estimates (Bodey et al. 2018). We use quantitative data from seven breeding seasons to compare mean egg-lay dates, clutch size, mean egg weight at laying, daily nest survival, hatchability of eggs from successful nests, and survival of chicks to fledging, between a large sample of birds fitted with ('PTT females') and without ('non-PTT females') satellite transmitters. We also quantify breeding probability for PTT females, although it was not possible to estimate this parameter for birds without PTTs.

Methods

Study area and population

Our study population of Asian houbara is located in the southern Kyzylkum Desert, Uzbekistan (39.34–40.56°N 62.21–65.20°E). Several aspects of this population (e.g. breeding productivity, habitat selection, migration and survival) have already been investigated (Koshkin et al. 2014; Burnside et al. 2016; Koshkin et al. 2016a; Koshkin et al. 2016b; Burnside et al. 2017, 2018; Guilherme et al. 2018). Fieldwork was conducted annually during the entire breeding season (March–July) from 2012 to 2018 inclusive, with a satellite-tagging and brood-monitoring programme from 2013. Continuous nest searching effort was made throughout the entire nesting season (mid-March until mid-May) in each year; nest monitoring continued until all nests had finished (with the latest hatching on 2 June). Brood monitoring started from the first successful hatch, as early as 5 April, and continued until early July, with visits to fledged broods from mid-May until the beginning of July. Opportunistic brood observations during fieldwork involved near-continuous effort until the end of nest monitoring, when driving time is reduced.

Fitting of satellite transmitters

Females were caught using snares placed around nests, as in Seddon et al. (1999), and fitted with solar-powered satellite GPS PTTs that incorporate a UHF radio transmitter (model 30 g solar Argos/GPS PTT-100 from Microwave Telemetry). We fitted PTTs to 38 wild female Asian houbara, using permanent 3-mm-wide Teflon backpack harnesses. We used a modification of the 'classic' full-body backpack harness (Brander 1968), in which the Teflon ribbons coming from the neck-loop pass between the legs before passing behind the wings to connect to the end of the transmitter, rather than directly passing behind the wings. In trials on captive individuals, this provided more balanced

placement of the PTT than could be achieved with the 'classic' method. This harness has been successfully used on another bustard, Bengal florican (Packman 2011), with ten individuals tracked through the lifetime of the attached transmitters up to 5 years (Mahood et al. 2016). We are only aware of this technique being used on houbara and Bengal florican, but perhaps it could be employed in other species with a similar morphology. For Asian houbara, the transmitter with harness (combined weight *c.* 34.5 g) represented 2.1–3.1% of the female's weight (range 1.11–1.59 kg; mean $1.28 \text{ kg} \pm 0.1 \text{ SD}$, $n = 38$). Individual females have been tracked up to 5 years within this study. Importantly, PTTs were fitted by well-trained biologists who had the opportunity to practise repeatedly on captive individuals before deploying transmitters on wild birds. Such expertise is crucial, as there is evidence that harnesses fitted incorrectly have led to increased mortality in great bustards (Ashbrook et al. 2016).

Nest and brood monitoring

Nests of non-PTT females and initial nests of females caught for PTT fitting (treated as part of the non-PTT sample) were located by tracking the footprints of females returning to the nest. Following transmitter attachment, subsequent nests of PTT-females were identified from GPS data and confirmed by a field visit. During egg-laying, females attended the nest-site only occasionally, but from the start of incubation they remained on the nest for long periods; so when three fixes involved the same point, the site was visited to confirm the nest and a standard nest-monitoring protocol was initiated. GPS transmissions from PTT females were received every 3 days.

In all years, after the first monitoring visit to the nest, it was subsequently visited every 6 days until hatching (incubation period 23 days). From 2013, during the first visit to each nest, all eggs were weighed (electronic scales to 0.1 g) and measured (length and breadth, dial callipers to 0.1 mm), and temperature loggers were placed inside and outside the nest scrape, at a depth of 1 cm, to determine the day and time incubation stopped. Monitoring protocols were designed to minimise the risks to the eggs from temperature extremes by limiting visits to 2–3 h after sunrise and before sunset (when it is neither very hot nor cold). Additionally, eggs were not turned during measurements and surgical gloves were worn to prevent scent and bacteria transmission. From 2014, 147 of the 298 monitored nests had cameras to validate outcomes and their interpretation from field-signs (for nest-monitoring see Koshkin et al. 2016b, Guilherme et al. 2018).

Asian houbara chicks leave the nest with their mother 1 day after hatching, fledge by 6 weeks and become independent after another 15 days (Hardouin et al. 2012). PTT females that had hatched a brood were tracked remotely. If they made a sudden movement longer than a distance that the chicks (accounting for their age) could manage, they were considered to have lost their

entire brood. Otherwise, chick survival to fledging was based on numbers alive during a visit (using their most recent GPS fix and UHF transmissions) made as close to their fledging date as possible (35–38 days after hatching). The number of chicks surviving was determined by the number of chicks seen and confirmed by searches to track footprints of the female and brood. The analysis of fledging probability (see below) included only broods for which the number of eggs hatched and the number of chicks fledged were certain. As non-PTT females could not be followed after leaving the nest, all non-PTT females with broods encountered opportunistically in the study area were recorded and investigated to locate all the chicks, again including searches of footprints. The age (in weeks) of chicks was estimated from size, development and feather growth, with chicks that flushed (i.e. were fledged) considered to be at least 35–50 days old (Combreaux et al. 2002).

Parameter estimation

A total of 38 females were marked with PTTs, and 114 of their nests were monitored and compared with 184 nests of non-PTT females. As not every nest yielded data on every parameter, the sample size for each test varied (Table 1). Generalised Linear Models (GLMs), with the appropriate error structure, were used to estimate each breeding parameter, and the fixed effect of PTT (categorical, carrying/not-carrying a PTT) was added to each model. When appropriate, other covariates (year; lay date; date in season; date of first monitoring visit and nest vegetation height) previously shown to influence a breeding parameter were included in models to account for their effects (see below; model details in Table 1) during parameter estimation.

Breeding probability Breeding probability of non-PTT females could not be estimated, so we simply estimated the probability of a PTT female nesting, as this can still give insights into the effect of the transmitter if it is particularly high or low. It updates the figure reported ($98.1\% \pm 1.9\% \text{ SE}$) in Dolman et al. (2018) with 21 additional observations. This parameter was estimated using a binomial GLM, coding birds that bred as 1 and those that did not as 0 (Table 1).

Mean lay date First nesting attempt lay dates for non-PTT birds could not be ascertained, so all lay dates from all nests across the season (i.e. first nests and renesting attempts) were used to estimate mean lay dates for both treatment groups (sample sizes in Table 1). For successful non-PTT nests, lay dates of the first egg were calculated as laying date = incubation onset – (final clutch · 1.5 days), assuming that incubation lasted 23 days (so that incubation onset = hatch date – 23), and each egg was laid approximately every 36 h (Saint Jalme et al. 1996). For unsuccessful non-PTT nests, lay dates were predicted following Combreaux et al.

Table 1 Estimated reproductive parameters of Asian houbara *Chlamydotis macqueenii* breeding in the southern Kyzylkum desert, showing error distributions. Sample sizes and model-averaged estimated parameter mean (\bar{x}) and uncertainty (\pm SE, unless stated otherwise) are

Breeding parameter Model error structure	Sample size of nests, n females shown in brackets and mean parameter estimates		Tested variables model-averaged beta coefficients \pm standard errors	
	Non-PTT females	PTT females	PTT	Additional covariates
Breeding probability Binomial	NA	71 nests (73 arrivals (33)) $\bar{x} = 97.3\% \pm 1.9\%$		
Lay date (Julian day) Gaussian	151 nests $\bar{x} = 91.7 \pm 12.3$ SD 2017: 114.2 \pm 19.9; all other years: 90.8 \pm 11.1	91 nests (31) $\bar{x} = 95.1 \pm 15.7$ SD 2017: 102.6 \pm 15.3; all other years: 93.1 \pm 15.3	1.11 \pm 1.81	Year = -13.70 ± 2.81 ***
Clutch size Poisson	184 nests Mean for nests laid in the first half of the season $\bar{x} = 3.30 \pm 0.68$ SD	107 nests (37) Mean for nests laid in the first half of the season $\bar{x} = 3.25 \pm 0.65$ SD	-0.04 ± 0.08	Lay date = -0.01 ± 0.003 *
Mean egg weight at laying within a clutch Gaussian	162 nests $\bar{x} = 66.1$ g \pm 5.4 SD	104 nests (36) $\bar{x} = 66.4$ g \pm 5.4 SD	0.761 \pm 0.73	Lay date = -0.049 ± 0.02 *
Nest survival Mark DSR Binomial	183 nests Mean for nests started after 2 April $\bar{x} = 57.08\% \pm 4.3$ SE	114 nests (38) Mean for nests started after 2 April $\bar{x} = 58.24\% \pm 4.5$ SE	0.126 \pm 0.214	Date = -0.1619 ± 0.0490 *** Date ² = 0.002 ± 0.001 *** Shrub height = 0.905 ± 0.382 **
Egg hatchability Binomial	88 nests Mean for nests first visited age 12 days $\bar{x} = 88.3\% \pm 2.2$	59 nests (31) Mean for nests first visited age 12 days $\bar{x} = 88.3\% \pm 2.6$	0.039 \pm 0.361	Lay date = 0.014 ± 0.011 Age visited = 0.049 ± 0.021 *
Chick survival to fledging Binomial	16 broods (opportunistic) \bar{x} chicks seen = 1.8 ± 0.66 SD $S_{chick} = 63.4\% \pm 4.2$	42 (25) broods visited \bar{x} chicks seen = 1.60 ± 0.74 SD $S_{chick} = 64.4\% \pm 4.7$	0.040 \pm 0.371	

(2002) using the estimated incubation stage in days during the first monitoring visit and the expected egg weight loss. Fresh egg weight at laying was predicted using the equation in Hoyt (1979): Weight = $Kw \cdot LB$ where L is egg length, B is egg breadth and Kw is the species-specific weight coefficient ($Kw = 0.00055$) and assuming a linear cumulative weight loss of 17.4% across incubation as estimated from artificially incubated eggs (Saint Jalme and Van Heezik 1995). For PTT females, lay date was taken as the first visit to the nest site. Nests of PTT females from the year they were caught were excluded from this estimate, as all initial non-PTT status nests (at catching) were early in the season (with catching occurring before 15 April), with subsequent (PTT status) renesting attempts initiated > 8.4 days after that event, so that their inclusion would have introduced systematic bias in first egg dates. As the onset of the breeding season differed between years (Dolman et al. 2018), year was included in the model, subsequently contrasting 2017 against the other 5 years combined (Table 1), which did not differ from each other (based on change in AICc, Akaike's Information Criterion corrected for small samples, on parameter merger following examination of coefficients).

shown for non-PTT and PTT females. Model-averaged beta parameters ($\beta \pm$ SE) are shown for PTT effect and each covariate. *, **, *** indicate that the parameter was significant to 5%, 1% and 0.1% threshold respectively.

Mean clutch size Only nests where clutches were confirmed as complete were included in the analysis (sample sizes in Table 1). Across the population, attempt number and lay date are only weakly correlated (Dolman et al. 2018), while first and second attempts overlap within a breeding season due to both staggered start (variance among individuals) and long incubation duration, so that renesting attempts following loss of first clutches occur across a wide period. Overall, clutch size declines between first and second nesting attempts (0.6 egg decrease) but not lay date; however, as the nesting attempt number could not be established for non-PTT birds, lay date was used as an imperfect proxy for attempt number. A GLM with Poisson errors was used to model clutch size, incorporating lay date as a continuous variable (Table 1).

Mean egg weight per clutch at laying Egg volume was used to calculate the initial weight of each egg within a clutch at laying (see fresh egg weight equation above), and the mean weight was calculated for each nest. Mean egg weight at laying (per clutch) was modelled using GLMs with Gaussian errors, again including lay date (Table 1) as a proxy for attempt number, as mean egg weight decreases with renesting attempts.

Daily nest survival Whether daily survival rate (DSR) of clutches varied between years, within season or across incubation was modelled in MARK (v. 6.2) using RMark package (Laake 2013) in R. Owing to the ephemeral emergence of predators as the desert warms, DSR is non-linearly related to date (Koshkin et al. 2016b). The mean height of shrubs within 50 m of the nest also influences the probability of nest predation (Koshkin et al. 2016b; Guilherme et al. 2018), so shrub height, date and date² were included in the nest survival model (Table 1).

Egg hatchability The probability of an egg hatching was analysed relating the number of successfully hatched eggs to the complete clutch size, considering only successful nests with known final clutch size and known number of hatched eggs (Table 1). Lay date was included to test for any date effects. As nests of PTT females were identified remotely, generally at inception or early incubation, they tended to be confirmed and visited earlier (mean first visit 3.5 days \pm 3.6 SD) than non-PTT nests (12.6 days \pm 7.2 SD). We had a priori reason to suspect that eggs in earlier stages of incubation are more vulnerable to failure, as lower hatching rates of houbara eggs collected from nests < 10 days old have been reported during establishment of breeding facilities, potentially related to embryo vulnerability during early incubation and either movement by females leaving the nest fast, handling by staff or inopportune exposure to a strong temperature gradient. Therefore, to account for potential lower hatchability in nests visited near the start of incubation, we included a variable for the age of the nest at the first monitoring visit.

Chick survival to fledging in successful broods The number of non-PTT females that lost their brood before fledging is unknown, precluding comparison of overall chick survival between PTT and non-PTT females. However, we were able to contrast the survival probability of chicks within successful broods (i.e. which fledged at least one chick) as follows. As the number of eggs that hatched in nests of non-PTT females was unknown, we randomly sampled a clutch size distribution and applied the mean egg hatchability (calculated above) to 1000 simulated clutches, using binomial trials to estimate the number of hatched eggs. To each non-PTT brood sampled, we then assigned an initial clutch size from this simulated population, constrained to be equal to or larger than the number of chicks observed. The eggs of all 16 opportunistically found broods were predicted to have been laid between 18 March and 2 April in their respective years—a short time-span relative to the length of the laying season (14 days vs 60), leading to a small predicted difference in clutch size of 0.17 eggs across this period. Therefore, the date effect on clutch size was not included in the simulation. The probability of chick survival to fledging was then estimated from this simulated hatching rate of the clutch and the chicks observed, with the

resampling process repeated 1000 times to generate a distribution of survival probabilities, allowing mean chick survival rate and uncertainty to be estimated. Chick survival was compared between (observed) PTT and (simulated) non-PTT broods at each simulation, using a GLM with binomial errors, coding each hatched individual within a brood as alive (1) or dead (0) at the time of the visit, generating a beta coefficient and SE for the difference at each simulation. We report the mean beta (untransformed difference) for the PTT variable and the proportion of times the simulated non-PTT group was statistically different (p value < 0.05) from the PTT group.

Statistical analysis

Each response (lay date, clutch size, mean egg weight per clutch, nest survival and egg hatchability) was tested using multi-model inference (MMI) assessing the support for each variable across candidate models. Model-averaged parameter estimates and relative variable importance (RVI; varying 0–1) of each variable were calculated from each set of all candidate models. Following Whittingham et al. (2005), a randomly generated variable (mean = 1, SD = 1) was incorporated in the candidate variable set to estimate the RVI that could occur by chance for predictors unrelated to the dependent variable, and the MMI analysis was repeated 1000 times, each with a newly generated random variable. Subsequently, candidate variables were considered strongly supported if (a) their RVI was above the 95% interval of the RVI distribution of the random variable and (b) the 95% confidence limit (standard error \times 1.96) of the model-averaged parameter did not span zero (following Boughey et al. 2011). All analyses were performed in R 3.1.1 (R Core Team 2013).

Results

When averaging across models that also accounted for other important factors, such as date (see model-averaged coefficients in Table 1; candidate models are presented within Online Resource 1), there was no support for a difference in any breeding parameter between PTT and non-PTT females (Fig. 1).

The probability of a PTT female nesting on spring arrival was 97.3% \pm 1.9% SE (71 nesting events from 73 spring arrivals of 33 unique PTT females). Mean lay date differed between years (Table 1, Fig. 1a & b), but there was no support for an influence of satellite transmitter (Table 1, Fig. 1b). Additionally, the variance in lay dates was similar between the PTT and non-PTT groups (on PTT variable removal from the full model: Δ deviance = -65.346 , $F = 0.378$, $p = 0.54$) confirming that the length of the laying window was the same for both groups. Mean clutch size was weakly ($r^2 = 1.5\%$) negatively associated with lay date (Fig. 1c & d), while there

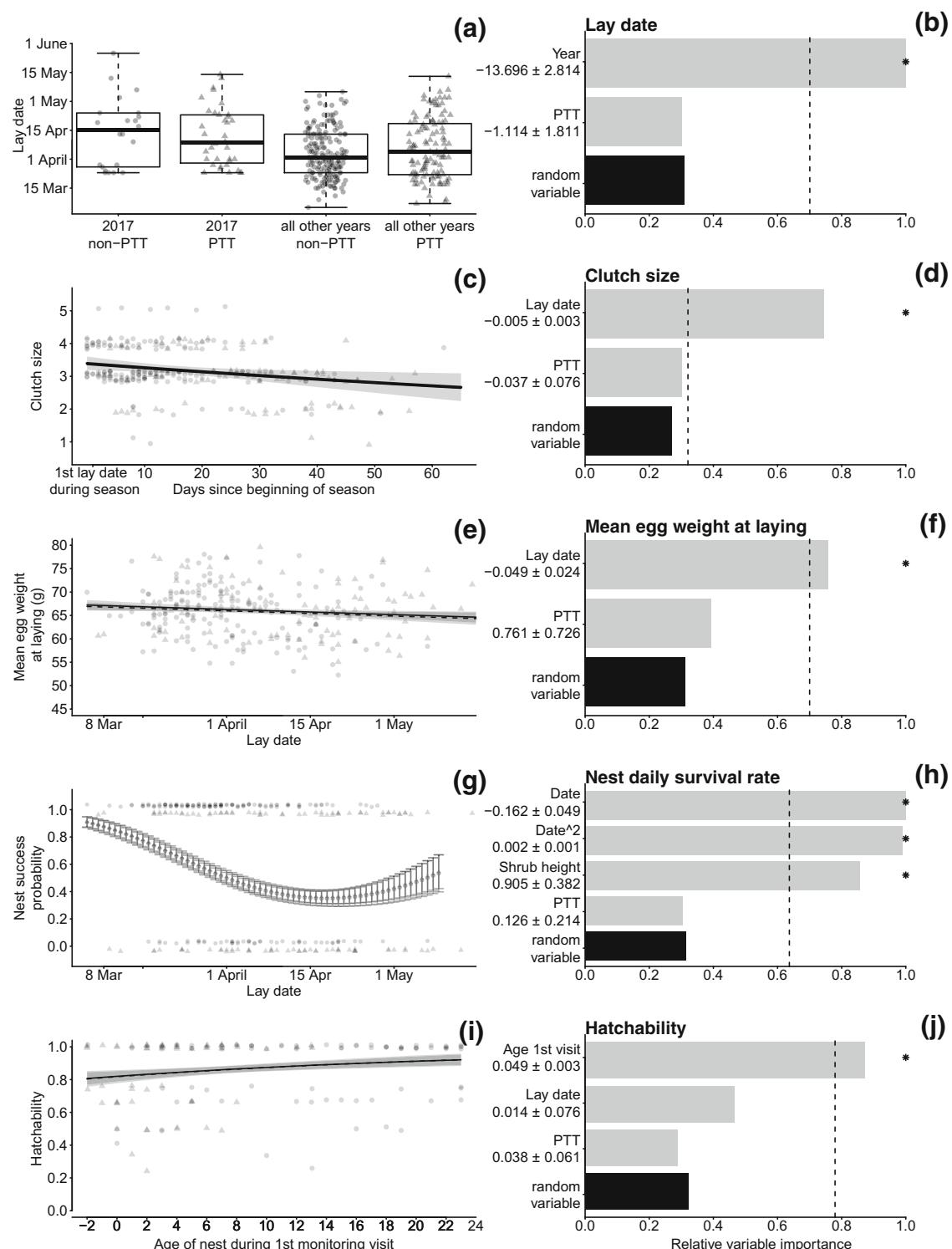


Fig. 1 Left column: five reproductive parameters of non-PTT and PTT Asian houbara *Chlamydotis macqueenii*, showing raw data and mean parameter estimates from multi-model inference (MMI) (non-PTT: triangles and dashed lines; PTT: circles and solid lines respectively). Uncertainty (\pm SE) shown as shading or bars. Owing to near-absence of effect (Table 1), lines are barely distinguishable. Jitter and transparency

were used to show overlapping points. Right column: relative variable importance of predictor variables included in the models of each breeding parameter, showing MMI estimated coefficients ($\beta \pm$ SE); a random variable was simulated for each MMI (see Methods) to denote 95% cut-off for support for variable importance (dashed vertical line)

was no support for an influence of satellite transmitter on clutch size (Table 1, Fig. 1c & d). Mean egg weight at laying (per clutch) was weakly ($r^2 = 2.4\%$) negatively related to lay date (Table 1, Fig. 1e & f), and there was no support for an influence of satellite transmitter on mean egg weight (Table 1, Fig. 1e & f). Daily nest survival rates (DSR) did not differ between PTT and non-PTT females (Table 1, Fig. 1g & h) but were influenced by (a) date (date and date²), decreasing through the season but increasing again towards the end, and (b) vegetation height, with taller shrubs conferring a survival advantage (Table 1, Fig. 1g). Egg hatchability was not affected by PTT (Table 1, Fig 1i & k). However, there was support for a positive relationship between nest age at first visit and subsequent egg hatchability (Table 1, Fig 1i & k), with earlier nest monitoring (i.e. first visit during pre-incubation) reducing hatching probability by approximately 5% relative to first visits made at the end of incubation (23 days).

For successful broods (where at least one chick survived to fledging) of PTT females, chick survival from hatching to fledging was $64.4\% \pm 4.7\%$ SE. For non-PTT females, chick survival to fledging, estimated (resampling a randomised clutch size and egg hatchability) for broods observed opportunistically, had a near-identical mean of $63.4\% \pm 4.2\%$ SE. After 1000 simulations of the opportunistic data with each simulation tested against the sample of observed PTT broods by a separate GLM, there were no cases in which the two means were significantly different and therefore no support for an influence of PTTs, with the mean PTT beta coefficient CI spanning zero (Table 1).

Discussion

We found no negative effects of backpack-mounted satellite transmitters on six breeding parameters in the Asian houbara; nor did we detect evidence of any effect on breeding probability. These findings have significant implications for using harness-mounted transmitters to measure demographic parameters of this species and are probably relevant to other large-bodied, cursorial, ground-nesting birds of open habitats, particularly other bustards.

Controlling for date, neither clutch size nor mean egg weight at laying (per clutch) differed between PTT and non-PTT females, which is in agreement with the meta-analyses of Barron et al. (2010). To protect their nests (and themselves) from predators, incubating Asian houbara females rely on crypsis, vegetation height and vigilance, allowing early departure (Guilherme et al. 2018). A backpack-mounted PTT may potentially make an incubating female more conspicuous to potential nest predators, owing to the 20-cm-long antenna and light reflection on the solar panel. Nevertheless, non-PTT and PTT females had similar nesting success (in models of daily nest survival, controlling for date and vegetation height),

although we acknowledge the study area holds no large corvids for which solar panels may be more visible. However, various species of raptor are present (those occurring commonly: steppe buzzard *Buteo buteo*, long-legged buzzard *B. rufinus*, marsh harrier *Circus aeruginosus*, golden eagle *Aquila chrysaetos* and steppe eagle *A. nipalensis*), but during the 7 years of this study we have no records of them predating nests. So PTTs do not increase the risk of nest depredation by those avian predators occurring in our study area. Egg hatchability was also similar between PTT and non-PTT females, suggesting that carrying a transmitter did not compromise nest attentiveness during cold or hot daily periods.

Mean lay date was similar for PTT and non-PTT females (even within different years), suggesting no delay in nest initiation following migratory return, and (given similar nest failure rates) also suggesting a similar seasonal pattern of renesting probability after failure (supported by similar variance in lay dates between the two groups). Accepting the potential limitations of the simulation method used to infer chick survival for opportunistically encountered non-PTT broods, estimated chick survival rates within successful broods were strikingly similar between PTT and non-PTT females. However, the proportion of non-PTT females that lost their entire broods could not be ascertained, because we did not monitor survival of broods from non-PTT females since catching and radio-tracking chicks can induce early chick mortality (Combrea et al. 2002; Bacon et al. 2018). Second, we could not test whether backpack mounts do (Bodey et al. 2018) or do not (Barron et al. 2010) affect offspring quality, as brood quality (chick size and weight) of most non-PTT females was not measured and exact age was not known.

We were unable to investigate if carrying PTTs led to increased energy expenditure or affected foraging efficiency relative to non-PTT birds, so we cannot exclude other potential fitness impacts, such as reduced provisioning rates, renesting rates and physiological reserves for post-nuptial moult, or compensatory increases in foraging time (Bodey et al. 2018) with consequent increased exposure to predation risk. We were also unable to compare annual survival between adults with and without PTTs. However, across species, transmitter effect-size is positively correlated ($r = 0.39$) between breeding-based and survival-based parameters (Bodey et al. 2018); thus the lack of breeding effects is consistent with low expectation of an effect on adult survival. Setting aside anthropogenic winter and summer adult mortality (powerlines, hunting and trapping, winter 53.9%, summer 53.7% respectively: Burnside et al. 2018), background annual survival of wild adult PTT-tagged Asian houbara was high, at 90.8% (Dolman et al. 2018), further suggesting that any detrimental effect of PTTs on survival is low or negligible. Furthermore, as migratory Asian houbara are considered to be 'capital

breeders', with females largely dependent on resources acquired on wintering grounds at least for their first clutch (Koshkin et al. 2016b), the extremely high nesting propensity (97.3%) shortly after migratory return to the breeding grounds, and lack of difference in clutch size and egg weights, together suggest that carrying a PTT did not compromise foraging ability and body condition over winter.

Hatchability was positively related to nest age at the first monitoring visit, with a predicted difference of 5% in hatchability between the youngest (at laying) and oldest (at hatching) nests found. While not measured systematically, early embryonic death (EED) is likely the main reason for unhatched eggs rather than infertility (4 EED vs 1 infertile from 5 eggs necropsied). The two most probable explanations for EED observed here are either trauma (jarring of the egg when the female runs from the nest as humans approach) at a critical stage in the formation of blood vessel organs, causing a loose air cell (Alcorn 2007), or stress to the egg through over-heating or chilling in the absence of the female (Alcorn 2007), although this is less likely as our nest-searching and monitoring visits avoided unfavourable temperatures. In traditional nest searching, it is not possible to avoid encountering newly laid nests. However, for PTT nests that are determined remotely, protocols could be adjusted to delay visits until eggs are older, *c.* 10 days.

The weight of evidence assembled here indicates that, when fitted by experienced biologists, PTTs have no discernible effect on female Asian houbara nesting performance. We are, therefore, confident that the welfare of the Asian houbara we are studying is not compromised and that our estimations of breeding parameters do not need correction. However, it should be noted that the Asian houbara has several characteristics that reduce the risk of transmitter effects. First, Asian houbara have annual weight fluctuation with an increase up to 200 g between the breeding and wintering periods. This equates to an 18% change from the lowest body weight (Saint Jalme et al. 1996), possibly making the small relative weight gain of 2–3% from the 30-g transmitter less influential. Second, Bodey et al. (2018) identified flapping flight as a characteristic that can make individuals susceptible to transmitter effects. Houbara are powerful and fast fliers, but they spend the majority of their time walking (cursorial), when aerodynamic concerns of drag do not apply. Furthermore, the harness technique used here brings the Teflon through the legs and not around the chest, behind the wings, and is considered less likely to interfere with the expansion and contraction of flight muscles during flapping. Third, Asian houbaras live in arid or semi-arid environments, thereby largely neutralising complications of moisture build-up on the neoprene bases of transmitters and issues affecting thermoregulation as seen for example in seabirds (Thaxter et al. 2016).

Conclusions

Transmitters have been deployed on a number of bustard species (see Introduction) because biologging is the only way to study many aspects of their biology, given their generally long-lived, cryptic nature (Dolman et al. 2018) and the legal restrictions on disturbing nesting birds for monitoring (Magaña et al. 2010; Morales et al. 2013; Silva et al. 2014) due to their threatened status (Collar et al. 2017). Nevertheless, this is the first quantitative assessment of the impact of transmitters on the reproductive performance of a bustard species. Our findings are encouraging, because backpack-mounted transmitters can give unbiased breeding parameters in the Asian houbara and likely in the other bustard family members, as well as other large-bodied, cursorial, ground-nesting birds of open habitats. However, for both ethical accountability and confidence in parameter estimates, thorough assessment of potential transmitter effects through harness testing in captivity and pilot studies in the wild are recommended before initiating a large-scale tagging programme.

Acknowledgements We are grateful to the State Committee for Nature Conservation of the Republic of Uzbekistan for permission to conduct fieldwork and the Emirates Bird Breeding Center for Conservation (EBBCC) for collaboration and logistical support. We warmly thank Alex Brighten, Elizabeth Grayshon, David Hodgkinson, Louise Jane, James Kennerley, Erasil Khaитov, Nurasil Khaитov, Maxim Koshkin, Judit Mateos-Herrero, Charlotte Packman, Philip Saunders, David Showler, Andrew Taylor, Elizabeth Taylor, Vladimir Terentyev and Jonathan Willans for their contribution to data collection in the field, and Marta Acácio, Adam Formica and Christopher Panter for monitoring satellite data.

Funding information This study was funded by the Ahmed bin Zayed Charitable Foundation.

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