Bird Study (2016), 1–11
http://dx.doi.org/10.1080/00063657.2015.1135104

Evidence for deleterious effects of harness-mounted satellite transmitters on Saker Falcons *Falco cherrug*

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Capsule This study identifies lethal and sub-lethal effects associated with the deployment of harness-mounted satellite transmitters on a large falcon species.

Aims We examined the effect of harness-mounted satellite transmitters and patagial tags on survival, behaviour and physical health of adult Saker Falcons.

Methods We compared breeding turnover of Saker Falcons deployed with harness-mounted satellite transmitters or patagial tags with unmarked birds identified by using genetic markers. In addition, observational data were recorded on the breeding behaviour and physical condition of birds with satellite transmitters.

Results This study found evidence of decreased survival, together with sub-lethal behavioural and physical effects, associated with the deployment of harness-mounted satellite transmitters on Saker Falcons. We found no effect of fitting patagial tags on breeding turnover, although the removal of patagial tags by several birds may have indicated they caused some degree of discomfort.

Conclusion Researchers using harness-mounted transmitters on this, and similar, falcon species need to assess how these deleterious effects may impact on species conservation, the welfare of individual birds and the interpretation of their studies.

The advent of satellite telemetry has revolutionized our understanding of the movements and migration of many birds (Meyburg & Fuller 2007), and technological advances have resulted in a reduction in the size and weight of the satellite-received transmitters (Platform Transmitter Terminals, PTTs), enabling a greater range of species to be tracked via satellite (Bridge *et al.* 2011), including small falcons weighing ca. 150–170 g (e.g. Liminana *et al.* 2012) and wading birds weighing ca. 200–300 g (e.g. Gill *et al.* 2009, Guzmán *et al.* 2011, Sheldon *et al.* 2011). Indeed, one of the smallest species currently tracked by satellite is the Common Cuckoo *Cuculus canorus*, weighing ca. 106 g (Willemoes *et al.* 2014). In addition to its use in studying movement ecology, satellite telemetry can also be deployed to measure survival rates (e.g. Millsap *et al.* 2004). However, it has long been known that some marking techniques, especially the use of harness-mounted radio transmitters, can have measurable, deleterious impacts on some birds (Calvo & Furness 1992, Murray & Fuller 2000). Nevertheless, relatively few studies using harness-mounted transmitters examine the potential impact of this marking technique (but see Barron *et al.* 2010). When determining the potential impact of harness-mounted tags, many researchers rely on an arbitrary 'maximum mass' that can be deployed, usually expressed as percentage of body weight, for example, 2–3% (Fuller *et al.* 2005) or 5% (Cochran 1980). This simple assessment fails to take into account differences in the life history of the study species (such as the time birds spend airborne), the age of the individuals tagged, the size/shape of transmitters, the effect on drag or the method of attachment (Vandenabeele *et al.* 2012).

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Satellite telemetry has been widely used on many raptor species, although early studies were confined mainly to large eagles that could ostensibly accommodate the relatively heavy and large PTTs available at the time (e.g. Meyberg *et al.* 1995a, 1995b, Brodeur *et al.* 1996). As the size and mass of PTTs reduced, satellite telemetry began to be applied to smaller raptors, including large falcons such as Saker Falcon *Falco cherrug* (hereafter Saker) and Peregrine Falcon *Falco peregrinus* (Fuller *et al.* 1998, Eastham *et al.* 2000, Ganusevich *et al.* 2004), which have a very different life history to the soaring raptors in that they rely more on active flight and speed for hunting. More recently, the development of lightweight transmitters (<9.5 g) has enabled the technology to be applied to small migratory falcons such as Eleonora's Falcon *Falco eleonorae* (Gschweng *et al.* 2008, López-López *et al.* 2009), Amur Falcon *Falco amurensis* (Dixon *et al.* 2011a) and Hobby *Falco subbuteo* (Meyburg *et al.* 2011).

In this paper we examine the effect of harness-mounted PTTs on the survival, behaviour and physical health of breeding Sakers in Mongolia, and discuss our findings in relation to the use of this technology in the study of Sakers and other falcon species.

METHODS

Our study area covered six grids of artificial nests established in 2006–07 in the Bayan and Bayantsagaan districts of Töv province in central Mongolia. Each grid comprised 25 pole-type nest boxes arranged in a 5 × 5 array, spaced at 1 km intervals over flat or undulating steppe landscape. Nest boxes were constructed from metal barrels 60 cm in diameter and approximately 60 cm tall with a rectangular side entrance hole 30 cm high by 40 cm wide. In 2009, 23 Sakers were caught at active nest sites when they were brooding small young by flushing them into a large fisherman's landing net that was held in front of the nest entrance. We deployed harness-mounted PTTs to ten breeding adult Sakers (six females and four males) and patagial tags to 13 breeding adults (seven females and six males). A further five PTTs were deployed to breeding adults in 2010 using the same methods. We recorded range occupancy and monitored breeding success at the artificial nests from 2006 to 2010.

Satellite tagging

All PTTs used on adults in this study were 22 g solar Argos/Global Positioning System (GPS) units (Microwave Telemetry Inc., Maryland, USA) and were mounted using an 8 mm wide Teflon coated tubular ribbon harness (Bally Ribbon Mills, Pennsylvania, USA). The combined weight of the PTT and harness represented approximately 1.7–2.8% of adult body weight (males: 885–1015 g; females: 1185–1470 g). The PTT units were 64 mm long, 23 mm wide and 17 mm high with a hard nylon-coated flexible stainless steel stranded antenna, 178 mm long and 1.8 mm in diameter, protruding from the back edge of the transmitter at an angle of 45 degrees. The tubular ribbon harness was attached to the PTT via a single anterior anchor point and two laterally positioned posterior anchor points. We used an 810 and 710 mm length of tubular ribbon for female and male Saker Falcons, respectively. The ribbon strand was tied at its midpoint to the anterior anchor of the PTT and stitched at a 45° crossover angle at a pre-determined point for female and male Sakers, that is, 145 and 135 mm from the PTT anterior anchor, respectively. The ribbon crossover was stitched using nylon polyester UV-resistant sail thread and nylon 'dental floss'. The PTT was mounted high along the dorsal midline and the harness ribbon crossover was positioned over the sternum with the trailing ends attached to the posterior anchor points of the PTT and adjusted so that there was ample space to fit two fingers between the dorsal midline and sponge-covered base of the PTT unit. Once fitted and 'preened' into the body feathers, the ends of tubular ribbon were knotted, stitched and sealed with quick-drying cyanoacrylate glue (Fig. 1).

In addition to the adult birds, we deployed 16 g Argos solar PTTs (North Star Science and Technology, VA, USA) on four nestlings (two male siblings and two females) from three different nests in the steppe zone of Tov province of central Mongolia in 2006. In 2009 we also deployed a 22 g GPS/Argos PTT (Microwave Telemetry, MA, USA) on a recently fledged (exact date not known) juvenile female from a natural nest site in the eastern Gobi desert of Omnogovi province.

Patagial tags

Patagial tags were made of coloured, UV-resistant PVC and woven fabric, which was cut to size with a dorsally positioned labelled portion measuring 40 mm wide and 60 mm long which tapered to a 20 mm wide, 50 mm long section that folded loosely over the leading edge of the patagium and was held in place dorsally and ventrally by a two nylon 10 mm diameter discs pinned by a 2 mm diameter hard nylon rivet (Fig. 2). Patagial

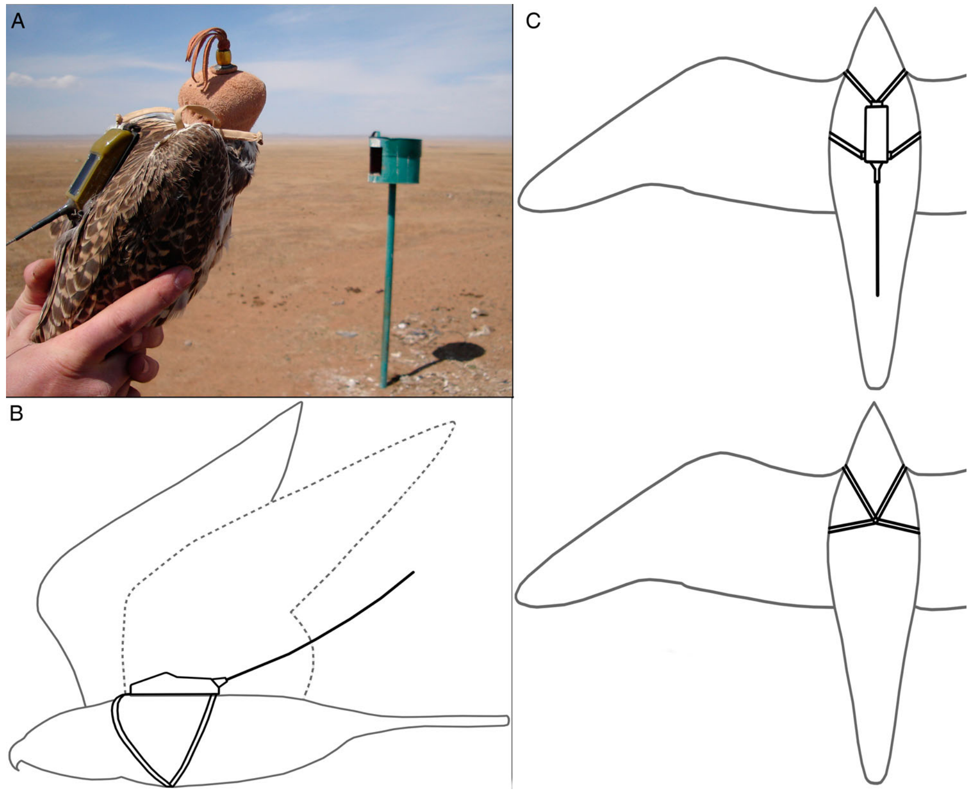

Figure 1. (A) Saker Falcon with harness-mounted PTT and artificial nest site. (B) Diagram to illustrate lateral view of PTT attachment. (C) Diagrams to illustrate dorsal (above) and ventral (below) views of PTT attachment.

tags were fitted to both wings and the colours used were black, blue, green, orange, red, white and yellow, each bearing a single letter code.

Genetic markers

We determined the return rate of adult Sakers that had not been trapped and fitted with a PTT or patagial tags, by genotyping DNA extracted from moulted feathers that were collected from nesting sites during the breeding season. In addition, DNA was also extracted from 1 to 2 breast feathers plucked from nestlings at the artificial nests. Moulted feathers were stored dry, in paper envelopes, whilst the tips of plucked feathers were cut with a scissors (5–15 mm lengths) immediately after being plucked from the nestlings and stored in 95% ethanol. Moulted feathers and plucked feather tips were transferred to Cardiff University, UK for genetic analysis.

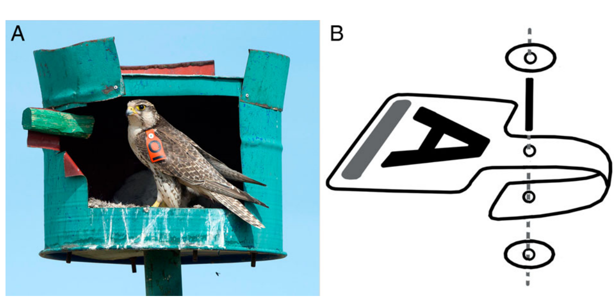

Figure 2. (A) Saker Falcon fitted with a patagial tag at its artificial nest site. (B) Diagram to illustrate mode of attachment of patagial tag.

Genetic analysis

For DNA extraction, feather samples were processed in a fume cupboard in a laboratory at Cardiff University, and DNA extracts were obtained using the Qiagen Blood and Tissue Extraction Kit (Qiagen, Germany). DNA samples were typed using ten polymorphic microsatellite DNA markers that had previously been reported in the literature: Age 7, Age 5 (Topinka & May 2004), NVHfp 92, NVHfp89, NVHfp31, NVHf46–1, NVHfp82–2, NVHfp54 (Nesje *et al.* 2000), NVHfr34 (Nesje & Røed 2000), μFpe1 (Dawnay *et al.* 2009). The primers were further divided into five multiplex groups (Age7 and NVHfp 92;

NVHfr34 and NVHfp89; NVHf46-1, Age5 and NVHfp31; NVHfp82-2 and µFpe1; NVHfp54).

PCR amplifications were performed in a GeneAmp® PCR System 9700 (Applied Biosystems, USA) in 10 µl containing 1 µl of template DNA, 0.4 µM of the forward and reverse primer, 4 µl of HotStar Taq Master Mix (Qiagen) and 0.2 µg/µl BSA (New England BioLabs). The amplification started with 94°C for 15 minutes, followed by 45 cycles (94°C/30 s, 94°C/90 s, 72°C/90s) and a final step of 72°C for 10 minutes. Products were resolved using an ABI 3730 prism automated sequencer, and analysed using Genemapper v3.2 (Applied Biosystems). To get reliable genotypes, we amplified each sample three times and loci that gave rise to the same genotype at least twice were accepted.

For adult samples, we checked matched individuals (genotypes) using the Microsatellite Toolkit (Park 2001) with genotypes from different samples across years considered to represent the same individual when all alleles at ten loci were identical. For nests without one or both parent samples, we inferred the possible father or mother from another year based on the offspring genotypes using Colony software (Jones & Wang 2009), which implements a likelihood method over the entire pedigree configuration for inferring parentage and sibship from marker data.

We used GenALEx (Peakall & Smouse 2012) to calculate the probability of identity (PI) and PI_{sibs} for each locus (Peakall & Sydes 1996); the former provides an estimate of the average probability that two unrelated individuals, drawn from the same randomly mating population, will by chance have the same multi-locus genotype and the latter statistic takes into account the genetic similarity amongst siblings (Taberlet & Luikart 1999, Waits *et al.* 2001).

Statistical analysis

When PTTs ceased transmission, we were not always able to distinguish between PTT malfunction, removal or destruction and bird mortality; this ambiguity complicates survival analysis. Thus, we also used the observed return rate to breed in the subsequent year, which enabled us to directly compare satellite-tagged, patagial-tagged and untagged birds in a Generalized Linear Mixed Effect Model, with prior breeding experience, sex, tagging method (satellite or patagial-tagged) as fixed factors, and individual identity as a random factor. We checked the assumptions of normality of the residuals and homogeneity of the variances using the full models for each response variable. We compared candidate models using Akaike Information Criterion (AIC) and the analysis was carried out in R software (R Development Core Team 2013) using the 'MuMIn' package for model selection and multi-model inference. Models with $\Delta AICc \leq 2$ were considered to be equally parsimonious (Burnham & Anderson 2002), and Akaike weights (w_i) were computed to assess the support in favour of each candidate model. We used multi-model inference to compute the model-averaged estimates and their corresponding 90% confidence intervals for the explanatory variables that had a normalized $\Delta AICc \leq 2$. The relative importance (RI) of each explanatory variable was calculated by summing the w_i across all the models in which the particular variable occurred.

In our survival analysis of satellite-tagged juveniles we have assumed that the PTTs stopped transmitting because the bird had died, though no birds or PTTs were subsequently recovered, thus it is possible that cessation of transmission was due to some reason other than death, such as PTT failure. Consequently our survival measure for PTT-tagged birds must be regarded as conservative.

RESULTS

Genetic identification

The ten microsatellite loci gave a combined PI of 0.75×10^{-7} and PI_{sibs} of 0.18×10^{-2} (Table 1). Six untagged adults were identified as having previously bred in our study population through identical genotypes across years, and a further nine were identified through parentage analysis of broods from earlier years. Similarly, three untagged adults were identified as having returned to breed in our study area through identical genotypes and one was identified through parentage of a brood in the subsequent year.

PTT and patagial tag recoveries

Of the ten PTTs deployed in 2009, three were subsequently recovered after they had been cut-off by falcon trappers, four stopped transmitting suddenly with no prior evidence of malfunction and three stopped transmitting due to malfunction after 166–563 days. Malfunction was identified from the engineering data received from the PTTs or inferred when signal transmission became sporadic prior to complete cessation. Only two of the satellite-tagged birds returned to breed in 2010, whilst an additional bird

Table 1. Variation in microsatellite loci used to identify unmarked individuals across years, 2008–2010. There was no significant deviation from Hardy-Weinberg equilibrium for any locus. Probability of Identity (PI) provides an indication of the statistical power of the loci for identifying individuals and siblings (PI_{sibs}) across years.

Locus	Size (bp)	*N*	H_O	H_E	PI	PI_{sibs}
NAGE7	202–208	3	0.512	0.419	0.38	0.64
NVHfp92	106–116	5	0.651	0.599	0.20	0.50
NVHfr34	146–152	3	0.465	0.462	0.39	0.62
NVHfp89	118–122	3	0.047	0.046	0.91	0.95
NVHf31	140–148	4	0.535	0.438	0.34	0.62
AGE5	149–170	7	0.605	0.621	0.20	0.49
NVHf46–1	120–124	4	0.209	0.194	0.66	0.82
UFpe1	152–208	12	0.907	0.889	0.02	0.31
NVHfp82–2	131–167	15	0.884	0.845	0.04	0.34
NVHfp54	99–129	10	0.667	0.781	0.07	0.38
Combined	–	6.6	0.548	0.529	0.75×10^{-7}	0.18×10^{-2}

returned but did not breed. All five PTTs malfunctioned and failed soon after deployment in 2010; this was a consequence of excessive battery drainage during storage, which triggered hibernation mode in the PTTs (Cathy Bykowsky, Microwave Telemetry Inc.). Consequently, we were not able to estimate the survival rate of these birds, though only one bird equipped with a PTT returned to breed the following year. Overall, only 3 of 15 birds fitted with PTTs returned to breed in the subsequent year. In 2010, we recovered one non-functioning PTT from beneath a regular perch of a male; the chest stitching of the harness had been bitten through. This male had a distinctive light head and was seen without its transmitter five months after it had been fitted. Similarly, a female in 2009 also bit through the cross-stitching of its PTT harness within a month of deployment, leaving the PTT hanging loose; she was recaptured in order to refit the PTT and harness.

Of the 14 birds deployed with patagial tags in 2009, seven returned to breed the following year. Of these, three birds had removed the patagial tags from both wings and a further two birds had removed a patagial tag from one wing; in all but one case where the patagial tags were removed the nylon discs remained attached to the patagium. DNA analysis indicated that over the period 2009–10 the annual return rate for unmarked breeding birds was 50% ($N = 8$), compared to 50% ($N = 14$) and 20% ($N = 10$) for birds with patagial tags and PTTs respectively.

Survival effect

We were able to track ten satellite-tagged birds for a total of 2528 days, and annual survival was estimated to be 36.3% when all birds with PTTs that ceased transmission for unknown reasons were considered to be dead and 64.8% if they were considered to be alive when transmission ceased (Table 2). Individuals that were captured for falconry are removed from the population, because trapping has the same biological effect as mortality in relation to breeding turnover. There was no clear difference in return rates of birds with PTTs deployed by different people: A. Dixon deployed PTTs on six birds, two of which returned the following year (33%), D. Ragyov and G. Purev-Ochir deployed PTTs on four birds, one of which returned the following year (25%).

Models that best explained the likelihood of birds returning to breed in a subsequent year all included prior breeding experience as a variable (RI = 1.00), with a model that included the additional influence of PTT deployment explaining the most variation (Table 3). Birds with prior breeding experience were more likely to return to breed the following year, whilst the deployment of satellite transmitters reduced the likelihood of subsequent return (Table 4).

The five juveniles deployed with PTTs survived for an average of 169 days (median = 157; range: 46–334 days) after fledging and their daily survival was 0.994, which equates to an annual survival rate of just 11.4%, with four of the five juveniles dying within 6 months of leaving their nests.

Behavioural effects

Nest desertion: We obtained video footage of the nest attendance behaviour of a breeding female that was fitted with a PTT on 25 May 2010. This female was caught at her nest site when the nest held four chicks

Table 2. PTT data for 10 adult Saker Falcons showing date of deployment, date PTT ceased transmission and number of days the bird was tracked. The fate of birds when transmission ceased was either 'unknown', that is, they could have been dead or alive, or 'alive', that is, transmission ceased due to PTT failure or because the bird was caught by falcon trappers.

PTT #	Deployed	Cessation	Days	Fate
90885	3 May 2009	30 August 2009	118	Unknown
90886	7 May 2009	22 November 2010	563	Alive (PTT failure)
90887	19 May 2009	13 November 2009	177	Alive (Trapped)
90888	13 May 2009	27 October 2009	166	Alive (PTT failure)
90889	3 May 2009	15 July 2009	73	Unknown
90890	12 May 2009	23 July 2010	436	Unknown
90891	29 April 2009	18 January 2010	263	Unknown
90892	29 April 2009	9 January 2010	254	Alive (Trapped)
90893	5 May 2009	28 February 2010	298	Alive (PTT failure)
90894	13 May 2009	10 November 2009	180	Alive (Trapped)

Table 3. Model selection results for annual return of breeding adults in relation to prior breeding, sex and deployment of PTTs or patagial wing tags.

Models	K	AICc	ΔAICc	w_i
Prior breeding experience + Satellite tag	5	43.3	0.00	0.32
Prior breeding experience	4	43.5	0.19	0.29
Prior breeding experience + Patagial tag	5	45.5	2.12	0.11
Prior breeding experience + Sex	5	46.1	2.80	0.08

Table 4. Model-averaged estimates of explanatory variables with their respective unconditional standard errors (se), 90% confidence intervals (CI) and relative importance (RI).

Variables	Est.	se	90% CI	RI
Prior breeding experience	1.32	0.93	−0.21, 2.86	1.00
Satellite tag	−1.76	1.04	−3.47, −0.05	0.52

aged approximately 8 days old. We obtained video footage of her nest attendance behaviour during four video sessions from 28 May to 6 June (3052 minutes observation) and four sessions from 10 to 27 June (4265 minutes observation). The female was observed feeding and brooding the chicks up to the 6 June but was not observed at the nest after this date; all subsequent nestling provisioning being undertaken by the male. Only the male was seen attending the nest during 134 minutes of visual observation at this nest site on 23 June. One nestling died between 16 and 22 June, aged 30–36 days old, and was partially eaten by the other nestlings; three chicks subsequently fledged at the end of June. The PTT was malfunctioning, so we only obtained three GPS locations for the female up to 6 June, two being within 2.4 km of the nest on 29 May and the other, on 4 June, being 73.5 km away. We obtained a further ten GPS locations from 10 June to 4 July where the female was mainly located >23.0 km from the nest (range 4.8–181.8 km).

A second female, deployed with a PTT in 2009 deserted its nest during the subsequent breeding season. This bird abandoned the nest area on 15 June 2010 when its chicks were approximately 28 days old. The nest held four chicks on the 8 June, 7 days prior to desertion, but one had died when the nest was next inspected on 18 June; three chicks fledged sometime between 7 and 11 July (minimum and maximum estimate of nestling period was 51 and 59 days), an unusually long nestling period (typically 44 days, se ± 0.4, $N = 69$; A. Dixon, unpubl. data) and one chick died at the nest site soon after fledging. Two observation bouts, totalling 301 minutes, were conducted at this nest during the nestling phase prior to desertion, and the female was present on both occasions (27 May and 8 June), but only the male was seen attending the nest in 150 minutes of observation on 15 June and no adults were seen attending the nest during a total of 318 minutes of observation on 23 June and 1 July. After deserting the nest, the female travelled a path of 980 km over a period of 127 hours, stopping each night and eventually reaching a settlement area in Inner Mongolia, China on 21 June, where it stayed until transmission stopped on 23 July. This settlement area was 720 linear km at a bearing of 120° from its nest site.

Non-breeding: Of the three satellite-tagged birds that returned to their breeding ranges one year after deployment, two (a male and a female) bred successfully with partners that were not deployed with PTTs. The non-breeding bird was a female, deployed with a PTT at its nest site in May 2009, which returned in 2010 to the range where it had previously bred. This female remained unmated in 2010 and stayed in its former nesting area until at least early May, after which its PTT stopped transmitting due to malfunction. Her mate of 2009 (fitted with a patagial tag in 2009) also returned in 2010 but shifted to a nest site 4 km away and bred with a new untagged female.

Physical effect

In June 2012, we recaptured an adult male and removed a PTT that had been deployed for 36 months. This bird had bred successfully each year since deployment of the PTT, despite the presence of physical injuries caused by the transmitter and its harness attachment. There was feather loss and damage on the dorsal body surface in the area under and immediately adjacent to the transmitter unit, and there was an area of raised, yellowish granulation tissue along the dorsal midline underneath the transmitter unit. On the ventral midline, where the harness was stitched over the sternum, there were further areas of yellow granulation tissue visible over the pectoral muscle. Further feather damage, areas of granulation tissue and lesions were evident laterally along the line of the harness running from the ventral midpoint to the rear anchor point of the PTT (Supplemental Fig. S1).

DISCUSSION

For medium-sized raptors, annual adult survival is typically 80–90%, for example, Goshawk *Accipiter gentilis* (Kenward *et al.* 1999); Common Buzzard *Buteo buteo* (Kenward *et al.* 2000) and Peregrine *Falco peregrines* (Mearns & Newton 1984). In Kazakhstan, return rates of breeding Sakers determined by DNA fingerprinting was 82 ± 5% (Wink *et al.* 1999, Kenward *et al.* 2007), which is higher than the annual return rate of untagged Sakers found in this study (50%). However, the annual breeding return rate of Sakers deployed with PTTs was even lower at 20%, although our estimate of annual survival of 36–65% based on daily survival rates was higher, suggesting that breeding dispersal may account for some of the difference in return rates between tagged and untagged adult Sakers. However, none of the Sakers that returned to breed with functioning satellite transmitters ($N = 2$), had dispersed from our study area, nor had the non-breeding bird.

Prior breeding experience was the most important variable in relation to the likelihood of birds returning to breed in the subsequent year. This could be due to differential survival, where birds with previous breeding experience are more likely to survive or to differences in breeding dispersal, where individuals that have previously demonstrated site fidelity are consistent in their behaviour, that is, if a bird returned after breeding in the previous year it is more likely to return to breed in the next year. The model that best explained variation in return rates incorporated the negative effect of PTT deployment, which held true when the non-breeding bird was also included as having returned (Supplemental Table S1 and S2), even though it would be difficult to detect similar instances of non-breeding return for patagial-tagged and untagged birds.

We were only able to recover three PTTs from the eight adults that did not return to breed in 2010; all were caught by falcon trappers in Mongolia and the harnesses had been cut-off and the PTTs discarded (enabling us to locate them as they continued to transmit from a stationary position). Differential trapping rates may account for the lower returns of satellite-tagged birds. Whilst there is no evidence that birds deployed with PTTs were more likely to be caught by trappers it is a possibility, perhaps because the trappers were curious to see what the PTTs were or because the birds were in poor condition and more likely to be trapped (Bloom *et al.* 2007). Juveniles fitted with patagial tags have been reported to us after being caught by falcon trappers in Mongolia, thus any possible increase in the likelihood of being trapped may simply be related to a bird carrying some form visible marker. It is also possible that Sakers encumbered with PTTs conserve energy by hunting more frequently from perches rather than in active flight, and are thus more likely to perch on power lines where they face an increased chance of being seen by trappers who frequently search for falcons along power lines, or risk electrocution (Dixon *et al.* 2013).

The low survival rate of birds deployed with harness-mounted PTTs, together with evidence of physical injury suggests that increased mortality is at least partly responsible for the low breeding returns of adult Sakers seen in this study. Mean annual survival of our PTT-tagged juveniles was just 0.11, with a median tracking period of 157 days, and 20% (1/5) transmitted signals until at least the second spring (i.e. 9 months after deployment). In Europe, 34% (21/62) of PTT-tagged juveniles transmitted signals for ≥9 months, with a median transmission period of 188 days (data from LIFE 2015), whilst the equivalent return rate was 23% (14/61) for juveniles deployed with harness-mounted backpack radio transmitters weighing 22 g in Kazakhstan (Kenward *et al.* 2007). In Europe, less than 5% of juveniles fitted with PTTs survived to breed (M. Prommer pers. comm.). The extremely low survival of adult and juvenile Sakers deployed with PTTs would not be expected for natural reasons because the study populations in Mongolia and Europe are increasing (Bagyura *et al.* 2012, Rahman *et al.* 2014).

In a previous study PTTs were believed to cause a significantly increased mortality of Sakers and Peregrines, with the cause attributed to the 'constrictive nature of the harness' (Eastham *et al.* 2000). In the Gyrfalcon *Falco rusticolus*, PTTs ceased transmission after an average of 145 days on adults and just 31 days on juveniles (Burnham & Newton 2011), again suggesting that the deployment of harness-mounted PTTs can impact survival in large falcons. Prairie Falcons *Falco mexicanus* that had shed their harness-mounted transmitters had an estimated annual survival rate of 87% compared with just 49% for those birds that retained their PTTs, providing clear evidence that harness-mounted PTTs reduced survival in this falcon species (Steenhof *et al.* 2006).

The removal of a harness-mounted PTT by one male in this study was achieved by biting through the stitched crossover of the Teflon harness on the sternum, and a female that also bit through this cross-stitching was recorded on video with the PTT hanging underneath her body as she fed her chicks. It is possible that falcons which bite through the cross-stitching may not succeed in completely removing the harness and could subsequently become entangled.

Reduced survival reflects a handicapping effect of harness-mounted PTTs that severely reduces fitness and condition. This handicapping can impose constraints on, or induce changes to, behaviour. Backpack transmitters have been shown to reduce flight velocity and body condition (Irvine *et al.* 2007), and influence migration behaviour (Ristow *et al.* 2000). In Gyrfalcons fitted with backpack transmitters, preening frequency increased after deployment and persisted for several weeks of observation, suggesting that the birds failed to adjust rapidly to the attachment of radio transmitters (Booms *et al.* 2011)

We found no evidence that the attachment of patagial tags influenced breeding return rates of Sakers, nor did we detect any adverse effect on breeding behaviour. The effects of using patagial tags can vary according to species (Kochert *et al.* 1983, Calvo & Furness 1992, Varland *et al.* 2007, Trefry *et al.* 2013) with some studies reporting little or no adverse impact of patagial tags (Smallwood & Natale 1998, Martin & Major 2010, Sergio *et al.* 2015), whereas others have reported increased mortality due to predation (Saunders 1988, Zuberogoitia *et al.* 2012.), sub-lethal effects on breeding ecology (Jackson 1982, Bustnes & Erikstad 1990), reduced nesting success (Trefry *et al.* 2013), physical effects such as feather wear and/or skin abrasion (Green *et al.* 2004) and behavioural impacts on hunting efficiency (Sherrod *et al.* 1981). The fact that five Sakers removed their patagial tags indicates that the markers were at least an irritation and possibly caused discomfort for the birds; removal of patagial tags has also been reported for Prairie Falcons (Kochert *et al.* 1983).

Non-breeding, following 'divorce' from its mate, was observed in one satellite-tagged female but from this single instance it is not clear whether the deployment of a PTT increased the likelihood of 'divorce' or non-breeding. Two satellite-tagged females deserted their nests during the nestling stage, something that was not detected in one patagial-tagged female and five untagged females whose nestling feeding behaviour was also monitored by video (A. Dixon, unpubl. data). However, desertion by one member of a breeding pair is not easy to detect during recurrent but infrequent nest monitoring visits, particularly when nestlings continue to be provisioned by the other partner. Nest desertion was inferred by Ellis *et al.* (2011) as an explanation for several Saker nests found in Mongolia with abandoned eggs or dead chicks, which they considered to be indicative of nomadic breeding behaviour. However, we found no evidence of nomadic behaviour in this study and breeding dispersal was very limited within our artificial nest grids (Rahman *et al.* 2014). Nest desertion during nestling provisioning may have been a response by females to a 'handicapping effect' of harness-mounted PTTs during an energy-demanding phase of the breeding cycle. The act of trapping the birds was unlikely to have caused the desertion as one female provisioned the chicks for at least 12 days after being caught and the other deserted its nest in the year after it had been caught. A case of nest desertion after deployment of a harness-mounted transmitter has been reported in the Gyrfalcon (Klugman *et al.* 1993), whilst another female trapped at its nest and deployed with a backpack transmitter temporarily deserted its nest during incubation (Booms *et al.* 2011).

The physical effects of encumbering a Saker with a harness-mounted PTT were exhibited in a male that had returned and bred successfully for three successive seasons after deployment. Skin lesions increase susceptibility to infection and the loss of insulating feathering under the body of the PTT and along the line of the Teflon harness is potentially costly in terms of thermoregulation for a bird that wintered each year in Mongolia where the average monthly temperatures are as low as −26°C. Similar injuries have been implicated in the mortality of Red Kites *Milvus milvus* fitted with harness-mounted transmitters (Peniche *et al.* 2011).

A great deal of attention has been focused on the Saker Falcon in recent years, including the compilation of an EU Single Species Action Plan, a Significant Trade Review by CITES, Appendix 1 listing and the establishment of a Saker Task Force by CMS and three IUCN Red List category revisions by BirdLife International between 2004 and 2011 (Dixon 2012). The Saker is categorized as Globally Endangered on the IUCN Red List and its Threatened status, together with its cultural importance in Arabic falconry, has resulted in the species being the subject of intensive study and management in Europe and Asia (e.g. Dixon *et al.* 2011a, 2011b, Bagyura *et al.* 2012) and much of this work has involved the use of satellite telemetry. From 1994 to 2013, at least 208 Sakers were deployed with PTTs, making it one of the most intensively satellite-tracked bird species, with at least 75 birds deployed in Europe (in Hungary, Slovakia, Romania, Ukraine: Prommer *et al.* 2012, M. Prommer in litt.) and 43 in Asia (in Russia, Kazakhstan, Mongolia, China: Eastham *et al.* 2000, Potopov *et al.* 2002, Karyakin *et al.* 2005, A. Dixon, unpubl. Data). In addition at least 73 Sakers that were released after being used for falconry or confiscated from smugglers have been tracked using satellite transmitters (Kenward & Pfeffer 1995, Judas 2011, M. Muller in litt.) and 17 captive-bred juveniles have been tracked after release in Austria and Bulgaria (Gamauf & Dosedal 2012, A. Dixon, unpubl. data). Researchers and conservation managers need to carefully assess the objective of any future tracking work on Sakers that involves using harness-mounted transmitters as the behavioural and survival effects of tagging can potentially compromise studies of survival, behaviour and movements.

ACKNOWLEDGEMENTS

We thank HE Mohammed Al Bowardi for his interest and support. We thank the following for their assistance: A. Adams, Amarkhuu G., Amarsaikhan S., Ariunzul L., I. Balazs, B. Batsukh, A. Bräunlich, N. Dixon, V. Ferdinandova, M. Fuss, M. Jessen, T. Kunca, N. Nedyalkov, J. Stacey, and Y. Tadehara.

FUNDING

This study was conducted on behalf of and funded by the Environment Agency – Abu Dhabi. X. Zhan was supported by the Recruitment Program of Global Youth Experts of China and the China Biodiversity Observation Networks (Sino BON). Additional support for the deployment of one PTT in 2009 was provided by The World Bank (Netherlands-Mongolia Trust Fund for Environmental Reform) and BirdLife International (the Rio Tinto – BirdLife Programme).

SUPPLEMENTAL DATA

Supplemental data for this article can be accessed at: 10.1080/00063657.2015.1135104.

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(MS received 14 July 2015; revised MS accepted 29 September 2015)