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ORIGINAL ARTICLE

Abdominally implanted satellite transmitters affect reproduction and survival rather than migration of large shorebirds

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Abstract Satellite telemetry has become a common technique to investigate avian life-histories, but whether such tagging will affect fitness is a critical unknown. In this study, we evaluate multi-year effects of implanted transmitters on migratory timing and reproductive performance in shorebirds. Shorebirds increasingly are recognized as good models in ecology and evolution. That many of them are of conservation concern adds to the research responsibilities. In May 2009, we captured 56 female Black-tailed Godwits *Limosa limosa limosa* during late incubation in The Netherlands. Of these, 15 birds were equipped with 26-g satellite transmitters with a percutaneous antenna (7.8 % ± 0.2 SD of body mass), surgically implanted in the coelom. We compared immediate nest survival, timing of migration, subsequent nest site fidelity and reproductive behaviour including egg laying with those of the remaining birds, a comparison group of 41 females. We found no effects on immediate nest survival. Fledging success and subsequent southward and northward migration patterns of the implanted birds conformed to the expectations, and arrival time on the breeding grounds in 2010–2012 did not differ from the comparison group. Compared with the comparison group, in the year after implantation, implanted birds were equally faithful to the nest site and showed equal territorial behaviour, but a paucity of behaviours indicating nests or clutches. In the 3 years after implantation, the yearly apparent survival of implanted birds was 16 % points lower. Despite intense searching, we found only three eggs of two implanted birds; all were deformed. A similarly deformed egg was reported in a similarly implanted Whimbrel *Numenius phaeopus* returning to breed in central Alaska. The presence in the body cavity of an object slightly smaller than a normal egg may thus lead to egg malformation and, likely, reduced egg viability. That the use of implanted satellite transmitters in these large shorebirds reduced nesting propensity and might also lead to fertility losses argues against the use of implanted transmitters for studies on breeding biology, and for a

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careful evaluation of the methodology in studies of migration.

Keywords Breeding success · Egg malformation · Implanted transmitter · *Limosa l. limosa* · Nesting propensity · *Numenius phaeopus* · Satellite telemetry · Survival

Zusammenfassung

Im Bauch implantierte Satellitensender beeinträchtigen bei großen Watvögeln eher Reproduktion und Überlebensfähigkeit als den Zug

Satellitentelemetrie hat sich zu einer gängigen Methode bei der Erforschung der Biologie von Vögeln entwickelt; ob allerdings eine solche Markierung die Fitness beeinträchtigt, ist ein kritischer unbekannter Faktor. In dieser Studie werteten wir die jahresübergreifenden Effekte implantierter Sender auf den zeitlichen Ablauf des Zuggeschehens und den Reproduktionserfolg bei Watvögeln aus. Watvögel werden zunehmend als geeignete Modelle für Ökologie und Evolution erkannt. Dass viele von ihnen schutzbedürftig sind, erhöht noch den Forschungsbedarf. Im Mai 2009 fingen wir in den Niederlanden 56 weibliche Uferschnepfen *Limosa limosa limosa* zu einem Zeitpunkt gegen Ende der Bebrütungsphase. Von diesen wurden 15 Vögel mit 26 g-Satellitensendern (7.8 % ± 0.2 SD der Körpermasse) mit einer perkutanen Antenne ausgestattet, welche operativ in die Leibeshöhle eingesetzt wurden. Wir verglichen die unmittelbare Nestüberlebensrate, den zeitlichen Ablauf des Zuggeschehens, die anschließende Brutorttreue sowie das Reproduktionsverhalten einschließlich der Eiablage mit denen der übrigen Vögel, einer Vergleichsgruppe aus 41 Weibchen. Wir konnten keinen Einfluss auf die unmittelbare Nestüberlebensrate feststellen. Der Ausfliegeerfolg und die anschließenden nach Süden beziehungsweise Norden gerichteten Zugmuster der implantierten Vögel entsprachen den Erwartungen, und die Ankunftszeit in den Brutgebieten in den Jahren 2010–2012 unterschied sich nicht von der Vergleichsgruppe. Gegenüber der Kontrollgruppe waren die implantierten Vögel im auf die Implantation folgenden Jahr genauso brutorttreu und zeigten vergleichbares Revierverhalten, dagegen aber kaum Verhaltensweisen, die auf Nester oder Gelege hindeuteten. In den drei auf die Implantation folgenden Jahren lag die scheinbare jährliche Überlebensrate von Vögeln mit Implantaten um 16 % niedriger. Trotz intensiver Suche fanden wir nur drei Eier von zwei implantierten Vögeln; diese waren alle missgebildet. Ein in ähnlicher Weise deformiertes Ei ist von einem Regenbrachvogel *Numenius phaeopus* mit einem vergleichbaren Implantat nach seiner Rückkehr ins Brutgebiet in Zentralalaska bekannt. So kann die Anwesenheit eines Objektes in der Leibeshöhle, welches etwas kleiner als ein normales Ei ist, zu Eimissbildungen und wahrscheinlich auch zu einer verringerten Lebensfähigkeit der Eier führen. Dass die Verwendung implantierter Satellitensender bei diesen großen Watvögeln die Nistbereitschaft reduziert und außerdem zu Fruchtbarkeitsausfällen führen könnte, spricht gegen die Verwendung implantierter Sender bei Studien zur Brutbiologie und für eine sorgfältige Prüfung der Methodik bei der Zugforschung.

Introduction

The science of animal tracking has seen major advances in the past three decades, primarily through the miniaturization of satellite transmitters, GPS devices and geolocators. For birds, the initial devices were so bulky that they could be used only on species as large as albatrosses and penguins (Hart and Hyrenbach 2009). Today, satellite tracking is possible in much smaller birds such as alcids (Falk et al. 2001) and the larger shorebirds (e.g. Driscoll and Ueta 2002; Watts et al. 2008; Gill et al. 2009; Johnson et al. 2010; Battley et al. 2012). However, the application of any tracking technology comes with costs to the experimental animal that can affect the quality of the data obtained (Calvo and Furness 1992; Barron et al. 2010; Fast et al. 2011; White et al. 2013).

To mitigate such effects, researchers need to critically evaluate their techniques and report their findings so others have a clear understanding of the potential consequences of a chosen application. Despite a sharp increase in the number of studies reporting results obtained from the use of remote sensing devices, many fewer reports address the effects these activities have on study subjects (McMahon et al. 2011; Vandenabeele et al. 2011). Studies reporting effects on the use of satellite- and GPS- tracking devices have initially addressed effects related to the external attachment of devices by harnesses (Rappole and Tipton 1991). Negative effects of such attachment include nest desertion (Falk and Møller 1995), mass loss and decreased colony attendance (Söhle 2003), decreased migration range (Pennycuick et al. 2012), and changes in behaviour (Robert et al. 2006). In albatrosses and petrels, negative effects on demographic traits varied with species and attachment method (Barbraud and Weimerskirch 2012; Philips et al. 2003).

While transmitters that have been surgically implanted in the coelomic cavity lessen drag that is incurred with externally attached devices (Pennycuick et al. 2012; White et al. 2013), implanted transmitters may affect aspects of behaviour, survival and reproduction. For example, captive Mallards *Anas platyrhynchos* with implanted transmitters developed mild to moderate localized air sac reactions, but neither behaviour nor activity of the birds was altered (Korschgen et al. 1996). During initial studies of Harlequin Ducks *Histrionicus histrionicus*, 2.3 and 3.4 % mortality occurred during the surgical implantation and immediate post-release periods, respectively. However, subsequent modifications to anaesthetic procedures reduced mortality to 1.5 % during surgery and 1.5 % during the immediate post-release period (Mulcahy and Esler 1999). In Common Eiders *Somateria mollissima*, 92 % of implanted females deserted their nest but no changes were observed in their time budgets (Fast et al. 2011). Following the surgical implantation of transmitters, Guillemots (*Uria aalge* and *U. lomvia*) ceased nesting activity (Meyers et al. 1998).

Investigators have also examined 'downstream' effects from implanted devices, particularly pertaining to reproduction and survival. For example, in Canada Geese *Branta canadensis* implanted with 26- and 35-g radio transmitters, no apparent effects were noted in survival of the first year after deployment or in behaviour, time budgets and fecundity during the subsequent nesting season (Hupp et al. 2003, 2006). In the Harlequin Ducks for which surgery-related mortality was documented, follow-up studies found no effects on subsequent survival (Esler et al. 2000). Fast et al. (2011) showed that surgical implantation led to a decline in first-year survival of Common Eiders, but there was no evidence for a survival difference in subsequent years and some implanted females were observed nesting.

Coelomically-implanted satellite transmitters have only recently been used in shorebirds and remain so novel that longer-term effects can only now be evaluated. In one study, Bar-tailed Godwits *Limosa lapponica* with implanted transmitters were tracked on all 3 long-distance legs of their annual flights around the Pacific Basin (Gill et al. 2009; Battley et al. 2012), apparently with little effect on their overall migratory performance. In contrast, Bar-tailed Godwits equipped with harness-attached 9.5-g PTTs did not complete their long-distance flight legs in one non-stop flight as did the implanted godwits, but rather stopped en route, or turned around and returned to non-breeding areas (R.E. Gill et al., unpublished data). Several of these birds then shed their transmitters upon making landfall, indicating to us that, for species that gain and lose a lot of weight during migration, harnesses are not a viable attachment method. In another study, however, two Black Oystercatchers *Haematopus bachmani*, a non-migratory species, with implanted satellite transmitters laid eggs that were aberrant in size and colour, apparently due to the transmitter's size and proximity to the shell gland (Johnson et al. 2010).

Here, we present an evaluation of the effects of implanted satellite transmitters on various aspects of the annual cycle of another species of large shorebird, the European continental subspecies of Black-tailed Godwit *Limosa limosa limosa*, with confirmatory information from Whimbrels *Numenius phaeopus* breeding in Alaska. We compare results obtained from birds implanted with satellite transmitters with those from a comparison group of Black-tailed Godwits that was captured and colour-ringed during the same year and in the same area in The Netherlands. We specifically compare the two groups in terms of the timing of their respective migrations and their reproductive performance both in the year they were surgically implanted and in the three subsequent breeding seasons. Our experience was not unique, but we should point out that in 2008–2009 there was a large body of literature describing deleterious effects of external harnesses on birds (see previous references). Nevertheless, the present study provides a strong qualifier to the suggestion in a recent meta-analysis by White et al. (2013) that properly implanted devices tend not to have negative fitness consequences. One of the main aims of the underlying study was to identify population-specific stopover and staging sites for conservation purposes. Geolocators do not yield location data that are detailed enough, and for this reason were not considered as an alternative for the use of satellite transmitters.

Methods

Study area

We have studied a breeding population of individually marked Black-tailed Godwits annually since 2004 on an 8,480-ha study area in southwest Friesland, The Netherlands (see, e.g., Groen et al. 2012; Schroeder et al. 2012; Kentie et al. 2013). The study area extends from Makkum (53°02′41″N, 05°23′14″E) in the north to Laaksum (52°50′59″N, 05°25′16″E) in the south. The area mainly consists of grassland (about 90 % of the surface area) managed intensively for dairy farming, with some arable land (about 10 %; mostly Maize *Zea mays* fields). About 10 % of the grassland area is located in nature reserves that are managed especially for Black-tailed Godwits and other meadow bird species.

Capture, implant procedure and cohort comparison

In spring 2009, we captured 56 female godwits on nests using walk-in traps. To enhance catching success and to minimize the likelihood of nest desertion, we set the traps during the last days of incubation or as eggs were hatching (Schroeder et al. 2008). In the period 10–17 May, 15 captured birds were selected for implantation; these females were transported to a three-person surgical team (veterinarian, anaesthetist and scribe) that worked from a mobile surgical laboratory immediately after capture. We performed the procedures following the protocol used for surgical implantation of satellite transmitters in other species of large shorebirds (Mulcahy et al. 2011). During the initial recovery period following surgical implantation, we ringed the birds with a unique combination of coloured rings, measured them, and took a sample of blood for molecular determination of sex (for details, see Schroeder et al. 2010, Trimbos et al. 2013). The remainder of the recovery took place in a closed holding box in a quiet area during which the birds were closely monitored. As soon as birds were fully alert and could stand and maintain their posture (usually less than 1 h after surgical implantation), we returned them to the capture site for release.

To assess the effects of the implant procedure, as a comparison group we used all other nesting females captured in spring 2009 in the study area ($n = 41$). These birds were treated to precisely the same capture, ringing, measuring, and blood-taking procedures as the implanted individuals, but were released immediately after data collection. Because these birds were not exposed to anaesthesia and surgery, we subsequently refer to a ‘comparison’ rather than a ‘control’ group. Molecular testing confirmed that all implanted and comparison birds were females.

We implanted godwits with the lightest internal satellite transmitter available in spring 2009 (25–26 g; ~54 × 18 × 17 mm; Microwave Telemetry; Fig. 1). We programmed the duty cycle of the units (i.e., the pattern of transmission and rest periods) so that the ca. 600 h of expected battery power would coincide with periods of our main study interest. Thus, 40 % of the battery power was

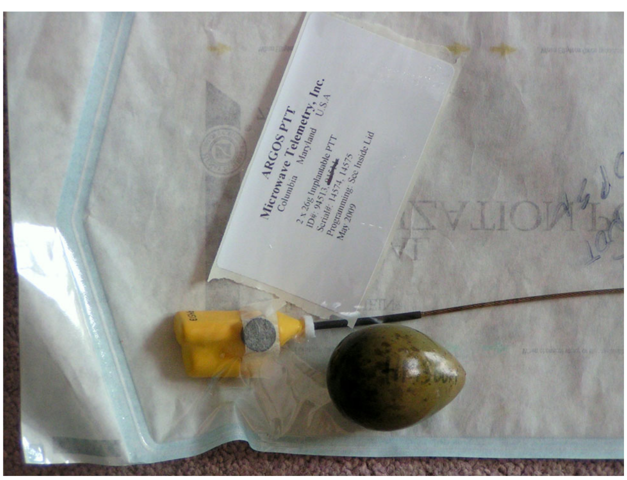

Fig. 1 Size and shape of an implantable satellite transmitter (in sterilized package) compared to a Black-tailed Godwit *Limosa limosa limosa* egg. The dark object on the yellow transmitter body is a magnet that activates a reed switch, preventing transmissions until it is removed. The white object at the base of the antenna is a collar made of polyester fabric that served as an anchor point for suturing to stabilize the transmitter within the bird’s body

programmed to be utilized in the first 3 months post-deployment to capture the southward migration and the arrival in the wintering areas, and the remainder of the power over the subsequent 8 months. In addition to the transmitter’s prescribed schedule for reporting positions, each also reported the activity (moving or not moving), the charge level of the transmitter battery, and either the bird’s internal temperature ($n = 11$) or the ambient air temperature ($n = 4$). Combined, these sensors allowed us, in most cases, to determine the fate of a bird (alive or dead).

The type of transmitter employed had previously been used on a large subspecies of Bar-tailed Godwit *Limosa lapponica baueri* just prior to migration (Gill et al. 2009). In this study, load factors (transmitter weight/body weight) ranged between 5.2 and 7.7 % (Mulcahy et al. 2011). Our Black-tailed Godwits are somewhat smaller than the *baueri* subspecies of Bar-tailed Godwits, and, like the other *Limosa* species, are sexually dimorphic in size with females being larger (Schroeder et al. 2008). We selected the largest individuals (>300 g) for surgical implantation, using the confirmed females in the lighter release group for the comparison. This resulted in an average load factor of 7.8 % (SD = 0.24, range = 7.50–8.30) at time of implantation, which is at the high end of the range in implanted Bar-tailed Godwits (Mulcahy et al. 2011). Note, however, that the studied Bar-tailed Godwits were actively fuelling and had considerably higher masses than they would have had during breeding.

Probably as a result of selecting the bigger individuals, at time of capture, implanted females were on average heavier (321 g; SD = 11) than females in the comparison group (312 g; SD = 19; $t_{42.62} = -2.03$; $P = 0.048$). To assess whether such large females were of larger structural size or carried larger body stores (Piersma 1984; van der Meer and Piersma 1994), we calculated the first principal component (PC1) in a principal component analysis (PCA). PC1 explained 53 % of the variation, with total head, bill length, tarsus, tarsus + toe and wing length to summarize the body size of the birds. We calculated the residuals from the regression between body mass and the PC1 ($R^2 = 0.31$). A comparison of these residuals indicated that, corrected for body size, mass was not different between satellite and comparison birds ($t_{46.81} = -0.689$, $P = 0.494$). At capture, implanted females were thus somewhat structurally larger, but with similar ‘body condition’ than females in the comparison group.

The total time elapsed from capture until release averaged 108 min (SD = 11, range = 90–135) with about 20, 30 and 50 % of the total time spent in transport, surgical implantation and recovery, respectively. We kept birds in the comparison group for less than 15 min. We lost contact with one bird 9 days after implantation, but it was resighted four times in the 6 weeks after surgery and returned to the study area in two subsequent breeding seasons. Another bird may have died within 3 days after deployment. It was alarming at the nest 24 h after surgery and was showing chick-guiding behaviour the next day. Both times, the bird was active and alert. On the third day, we found a bunch of feathers at the site where it was last seen and concluded that it was probably depredated. As the disappearance of these birds seems unrelated to capture or surgery, and as such events could also easily happen to birds in the comparison group, we incorporated them in the survival analysis introduced below (i.e., $n = 15$).

Monitoring methods

We followed both groups for 3 years until July 2012. Initially, we monitored several parameters in the period between their capture and departure on migration. Roughly 24 h after the initial capture, we visited the nest site and noted the status of the nest and the presence or absence of the birds. After this initial visit, we monitored the fate of the nest about every 2 days until hatching. If nests of implanted birds hatched, then, about every 5 days thereafter, we determined the status of the brood, either by visually sighting chicks or by noting behaviours of the marked birds that were indicative of having a brood. We did not follow all broods in the comparison group as systematically (i.e. noting intensive alarming, chick-guiding).

We used satellite telemetry to assess the status of implanted birds during the period between departure on migration in 2009 and their return to the breeding grounds in 2010. We followed most birds for some or all of their southward migration in 2009 during which we collected information on the timing and route of the flights as well as the status of the birds. Of the 15 birds, only 4 carried functioning transmitters through their return to the breeding grounds in spring 2010. Of the other 11 birds, we lost contact with 9 prematurely through battery and/or transmitter failure, whereas 2 birds died. To help locate birds of both cohorts during the 2010–2012 breeding seasons (15 March–15 July), we relied on a team of 8 trained and experienced observers in 2010 and 2012 and a team of 4 in 2011. They searched the study area daily to determine arrival dates, record territorial (i.e., paired, fighting, displaying, copulating, nest-building), nesting (i.e., alarming, incubating) or brooding (i.e., chick-guiding, intensive alarming) behaviour, and to locate nest sites of birds in both groups.

As the arrival date in a given year, we considered the first sighting of an individual prior to 1 May (Lourenço et al. 2011). We defined nest site fidelity as a bird's return to the same polder (i.e., tract of low-lying land reclaimed from the sea or former lakes, in which the parcels in general have the same (a)biotic characteristics) in which it nested in 2009. The average size of a polder in our study area is 197 ha (SD = 133, Groen et al. 2012). For the 4 birds that returned with functioning transmitters, we used satellite-fixed location data to find general territories over which we conducted intensive ground-searches to locate nests and document nest fate. Determining nesting status of birds that returned with non-functioning transmitters and of those in the comparison group required more effort. This involved identifying the unique combination of markers each bird carried on its legs. Because Black-tailed Godwits are generally faithful to the nest site of the previous year (Groen 1993; van den Brink et al. 2008), we intensively searched the nesting area that a marked bird used the previous year and, if no evidence of nesting was found, expanded the search farther afield. We considered a breeder failed if it was never observed exhibiting nesting or brooding behaviour (i.e., egg-laying, breeding, intensively alarming, chick-guiding).

This study was conducted under Dutch Animal Welfare Act Article 9 (license number DEC 4339F).

Statistical analyses

We used mark–recapture analysis to estimate apparent survival rates of both implanted and comparison birds and tested if these differed from each other. To avoid false positives, we only used visual resightings of birds seen twice within the breeding seasons 2009–2012 on different days or by different observers. Because of the small sample size ($n = 15$), we did not test for year-specific survival and resighting probabilities. The two models we tested were $\varphi(_{sat})p(.)$ and $(.)p(.)$. As only four transmitters still worked in the subsequent year and none in the years after, and as resighting probabilities are high for godwits in our study area (Schroeder et al. 2010), we expect no difference in resighting probability between the two groups.

We tested for differences in nest survival with a generalized linear model (GLM) with a binary response (successful/unsuccessful), using laying date as covariate; we regarded a nest successful if it hatched at least one chick. We used an analysis of variance (ANOVA) to test if the arrival dates of implanted birds differed from the comparison group and included the factor year and the interaction year × group. We used a GLM for binomial data to test if the two groups of Godwits differed in territorial and nest-indicating behaviour, including the factor year and the interaction year × group. All categorical data were analysed using Fisher's exact test. All analyses were conducted using the R Project for Statistical Computing (R Development Core Team 2008) and results were considered significant when $P < 0.05$. All values represent mean ± SD, unless indicated differently. The mark–recapture analysis was done with MARK (White and

Table 1 Comparison of breeding and migration season parameters of female Black-tailed Godwits *Limosa limosa limosa* with ("implanted birds") or without ("comparison birds") coelomically implanted satellite transmitters in southwest Friesland, the Netherlands in 2009–2012

Parameter	Implanted birds	*n*	Comparison birds	*n*	*P*
First year after implantation					
Nest survival after 1 week, 2009	0.80	15	0.85	41	0.40
Proportion of nests that fledged chicks, 2009	≥0.13	15	No information		
Departure date from W Europe, 2009	27 June ± 17 days	13	No information		
Subsequent breeding seasons					
Arrival date on study area, 2010–2012	29 March ± 11 days	18	26 March ± 12 days	87	0.21
Apparent survival, averaged model, 2010–2012	0.74	15	0.90	41	na
Fidelity to 2009 nest site, 2010	0.73	11	0.85	40	0.43
Proportion exhibiting territorial behaviour, 2010–2012	0.33	21	0.53	100	0.31
Proportion of birds with likely nests, 2010–2012	0.19	21	0.45	100	0.035
Proportion of viable eggs, 2010	0[a]	2	0.98	41	0.003

Given values expressed as percent, mean ± SD

na not applicable

[a] Eggs in the one nest found in 2010 likely were not viable, but the nest was depredated before this could be determined

Burnham 1999). Because the global model was not the full-time and group-dependent model, we used the median $\hat{c}$ method with 100 iterations integrated in the program MARK to test for goodness-of-fit. Because the data were slightly overdispersed ($\hat{c} = 1.96$, SE = 0.03), we used QAICc (Akaike's information criterion, corrected for overdispersion and small sample size) for model interpretation (Burnham and Anderson 2002).

Results

First year after implantation

We found no difference in nest survival between implanted and comparison birds following capture in 2009 [$\beta = 0.57$, SE = 0.72, $P = 0.42$, Table 1; effect of lay date was not significant ($P = 0.50$) and was removed from the analysis]. During the initial nest check within 24 h following implantation, 14 nests of the implanted birds were being incubated (1 was depredated), while at the end of the first week post-capture 12 of the 14 nests had hatched and potentially produced a total of 46 hatchlings (based on number of viable eggs present at last check). Of the 2 nests that did not hatch, the eggs in 1 were cold and the nest was apparently abandoned, while the second nest was apparently depredated. Rates of hatching, depredation and abandonment were 80, 13 and 7 %, respectively, for this group. The degree to which the implanted birds participated in incubation was unclear; only 1 implanted bird was actually seen on its nest and 3 birds might have departed, leaving the final days of incubation to their partners based on prolonged absences from their territories during this period. One bird was apparently depredated 3 days after its nest hatched. We were able to verify hatching status in 37 of the 41 nests of colour-ringed comparison birds that we checked within 24 h of ringing. Of these 37 nests, 18 had hatched, 17 were still being incubated and 2 had apparently been abandoned. A week following banding, we were able to check all 41 nests of comparison birds and found that 34 had hatched (83 %), 4 were depredated (10 %) and 3 had been abandoned (7 %).

Nine of the satellite-tagged birds were seen with chicks within the first week post-hatch. We were unable to obtain detailed information on fledging rates of either experimental or comparison group, primarily because godwit broods are very mobile—moving kilometres in a day—and, for implanted birds, there was a 36-h lag time in obtaining location data due to the duty cycle of the transmitter. Nevertheless, in 2009, two pairs of birds, of which one member of the pair carried an implanted transmitter, were seen with at least one fledged (>25 days old) chick, two pairs were seen with chicks 16 days old, and six pairs with chicks <8 days old. Thus, fledging success of the implanted birds was at least 0.13 chick per pair, but likely higher. Without the help of satellite or radio telemetry to relocate birds at either broad- or fine-scales, the resighting probability during this period of birds in the comparison group was too low to assess either fledging success or the date they departed the breeding grounds (Table 1).

The 13 implanted birds that were alive at the end of the breeding season and still had a functioning transmitter at that time, departed the breeding grounds on average 27 June (±17 days, range = 5 June–5 August), or on average 46 days post-implantation. Of the initial 15 birds, only 4 carried functioning transmitters through their return to the breeding grounds in spring 2010. One bird died within 3 days after deployment, and the PTTs of the remaining 10 birds did not perform as well as expected, but did transmit for a median of 88 days (range 3–232 days). This was long enough to provide detailed information on the location of southward migration routes (2 birds) and southward routes plus wintering areas (11 birds). Thirteen implanted birds could be tracked to the Mediterranean, where at least 3 birds spent the whole winter. Eight birds were tracked to wintering sites in coastal West Africa, either on direct flights from the breeding grounds or from intermediate staging areas in southern Europe. One migrant to West Africa died when it was inadvertently captured in a fishing net (B. Kone, Wetlands International Mali, personal communication). As we have seen, 1 bird may have died within 3 days of deployment (likely depredated) and 1 PTT failed for unknown reasons within 9 days of deployment so that we obtained little information.

Subsequent breeding seasons

We resighted 11 implanted birds in 2010, 9 in 2011 (including 1 not seen in 2010) and 1 in 2012. In contrast, we resighted 40 of the 41 comparison group birds in 2010, 29 in 2011, and 31 in 2012. During springs 2010–2012, the mean arrival date of implanted birds (29 March ± 11 days, $n = 18$) did not differ ($F_{1,103} = 1.93$, $P = 0.2$) from that of comparison birds [26 March ± 12 days, $n = 87$; Table 1; we removed the interaction year × groups ($P = 0.4$) and year ($P = 0.1$)]. There was also no difference between the groups in 2010 in their rates of apparent fidelity to their 2009 nest sites ($P = 0.4$, Table 1). In another measure of apparent reproductive success, 33 % of the observed implanted birds showed territorial behaviour in 2010–2012, compared to 53 % of the comparison group [$\beta = -0.81$, SE = 0.50, $P = 0.1$; Table 1; note that the interaction year × group was not significant ($P = 0.2$), nor was the term year ($P = 0.7$), so both were removed from the analysis]. Based on all observed behaviours, fewer implanted birds initiated nesting: 19 % of the implanted birds versus 45 % of the observed birds in the comparison group [$\beta = -1.25$, SE = 0.59, $P = 0.035$; Table 1; note that the interaction term year × group was not significant ($P = 0.1$) and neither was year ($P = 0.6$) and both were removed].

Apparent annual survival was 0.90 (SE = 0.05, CI = 0.72–0.97) for the comparison group and 0.74 (SE = 0.13, CI = 0.41–0.92) for the implanted birds. As the model $\varphi(_{\text{sat}})p(.)$ (Qdeviance = 13.00) was better supported than the model without implantation effect on survival $\varphi(.)p(.)$ (Qdeviance = 16.87), with a ΔQAICc of 1.77 less (with an Akaike weight of 0.71 above 0.29), comparison birds had a 16 % higher apparent survival than implanted birds. As the ΔQAICc of the models were within a difference of 2 (which might be caused by the small sample size), we opted for model averaging. The resighting

Fig. 2 Deformed eggs (*left*) from the only nest of a Black-tailed Godwit intra-coelomically implanted with a satellite transmitter in 2009 that was found in SW Friesland, The Netherlands in 2010 in comparison to a series of normal godwit eggs (on the *right*, they measure approximately 55 by 38 mm). Dimensions of the deformed eggs: 35.9 × 26.4 mm (*left*), 54.2 × 27.5 mm (*right*). Photos by Bram Verheijen (*left*) and Astrid Kant (*right*)

probability after model averaging was estimated as 0.83 (SE = 0.07, CI = 0.66–0.92).

Despite intensive searching, we found only 1 nest of an implanted bird in the 3 years after implantation, whereas we found nests or observed broods for 50 % of the birds of the comparison group in 2010, 48 % in 2011 and 35 % in 2012. The single nest of an implanted bird found in 2010 contained only two eggs at the time of finding (Fig. 2), whereas average clutch size in our study area was 3.7 (R. Kentie, unpublished data). The eggs were either markedly narrower or shorter (35.9 × 26.4 and 54.2 × 27.5 mm) than the average-sized egg measured on the study area (54.5 ± 2.2 × 37.7 ± 1.2 mm: $n = 11{,}112$), with a more bluish shine than is normal and with fewer spots. None of the 99 eggs of the comparison birds found were deformed. Both eggs were depredated before we could assess their viability or if any additional eggs had been laid. If we considered them to be unviable, the viability of the eggs in the two groups would have been markedly different ($P = 0.003$; Table 1). In April 2011, we found a deformed egg similar in pigmentation and size to the oblong egg we found in 2010. It was depredated before dimensions could be recorded, but we were able to assign it to one of the implanted birds using molecular DNA techniques (van der Velde et al. 2011). In 2012, the only implanted bird that was observed in the study area was showing chick guiding behaviour but its nest was not found. This bird had also demonstrated nest-indicative behaviour in 2010, but not in 2011.

Discussion

Direct implantation effects

We noted no outward effects of the surgical implantation and no mortalities occurred during and immediately after surgery. The apparent depredation of one bird within a few days of surgical implantation is unlikely to be related to the surgical implantation as it was actively defending its chicks 2 days after the surgical implantation and appeared healthy. Nest survival after capture was high and independent of treatment, and we have no indication that surgical implantation might have led to nest abandonment. Yet, we cannot exclude the possibility that males took over incubation duties to compensate for lack of incubation by their implanted mates. Depredation rates of nests of implanted and comparison birds were comparable between the experimental and comparison groups and probably not related to implantation. The two nests of implanted birds that were depredated were in fields that were mown shortly after the birds were captured; all other nests that hatched were in unmown fields. This suggests that their loss was due to external factors related to mowing. Farmers usually try to avoid a nest and its direct surroundings during mowing, helped by volunteers that mark nests. Nests in mowed fields are therefore always clearly recognizable as small patches of long grass. They generally have lower survival probability, likely because unmown patches attract predators (R. Kentie, J. Hooijmeijer and T. Piersma, unpublished data).

Without the use of radio telemetry to track fine-scale local movements, it was difficult to locate parents and broods for either group of birds in order to make accurate estimates of fledging success. However, we did determine that, in the year of surgical implantation, at least two chicks of implanted birds fledged, as we suspect did several other chicks based on their advanced age when last detected. Note that, if just 1 of the other 44 hatchlings from nests of implanted birds had fledged, then fledging success of implanted birds in 2009 would have been within the range of 0.2–0.6 godwit chicks per pair reported for other areas in The Netherlands (Schekkerman et al. 2008).

Departures of implanted birds occurred within the period that Black-tailed Godwits normally leave The Netherlands (Zwarts et al. 2009). Similarly, implanted birds returned to the breeding grounds at the same time as comparison birds in the 2 years after implantation. Further, migration routes and use of staging and wintering areas by the implanted birds in the year after implantation confirmed known routes and areas (Zwarts et al. 2009; Márquez-Ferrando et al. 2011). Flight behaviour also did not seem to be compromised since several birds made 4,500-km-long nonstop flights to West Africa. This is further evidence that implanted transmitters have no great effect on migratory or wintering behaviour (Gill et al. 2009; Battley et al. 2012).

Of the 60 implanted curlews and godwits that we had tracked prior to this study, and on which we based our planning, 26 of their PTTs (43 %) went off the air prematurely (i.e., worked for <400 h in 2006 units and <500 h in 2007 and 2008 models). Of these, 7 failures were due to battery failure, 5 to bird deaths 1,000 s of km away from banding sites, and 13 to unknown causes (several of these birds were resighted). Nevertheless, the average battery life of these failed units was still 218 h ± 78 SD (and almost half of these failures were in the 2006 models, indicating to us that the technology was improving). The 34 units (57 %) that met or exceeded their battery life expectancy stayed on the air for an average of 690 h ± 107. Thus, we had good reasons to expect to be able to track the majority of Black-tailed Godwits for the majority of their battery life expectation of 600 h.

Mid-term implantation effects

In the subsequent year(s) after surgical implantation, nest site fidelity and territorial behaviour of the implanted

Black-tailed Godwits were not different from the comparison group, but annual survival and nesting propensity were reduced. Additionally, egg viability appeared affected by implanted transmitters, as we noted aberrant eggs in the experimental group in years following implantation. Performance of territorial behaviours such as displaying and copulating were not accurate indicators of whether implanted birds actually nested. Further, long lengths of stay and localized movements at breeding sites by implanted birds were not good indicators of breeding propensity; a finding that has implications for studies of remotely tracked birds. For example, in a study of Bar-tailed Godwits implanted with satellite transmitters in New Zealand and tracked to Alaska, it was assumed that birds had bred successfully if they were present at a breeding site for 7 weeks (Battley et al. 2012). In other studies, successful breeding by implanted birds is confirmed for Common Eiders and Canada Geese (Hupp et al. 2006; Fast et al. 2011), but in Black Oystercatchers (Johnson et al. 2010), two implanted females laid malformed eggs similar to those we found in the one Black-tailed Godwit nest reported here. Although, as in our study, viability could not be established due to depredation of the eggs, it is fair to assume that viability of such small eggs is likely low given that there is inadequate space for a normal-sized chick.

That malformed eggs may be a general concern with implanted large shorebirds is also supported by finding one in the nest of a Whimbrel that had been captured on the nesting grounds in Kanuti National Wildlife Refuge, Alaska, in 2009, implanted with a 26-g transmitter, and found nesting there in 2010 (C.M. Harwood, R.E. Gill, unpublished data). The egg measured 65.4 × 31.8 mm and had two thin-shelled, unusually bluish, depressions (ca. 5 and 15 mm diameter, respectively) on opposite sides of the egg. The average size of Whimbrel eggs in 2010–2012 at this location was $58.5 \pm 2.3 \times 41.2 \pm 1.1$ mm ($n = 76$). The egg was depredated before viability could be checked.

The fact that three species of shorebirds implanted with the same type of satellite transmitter have all laid malformed eggs strongly suggests mechanical obstruction of the oviduct by the transmitter. Given the successful migrations of implanted shorebirds, we suggest that it is not simply the mass of the transmitter or the percentage of body mass it represents, but the size and shape of implanted transmitters, and its location within the body, that causes the production of malformed eggs. This means that general lack of negative fitness effects of implanted bio-logging devices relative to externally mounted ones (White et al. 2013) requires qualification.

Many shorebirds currently are declining (e.g. International Wader Study Group 2003; Piersma 2007; MacKinnon et al. 2012). The kind of information gained from implanted satellite transmitters can be critical in establishing the importance of sites within migration networks (Battley et al. 2012), especially at a time when conservation actions can still be decisive (e.g. Yang et al. 2011; MacKinnon et al. 2012). In this framework, our results offer guidance for the use of coelomic implantation of tracking devices in wild birds. Specifically, all uses of such techniques should be carefully weighed against potential consequences for the individual and population. If the technique is used on breeding birds, it should be employed only during late incubation or at hatch. This will assure normal rates of hatching and likely fledging success, but in subsequent seasons there may be reduced adult survival, reduced nesting propensity and greatly reduced fertility. The application of the technique should be carefully considered for use among individuals of sensitive populations during any season. We do, however, believe that this application has use in obtaining important conservation information pertaining to migration routes, use of staging and stopover sites, migration phenology, and the extent of individual variation among these.

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