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ORIGINAL ARTICLE

Testing an attachment method for solar-powered tracking devices on a long-distance migrating shorebird

Ying-Chi Chan[1] · Maarten Brugge[1] · T. Lee Tibbitts[2] · Anne Dekinga[1] · Ron Porter[3] · Raymond H. G. Klaassen[4] · Theunis Piersma[1,4]

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Abstract Small solar-powered satellite transmitters and GPS data loggers enable continuous, multi-year, and global tracking of birds. What is lacking, however, are reliable methods to attach these tracking devices to small migratory birds so that (1) flight performance is not impacted and (2) tags are retained during periods of substantial mass change associated with long-distance migration. We developed a full-body harness to attach tags to Red Knots (*Calidris canutus*), a medium-sized shorebird (average mass 124 g) that undertakes long-distance migrations. First, we deployed dummy tags on captive birds and monitored them over a complete migratory fattening cycle (February–July 2013) during which time they gained and lost 31–110 g and underwent a pre-alternate moult of body feathers. Using each individual's previous year fattening and moult data in captivity as controls, we compared individual mass and moult differences between years between the tagged and reference groups, and concluded that the attachment did not impact mass and moult cycles. However, some birds shed feathers under the tags and under the polyester harness line commonly used in avian harnesses. Feather shedding was alleviated by switching to smoothed-bottom tags and monofilament harness lines. To field-trial this design, we deployed 5-g satellite transmitters on ten Red Knots released on 3 October 2013 in the Dutch Wadden Sea. Bird movements and tag performance appeared normal. However, nine tags stopped transmitting 11–170 days post-release which was earlier than expected. We attribute this to bird mortality rather than failure of the attachments or transmitters and suggest that the extra weight and drag caused by the tag and its feather-blocking shield increased the chance of depredation by the locally common Peregrine Falcons (*Falco peregrinus*). Our results demonstrate that species- and place-specific contexts can strongly determine tagging success. While captive trials are an important first step in developing an attachment method, field trials are essential to fully assess attachment designs.

Keywords *Calidris canutus* · Harness design · Satellite transmitter · Tag retention · Telemetry

Zusammenfassung

Test einer Befestigungsmethode für solargetriebene Peilsender bei einem langstreckenziehenden Watvogel

Kleine solargetriebene Satellitensender und GPS-Datenlogger ermöglichen das kontinuierliche und globale Verfolgen von Vögeln über mehrere Jahre. Was jedoch fehlt sind verlässliche Methoden, die Geräte an kleinen Zugvögeln zu befestigen, so dass (1) die Flugleistung nicht beeinträchtigt wird und (2) die Geräte in Zeiten erheblicher Körpermasseschwankungen, wie sie während des Langstreckenzuges auftreten, befestigt bleiben. Wir haben ein Ganzkörpergeschirr entwickelt, um Geräte am Knutt (*Calidris canutus*), einem mittelgroßen langstreckenziehenden

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✉ Ying-Chi Chan
yingchi.chan@nioz.nl

[1] Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, P. O. Box 59, 1790AB Den Burg (Texel), The Netherlands

[2] US Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage AK 99508, USA

[3] 800 Quinard Court, Ambler PA 19002, USA

[4] Animal Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands

Watvogel (durchschnittliche Köpermasse 124 g), zu befestigen. Zunächst haben wir Geräteattrappen bei in Gefangenschaft gehaltenen Vögeln eingesetzt und die Tiere über einen gesamten Zugzyklus hinweg beobachtet (Februar bis Juli 2013). In diesem Zeitraum gewannen und verloren sie 31–110 g an Masse und machten eine Pränuptialmauser der Körperfedern durch. Für jedes Individuum verwendeten wir die in Gefangenschaft gewonnenen Daten zu Fettreserven und Mauser aus dem vorherigen Jahr als Kontrolldaten und verglichen dann die individuellen Köpermasse- und Mauserunterschiede zwischen den Jahren von besenderten Tieren und unbesenderten Referenztieren. Wir fanden keinen Einfluss auf Körpermasse- und Mauserzyklen. Einige Tiere verloren allerdings Federn unter den Geräten und unter den bei Vögeln üblicherweise verwendeten Polyester-Geschirrschnüren. Der Federverlust wurde durch das Verwenden von Geräten mit glatter Unterseite und Monofilament-Geschirrschnüren gemindert. Um dieses Design im Freiland zu testen, statteten wir zehn Knutts mit 5 g schweren Satellitensendern aus und ließen sie am 3. Oktober 2013 im niederländischen Wattenmeer frei. Die Bewegungen der Vögel und die Geräteleistung erschienen normal. Neun Sender stellten allerdings das Senden 11–170 Tage nach der Freilassung der Tiere ein, was früher als erwartet war. Wir führen dies nicht auf das Versagen der Sender oder ihrer Befestigung zurück. Vielmehr vermuten wir eine höhere Mortalität der Vögel aufgrund einer durch das zusätzlich Gewicht und den zusätzlichen Luftwiderstandes durch das Gerät sowie dessen die Federn abdeckenden Schirm erhöhten Prädation durch den lokal häufigen Wanderfalken (*Falco peregrinus*). Unsere Ergebnisse zeigen, dass der art- und ortsspezifische Kontext den Besenderungserfolg deutlich beeinflussen kann. Während Vorversuche an in Gefangenschaft gehaltenen Vögeln einen wichtigen ersten Schritt beim Entwickeln einer Befestigungsmethode darstellen, sind Freilandversuche essenziell, um Befestigungsdesigns vollständig zu beurteilen.

Introduction

In the past decade, satellite telemetry and GPS (Global Positioning System) tracking studies have revolutionized our understanding of local movements, dispersal and migration patterns (Tomkiewicz et al. 2010; Bridge et al. 2011). Satellite transmitters, also called platform transmitter terminals (PTTs), send signals at interval of 60–65 s during pre-programmed transmitting periods. The Argos receiving system (CLS, Collecte Localization Satellites, http://www.argos-system.org) collects the signals via satellite, and a bird's position is subsequently calculated. GPS tags receive signals from a network of GPS satellites and store the position data within the device. Depending on tag design, tag retrieval, remote downloading, or data transmission via satellites are required to download the data (for reviews, see Bridge et al. 2011; Klaassen et al. 2014). Both satellite and GPS technologies enable animal tracking at a global scale. Solar-powered (i.e. rechargeable) satellite transmitters are now as small as 5 g (Microwave Telemetry), while solar-powered GPS data loggers are as small as 6 g (UvA-BiTS http://www.uva-bits.nl; Bouten et al. 2013), enabling multi-year tracking of small bird species.

Tracking devices can be implanted or externally attached (see Hooijmeijer et al. 2014), but, for solar-harvesting devices, external attachment is necessary. For external devices, the design components that facilitate charging (e.g. feather shields, elevating platforms) are important considerations. Since the early days of VHF radio tagging, various external attachment techniques have been developed. For shorebirds, gluing the radio tag onto the bird's back (Warnock and Warnock 1993) has been a preferred and very successful method. For example, 1.3- to 1.8-g glue-mounted radio tags have been used to successfully track movements of Red Knots (*Calidris canutus*) in both the Dutch Wadden Sea (van Gils and Piersma 1999; Nebel et al. 2000; van Gils et al. 2005, 2006; Spaans et al. 2009) and in northwest Australia (Battley et al. 2005; Rogers et al. 2006). Gluing is a relatively simple process that can be completed at the banding site, and birds will shed the tag at or before the next moult. However, glue-mounted tags weighing more than 2.0 g are likely to be shed prematurely, within a few weeks after deployment, especially in hot and humid conditions (Y.C.C., T.P., T.L.T., C. Hassell, personal observations). Since most studies using satellite transmitters and GPS tags seek to track local movements and migration over a few months or years, developing methods for long-term attachment is necessary. Leg-loop harnesses (described in Rappole and Tipton 1991) have been applied in some long-legged shorebird species (Sanzenbacher et al. 2000; Watts et al. 2008; Page et al. 2014), but this harness design is unsuitable for more compact species such as the Red Knot. This is because Red Knots have no external 'knee', so a leg-loop harness slips off the legs within seconds after deployment, no matter whether the harness is made of fixed or elastic materials (T.P. and R.P., personal observations). An alternative is a full-body harness consisting a neck and a body loop, first described by Brander (1968). This design has been used for attaching satellite and GPS tags on several bird taxa, such as raptors (e.g. Fuller et al. 1998; Hake et al. 2001; Klaassen et al. 2010), waterfowl (e.g. Roshier and Asmus 2009), gulls (e.g. Klaassen et al. 2012; Shamoun-Baranes et al. 2011) and Crab Plovers *Dromas ardeola* (R. Bom, personal communication).

An important issue confronting attachment in many long-distance migrants relates to their dramatic changes in body mass before and after migratory flights. For example, the body mass of Red Knots increases up to 190 % before making long-distance migratory flights (Piersma et al. 1995, 2005), resulting in a marked change in circumference. For small migratory bird species that cannot wear a leg-loop harness, no harness designs have been developed to cope with these regular, substantial changes in bird size. A potential solution is fitting a full-body harness with dimensions larger than the maximum size the bird could attain; such a harness would need to fit loosely but securely when a bird is not at its peak mass. We set out to investigate the effects of full-body harnesses on Red Knots in captivity and subsequently in a field setting, in preparation for a world-wide tracking study of the migratory behaviour of this species (see Piersma 2007 for context).

We used an iterative refinement approach involving two captive trials. Our first captive trial lasted for 4 months in spring and tested the effect of this attachment design on bird behaviour, body mass and moult cycles. The individual Red Knots we instrumented show seasonal cycles in mass and moult, with a mass peak in May to June (Piersma et al. 1995). Since their mass and moult cycles are highly repeatable between years (J. Karagicheva, M.B., T.P., unpublished data), we were able to compare an individual's weekly body mass and plumage score between years in both tagged and untagged birds to assess effects of tag attachment.

During the first trial, we observed problems of irritation associated with wearing the harness. We examined the possible causes of these problems and came up with further refinements of the attachment technique, and then conducted a second trial to test our improved design on a subset of the captive birds. On the basis of improved results from the second trial, we deployed 5-g solar-powered satellite transmitters on ten free-ranging Red Knots to test field performance of our attachment method.

Methods

Testing the effect of the attachment on mass and moult cycles

Study animals and housing

The Red Knots used in the captive trials were caught in the Dutch Wadden Sea between 1994 and 2004, and since then have been held in captivity at the NIOZ Royal Netherlands Institute for Sea Research on Texel, the Netherlands. The birds are housed in aviaries of approximately 4 m × 2 m and 2.5 m high, in groups of 6–7 birds per aviary. During the harness trials, birds were fed ad libitum with protein-rich trout pellets (Produits Trouw, Vervins, France). Each aviary contained a tray with running fresh water for the birds to bathe and drink, and a patch of mudflat with running salt water where the birds could probe the sediment.

Attachment design and deployment

Using a 3D printer, we produced Acrylonitrile Butadiene Styrene (ABS) dummy tags of 24 × 14 × 8 mm, weighing 3.5 g each, in the same shape of the 5-g satellite transmitters manufactured by Microwave Telemetry that we intended to use in the field. We glued a 3-mm layer of neoprene to the underside of the dummy tags to give them a higher profile in anticipation that the real tags would need this extra height to prevent feathers from covering the solar panels (as observed in Cohen et al. 2007). Our first harness was made of inelastic braided polyester line (1.5 mm wide; Kivikangas Oy, Finland) that has been used successfully in many tagging studies of raptors (R.H.G.K., personal observations). It consisted of a neck loop and a body loop that went underneath the wings and in front of the legs (Fig. 1). We first constructed the neck loop that measured 55–65 mm when stretched by a calliper placed within the loop, and then attached this loop to the front end of the tag. Then, the neck loop was put over the bird's head and neck. The tag sat on the bird's back and was held in place while the body loop was constructed, for which we slid the two lines underneath the wings, passed them through the mounting loops at the tag's rear end, and tied them to the tag. In our first deployment session, to ensure the body loop was not too tight, we placed a finger between the tag and the back of the bird when tightening the 'rear knot' (see Fig. 1). However, we found that it was difficult to tell the actual size of the body loops when tightening it on the bird, therefore in later sessions, we drew a mark on each of the harness lines at 120 mm from the 'breast knot' (Fig. 1), and tightened the rear knot at 15–25 mm (to create variation in body loop widths) away from the marks. The exact size of the body loop was measured after removing the harness at the end of the trial. We deployed the dummy tags with harnesses on 1 Red Knot on 5 November 2012 during a pilot trial, and on 22 Red Knots between 25 February 2013 and 7 March 2013. At deployment, the dummy tag with harness weighed about 3 % of the body mass of the birds.

Monitoring bird's response to the attachment

Bird response was assessed by observing their behaviour through the one-way aviary window at least 3 times a day for the first 72 h after tagging; afterwards, they were checked daily and weighed weekly. We noted if abnormal behaviours (e.g. excessive preening, movements to remove the tag and harness) occurred. From late April onwards, we observed that a few birds had shed feathers beneath the tag

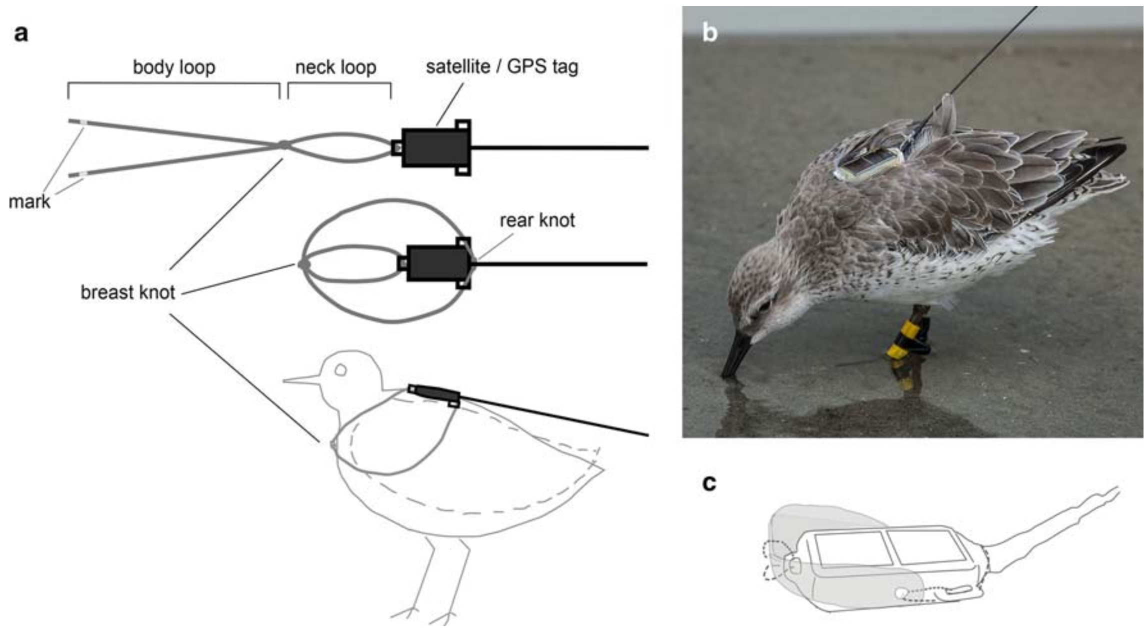

Fig. 1 **a** The loose neck-body loop harness attached to Red Knots (*Calidris canutus*). *Top* the harness before deployment, where a mark at 120 mm from the breast knot is drawn on each side of the line forming the body loop. *Middle* dorsal view of the harness after deployment. *Bottom* the position of the harness on a Red Knot. **b** A Red Knot with a 5-g solar satellite transmitter deployed. **c** A small transparent plastic shield (in *grey* in the diagram for illustration purposes) was tied to the transmitter to prevent feathers from covering the solar panels

and on the breast especially around the area of the 'breast knot', to the extent that the skin had become bare. Subsequently, during weekly handling, we closely examined birds for skin irritations and scored the degree of feather shedding under the tag and on the breast under the harness lines (quantified by a score from 0, no feather shedding, to 3, large area of bare skin similar in size to the surface area of the tag). As feather shedding could have been related to constant rubbing of harness/dummy tag on the feathers, we hypothesised that the tighter the harness, the more feathers the bird would shed. Using Poisson regression, we tested whether (1) the maximum body mass, (2) the length of the neck loop and (3) the length of the body loop predicted the degree of feather shedding (quantified by a score from 0, no feather shedding, to 3). Statistical analysis was conducted in R v.3.01 (R Core Team 2013).

Six birds that were clearly irritated by the harness lines in the first few weeks after deployment were relieved of their harnesses by 1 April. Together with five birds that never wore harnesses, they served as the reference group ($n = 11$ birds) in analyses of timing and magnitude of mass and moult changes in the birds that wore harnesses for 4 months until the end of the trial on 8 July 2013 ($n = 13$).

Body mass cycle

To determine if the harness attachment prevented birds from following normal fattening patterns, we calculated the between-year differences in mass by week of individuals between 2012 and 2013, from the start of April (week 14), which was the onset of mass increase, until the end of the trial on 8 July (week 27). This weekly mass difference was then compared between the reference group and the harness group by two-way ANOVA.

Moult cycle

During the weekly handling, we scored the amount of breeding plumage (from 1, complete winter plumage, to 7, complete breeding plumage using methods described in Piersma et al. 2008). The plumage score could differ by one score point between observers scoring the same bird, or within observers scoring the same bird again on the following day; therefore, a difference of one point would not indicate plumage differences. To assess whether between-year differences in the timing of plumage gains were different between the reference group and harness group, we visually examined each individual's plot of plumage score against time.

Testing alternative attachment materials

In an attempt to alleviate the feather shedding and skin irritation problems observed in the first trial, we produced a new batch of ABS dummy tags. To prevent feather shedding underneath the tag, we did not glue neoprene on the underside surface of the tag; instead, we smoothed the surface by wiping it with a solvent (Tangit PVC-U/C/ABS Cleaner). Two other types of harness lines were tested: (1) multifilament Dacron (Micron) fly line backing (0.5 mm diameter; Cortland, USA) and (2) monofilament nylon fishing line (0.5 mm diameter; Albatros, Netherlands). For the nylon harness, we wrapped a heat-shrink tubing around the 'breast knot' (Fig. 1) so that it was less irritable to the bird, and prevented the 'breast knot' from loosening.

We applied these attachment designs to birds that had their harnesses removed during the spring trial due to irritation. Birds were checked by watching their behaviour through the one-way aviary window at least three times a day for the first 72 h after tagging; afterwards, they were checked daily and weighed weekly. During the weekly handling, we checked for any feather shedding beneath the tag and the harness lines.

Initially, we applied the monofilament nylon harness to two birds on 4 July 2013, and then on 24 July we equipped one bird with the monofilament nylon harness and three with the Dacron harness. Three more birds were equipped with monofilament nylon harness on 30 July, two of which had worn the Dacron harness but had it removed (see "Results"). From 30 July onwards, six birds in total were wearing the monofilament nylon harness, and this second trial ended on 18 September 2013.

Field test

Five second calendar year and five adult Red Knots (*C. c. islandica*) were caught in Richel (53.3°N, 5.1°E) on 6 September 2013 and transported about 40 km to the NIOZ aviary facilities. The housing conditions were the same as described in "Study animals and housing". By housing the new birds with birds that have been kept in captivity for years, the new birds learnt to feed on trout pellets within 2 days, and were fed ad libitum.

We deployed satellite transmitters (5.0 g solar PTT; Microwave Telemetry) on these 10 birds on 27 September 2013, using a harness constructed with monofilament nylon line as described above. We tied a small transparent plastic shield with a height of 7–8 mm around the front of the transmitter (Fig. 1c) to block feathers from covering the solar panels. The tag with shield and attachment weighed c. 3.1–4.0 % of body mass at release. After deployment, we kept the birds for 7 days in the aviaries so they could acclimate to the harness and tag, and we could monitor their condition.

We released the birds on 3 October 2013 at mudflats at De Schorren, Texel (53.1°N, 4.9°E), 25 km from the capture site. We chose this location over the capture location because it is easily reached by car from the NIOZ aviaries, thus minimizing stress caused by transportation; moreover, a Red Knot's wintering home range is much wider than 25 km (Piersma et al. 1993; van Gils and Piersma 1999; Spaans et al. 2009) and birds released at De Schorren in the past were subsequently resighted at Richel and locations further away (NIOZ resighting database).

Transmitters were programmed to operate on a duty cycle of 10 h on and 48 h off and data were collected via the Argos data collection system. Received data were converted to locations which were classified according to accuracy (CLS 2015); generally four or more messages received during a satellite overpass resulted in a 'standard' location with an estimated radius of error, whereas fewer messages, or overpasses low on the horizon, resulted in an 'auxiliary' location without an estimate of accuracy. The transmitters also measured battery voltage.

We evaluated the field performance of our attachment method by assessing the duration of tag retention (as determined by length of satellite contact with the tags) and its effect on tracked bird movements as compared to what is known of typical movements of Red Knots in the Wadden Sea (van Gils and Piersma 1999; van Gils et al. 2006). We also assessed patterns of battery voltage and the ratio of standard to auxiliary locations, since these variables reflect how well a tag is positioned on a bird, i.e. how well it is receiving sunlight and how well the antenna is oriented. Regular field observations were also conducted in a section of the Wadden Sea for an unrelated mark–resighting project, in which the tagged Knots were searched for and recorded.

Results

Testing the effect of the attachment on mass and moult cycles

Harness effects

When captive birds gained weight, harnesses became tighter and the tags moved upwards along the back. However, with the exception of one bird, a small gap always remained between the bird's back and the tag even when birds were at their maximum masses. For the exception, the neck loop circumference was 132 mm (widest of all birds) and body loop was 145 mm; the harness was so tight that we had to remove it before the end of the trial. A different bird repeatedly put one foot into the body loop which was 189 mm; however, it was behaving normally otherwise so we did not remove the harness.

In the course of the experiment, but mainly early on, the harnesses were removed from ten birds which were clearly irritated by the inelastic braided polyester line and/or the tag. These individuals either got their bills stuck in the harness multiple times as a result of intense preening around the harness (seven birds); or the harness became very tight during fattening up in May (one bird); or many feathers were shed beneath the tag and on the breast (two birds). For the remaining 13 birds, their harnesses were completely covered by feathers within a few days as the birds preened the harness lines down towards their skin. These birds went through the cycle of fattening up and slimming down from April to June without obvious problems and were the ‘harness group’ in the analysis of the body mass and moult cycles.

Feather shedding

The amount of feathers shed in the 13 birds in the harness group varied between individuals, and even within individuals; some individuals shed feathers on the back but none on the breast, or vice versa. In mid-June, new feathers started to grow on the bare parts, and by mid-July, all bare parts were covered by new feathers. We did not find any associations between the lengths of the neck and body loops, or the maximum body mass, with the degree of feather shedding at the back or the breast (all $P > 0.1$).

Body mass cycle

Body masses of all captive birds increased from early April onward and peaked in mid- to late May (Fig. 2a). The pattern was similar in both years, but in 2013 the decline in masses occurred earlier than in 2012; thus, the mass differences ($mass_{2013} - mass_{2012}$) in weeks 26 and 27 were significantly more negative than in other weeks ($t_{week26} = -4.725$, $t_{week27} = -6.405$, both $P < 0.001$; Fig. 2b). The individual mass differences were the same between the harness group and reference group for all weeks (ANOVA, $F = 1.7885$, $P = 0.1822$; Fig. 2b).

Moult cycle

Starting in March, plumage scores increased and reached a plateau in early May; birds then kept their breeding plumage until the end of the experiment. No differences in plumage progression were detected in the majority ($n = 22$) of the birds (Fig. 3). However, for one bird, the increase in plumage score was faster in 2013 than in 2012, and for a second bird, the maximum plumage reached was higher in 2013 than in 2012 (birds 427 and 609 in Fig. 3). Both birds belonged to the harness group.

Testing alternative attachment materials

Within the first 24 h of wearing the Dacron harness, all three birds had their bills stuck multiple times and we had to remove the harnesses. Three of the six birds wearing the

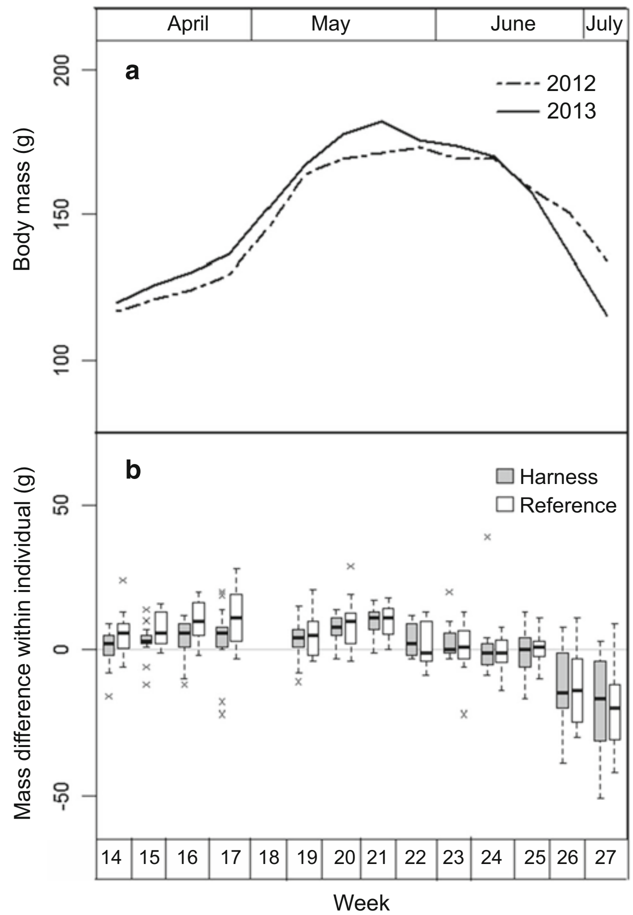

Fig. 2 **a** Body masses of captive Red Knots carrying dummy tags in 2013 from week 14 (2 April 2012; 1 April 2013) to 27 (2 July 2012; 1 July 2013). **b** The weekly within-individual mass difference ($mass_{2013} - mass_{2012}$) of the harness group (*grey*) and the reference group (*white*)

monofilament nylon harness also stuck their bills in the harness: for one bird this occurred once, and for another bird twice, both within the first 24 h; for a third bird, this was observed once at 53 h after deployment. We did not detect this behaviour again for the remaining 7–10 weeks of the trial. All six birds spent almost no time preening around the monofilament harness, in contrast to the intense preening exhibited when they were wearing harnesses made of the multifilament braided polyester or Dacron. When the trial ended, the birds had almost completed their contour feather and wing moult, and none of these birds showed any feather shedding on their backs or breasts.

Field test

During their 1 week in captivity, none of the 10 field-trial birds stuck their bills into the harness. Of the 10 tags, we lost contact with 2 in the first month: the last signals were obtained 9 and 19 days after release. From December

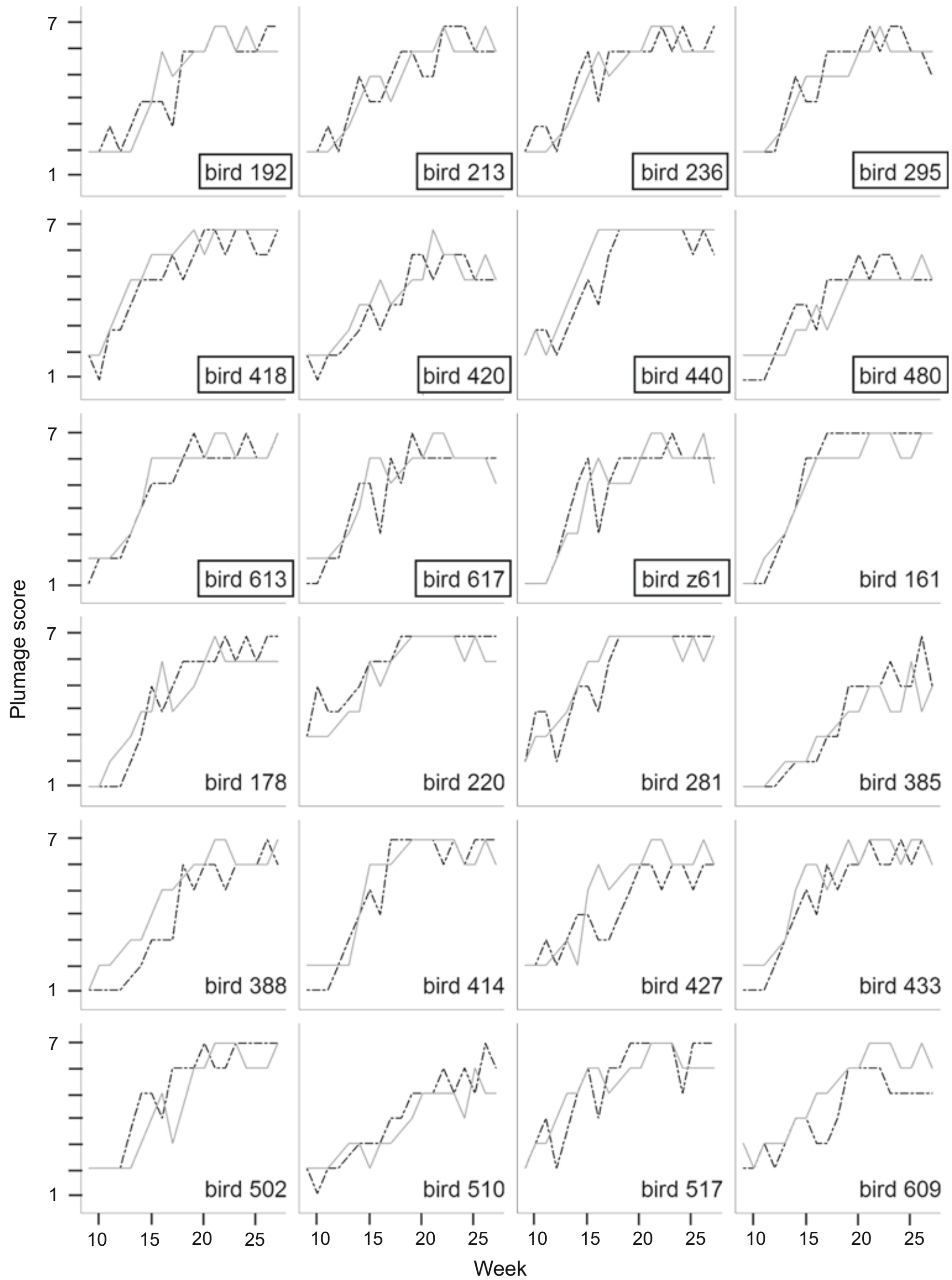

Fig. 3 Plots of individual plumage scores in 2012 (*dotted line*) and 2013 (*grey line*) by week. Bird IDs belonged to the reference group are enclosed in *rectangles*

onwards, we lost contact with more tags (Fig. 4), and by mid-March we were only receiving continuous data from one tag (which is still transmitting from a live bird as of July 2015). Median retention time for the nine tags was 65 days. A few signals were received from three tags at certain times afterwards, but no locations were generated, therefore it is doubtful whether these signals came from tags on live birds; they also could have been parity errors. Battery voltage and number of locations per duty cycle dropped from October through December and then increased gradually from January onwards (Fig. 4), while the percentage of 'standard quality' locations (Argos location classes 3, 2 and 1) received per duty cycle ranged from 23 to 37 %. On average, we received 2.8 standard quality locations per duty cycle of 10 h.

Two birds moved more than 300 km from the release site shortly after release: one bird travelled over 300 km to mudflats around the islands Föhr and Sylt (54.7°N, 8.6°E)

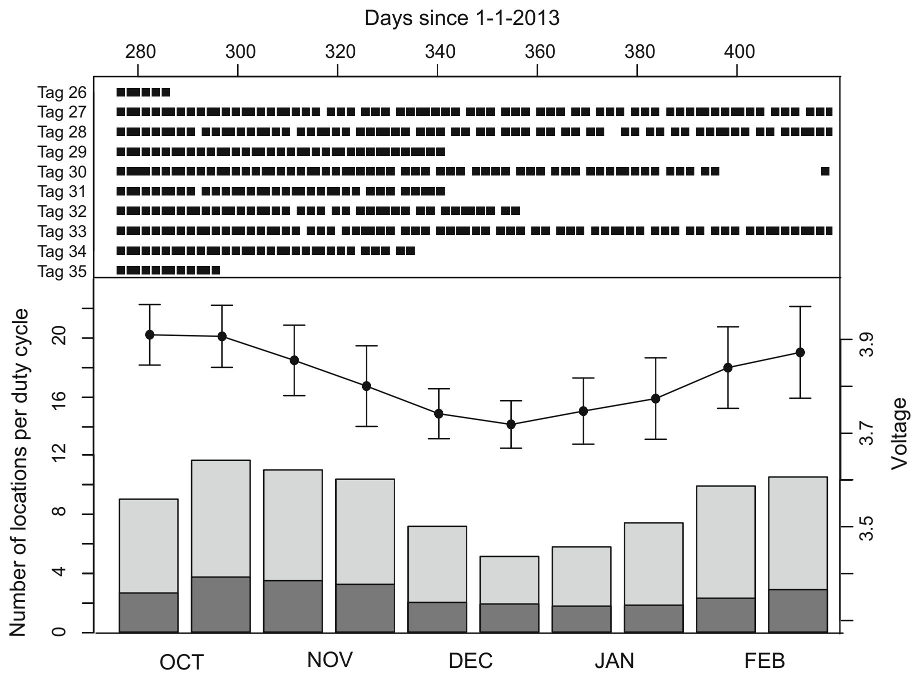

Fig. 4 (*Upper graph*) signals received from each tag per duty cycle, (*middle line*) mean battery voltage within the first 2 h of a duty cycle and (*lower bars*) number of standard (*dark grey*) and all locations (*whole bars*) per duty cycle per half-month (first half, 1–15, second half, 16 onwards), from satellite-tagged Red Knots released on 3 October 2013 at De Schorren, Texel (53.1°N, 4.9°E) in the Wadden Sea

in northern Germany within 2 days of release, and another bird flew 340 km to the Wash (52.9°N, 0.1°E) in England within 9 days. Most other birds remained in the Wadden Sea within 150 km of the release site. As the area where the tagged Red Knots occurred is large and mostly difficult to access (e.g. Piersma et al. 1993), we had only two field observations of tagged birds, and in both cases the bird had normal appearance and behaviour.

Discussion

Through our first and second captive trials, we developed a method of attaching small solar-powered tags onto Red Knots that showed more potential for successful field application than any other method had shown previously. Provided that the harness was constructed large enough, it could accommodate the seasonal changes in body size of Red Knots. By using suitable harness line material, any skin irritation to the birds was minimal. We first discuss several aspects in attachment methodology that we learnt from our captive trials. Then, based on the field test results, we discuss how attachment design, tag properties, and the specific 'environment' that the birds experience jointly determine the success of a field application.

Harness construction

Before actual deployments using our harness, trials with captive birds are necessary to determine the appropriate size for each (sub-) species. Although wider loops will prevent the harness from getting too tight when a bird fattens, a neck loop that is too wide will not lie on the bird's shoulder and might fall sideways, possibly affecting wing movement. If the body loop is too wide, there is a risk of the bird putting its foot into the loop; moreover, the tag will be lower on the bird's back away from the centre of gravity. Thus, we determined that the suitable harness size for *islandica* Red Knots is a neck loop of 100–110 mm in circumference, and a body loop of 160–170 mm. Visible marks at equal distances from where the 'rear knot' is tied (in this case, about 120 mm from the 'breast knot') are very useful for checking whether the two sides of the body loop are symmetrical during deployment (Fig. 1). Symmetry of the loops will ensure that the tag sits on the central axis of the bird and that the weight load is balanced. As birds preened the harness so that it is trapped by feathers, the harness position on the body was stabilised and the harness sat close to the skin; therefore, there is very little risk of the harnesses getting tangled with vegetation.

Materials

We reasoned that the feather shedding we observed was caused by the multifilament polyester lines and the neoprene layer constantly rubbing against the tiny barbs and hooks and bases of feathers which are connected to nerves. This resulted in irritation to birds (as manifested in increased preening) and wearing of the feathers. Our second trial tackled this particular problem by testing materials that would minimize irritation. Monofilament nylon line had a smooth surface and did not appear to rub against feathers as much as multi-threaded Dacron and polyester lines. We found it to be the least irritating among the three materials we tested. Although tubular Teflon Ribbon is the most commonly used material for harnesses (e.g. Klaassen et al. 2012; Kesler et al. 2014; Page et al. 2014), we did not test this material because of its extra weight and thickness (thinnest available Teflon thread is 3.5 mm width, weighing 1.0 g per 40 cm, whereas the nylon line weighs 0.1 g per 40 cm).

In many satellite/GPS tag deployments, a layer of neoprene is attached to the underside of the tag (T.L.T., K. Camphuysen, personal communication), to (1) insulate the tag from the bird's back; (2) raise the height of the tag so that the solar panels are not covered by feathers; and (3) act as a 'padding' so that the bird feels more comfortable. However, our first trials showed that this material irritated birds. K. Camphuysen (personal communication) also observed that Herring Gulls *Larus argentatus* constantly pecked and eventually removed the neoprene. While neoprene could still be useful for tags attached by gluing onto the skin, a smooth surface seems more suitable for tags attached with our harness design for Red Knots.

Deployment protocol

The chance of birds trapping their bills in the harness was related to the type of harness material used, as some materials were more irritating to birds than others. This response was very individualistic—some individuals preened furiously around the harnesses which provided many more opportunities for the bill to become trapped. Even for the nylon monofilament lines, the least irritating material, the chance of getting stuck was high during the first 24 h of wearing the harness (2 of 6 birds). This problem still persisted when using a flexible material such as an elastic nylon line and silicon-rubber line (Y.C.C. et al., unpublished data). Based on these observations, we strongly recommend keeping birds in captivity for at least 24 h prior to release so that they can acclimate to the harness and tag in a safe environment. Then, those individuals that do not appear suitable for satellite tagging, i.e. those that are stressed or repeatedly putting their bills into the harness, can be identified and their tags removed. It follows that tagging should not be done for species that could become too stressed in captivity, or when this observation period is not possible, e.g. the breeding season when birds need to care for young. As keeping birds in captivity requires a lot of effort and can be carried out adequately only by experienced bird handlers, some researchers might opt to skip this procedure; however, we feel that in such cases they would be introducing an avoidable source of mortality by including some 'unsuitable' birds. Although the risks get smaller with time, it is still possible that birds will get stuck after the first 24 h, so we further recommend a longer assessment period (e.g. 7 days for our field trial) in those situations where the infrastructure is suitable for keeping birds and the tagged species can be maintained in good condition. Finally, keeping extra birds in captivity along with the tagged birds helps distinguish tag-induced behaviours from captivity-induced behaviours, thus helping to focus the assessment.

Field performance

Initially, the full-body harness appeared to have minimal negative effects on free-ranging Red Knots as all birds moved between tidal basins of the Wadden Sea, and two birds performed long-distance flights within the first 2 weeks in the wild. These latter movements were much longer than the typical daily flights between roosting and foraging areas performed by Red Knots in the region (van Gils and Piersma 1999; van Gils et al. 2006) and would require considerable energy expenditure.

The voltage levels of the transmitters closely tracked the winter decrease/spring increase in day length and sun angle, indicating that the tags were positioned well and that feathers were not interfering with charging. The ample number of total and standard class Argos locations also indicated that the antennas were positioned well. Overall, the percentage of standard class locations (31 % of locations were standard class) was sufficient to describe wintering movements of Red Knots in good detail even though it was lower than the published figures of 55 % in Marbled Godwits (*Limosa fedoa*) with 9.5-g tags (Olson et al. 2014) and 58 % in Long-billed Curlews (*Numenius americanus*) with 18-g tags (Page et al. 2014).

We lost contact with nine of the ten transmitters 10 days to 5 months after releasing the birds into the wild. We considered insufficient battery charging as an unlikely cause, since we did not receive signals from the lost tags when battery charge began increasing in the functioning tags in spring. We doubt that birds could have escaped their harnesses, since none ever slipped a harness during the 4-month captive trial and the harnesses were unlikely to break. Although malfunctioning of a small percentage of transmitters has been observed in some studies (R.H.G.K., Y.C.C., T.L.T., C. Hassell, unpublished data), it is unlikely that all nine of the missing transmitters failed. Transmitter failure is usually confirmed by resighting a live bird wearing a non-transmitting device, but the low resighting rate of 0.26 year^{-1} of colour-marked Red Knots in the Dutch Wadden Sea (Rakhimberdiev et al. 2015) precluded us from using resightings to assess transmitter failure. If the birds died and their transmitters were subsequently 'lost' in sea, mud or vegetation, their survival rate would have been lower than the wild population's average survival rate of 0.81 $year^{-1}$ calculated from mark–resighting data of colour-ringed individuals from 1999 to 2013 (Rakhimberdiev et al. 2015). A likely explanation of the high mortality rate of our tagged birds is that they experienced high predation. In the Wadden Sea, predators like Peregrine Falcon are common in winter (van den Hout 2010, p. 59). The tactic knots use to escape predation by falcons is persistent coordinated aerial escape flight manoeuvres performed by the whole flock (van den Hout et al. 2010). Even if the extra load and drag from the 5 g transmitter is relatively small, any slight handicap in maneuverability experienced by a tagged bird could have led to a higher probability of them being singled out of the flock into a one-to-one chase with a raptor and being killed.

When determining the suitability of tags, much emphasis is placed on tag mass (e.g. the 5 % rule in Kenward 2001), whereas tag size and associated drag are often not considered (Barron et al. 2010). As turning maneuverability is determined by weight and drag (van den Hout et al. 2010), a tag's effects on these aspects need to be considered such that agility is not significantly hampered. Although the feather-blocking shield likely contributed to the overall good performance of the transmitters, the shield rises an extra 3–4 mm above the tag which significantly increases the drag coefficient (Pennycuick et al. 2012). Consequently, we do not recommend using the shield when tagging Red Knots or other species where flocks are attacked at high rates by aerial predators and individuals must successfully evade them (van den Hout et al. 2010). Experiments to examine the effects on aerodynamics of different tag sizes, shapes, and varying antenna length and angle would greatly aid future tag design. These experiments would also help researchers balance the risk of negative effects on survival caused by the increased drag of tags or feather-blocking shields against benefits of data collection during months or situations with low solar radiation.

In our study, deleterious effects of the tagging, beyond what could be tested in captivity, appeared to be determined by species and environmental factors in the wild, including the presence of certain species of predators. The loss of so many of the tagged birds in the field, after using what we thought was a suitable tag attachment method, points to the need for further refinement of our methods for Red Knots. Given that the harness worked well in the captive trials, and if the missing birds were indeed predated, the reduced agility caused by a large tag was limiting the success of the field applications. If this is indeed the case, our harness design may currently be suitable for attaching 5-g satellite transmitters to larger shorebird species with Red Knot-like body structure, or for studies of Red Knot-sized shorebirds in areas with few aerial predators.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This study was carried out under protocol DEC-NIOZ 12.04 and DEC-NIOZ 13.01 approved by the Animal Experiments Committee under the Royal Netherlands Academy of Arts and Sciences (KNAW).

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