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Geolocator wetness data accurately detect periods of migratory flight in two species of shorebird

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While the principal use of light-recording geolocators is to determine geographical locations of migratory birds, supplementary wetness data have been used to refine estimates of minimum flight duration, on the assumption that a wet logger indicates the bird is on the ground. We provide a test of this assumption, by comparing wetness values against directly observed migratory departures of logger-equipped Bar-tailed Godwits *Limosa lapponica* and Red Knots *Calidris canutus* from the Manawatu River Estuary, New Zealand. Loggers recorded wetness every 10 min (Biotrack MK4093 and MK5093) or every one or four hours (Migrate Technology C65K). We retrieved loggers from 41 godwits from 2008–2014 and from seven Red Knots in 2013–2014 for which we had corresponding departure information; in total there were 51 departures of godwits and seven of knots that we could match to actual departure times (this included multiple years for some godwits). Overall, 10-min wetness data were very accurate for both godwits and knots (median estimated departure times were 14 min and one min later than true departure, respectively), as were the 60-min and 240-min loggers on godwits if corrected by the wet counts that are recorded within measurement intervals (medians of 16 min earlier and 8 min earlier, respectively). These longer-interval loggers were still reasonably accurate without this adjustment (medians of 37 min and 74 min later, respectively). There was substantial variation between individuals and logger types, with 10-min loggers going dry up to 148 min (godwit) or 55 min (knot) earlier than true departure, while the 60-min and 240-min loggers recorded wetness up to 142 min or 124 min later than true departure (or 195 min or 232 min later, if unadjusted). Some of this variation simply reflects the interval over which wetness is recorded, but bird behaviour and/or logger performance must play a role in some cases (e.g. the logger going dry before departure or remaining wet after departure). Given observed bird behaviour upon arrival after migration (feeding on wet tidal flats), the wetness recording of geolocators is likely to give an accurate estimate of migratory flight duration, at least for species that frequent wet, particularly marine, habitats.

Keywords

shorebird

migration

geolocation

tracking

conductivity

Scolopacidae

Charadriiformes

INTRODUCTION

Small light-sensitive geolocators are now commonly used to study movements and migration timing of small to medium-sized birds including shorebirds (e.g. Conklin *et al.* 2010, Minton *et al.* 2011, Bates *et al.* 2012, Johnson *et al.* 2012, Hedenström *et al.* 2013, Lanctot *et al.* 2016). While generally adequate for describing large-scale movements, they provide only twice-daily estimates of locations, so the accuracy of estimating migratory flight durations is inevitably low, given both the geographical error around departure and arrival locations and the uncertainty about when a bird actually departed or arrived (with positions generated only every 12 hr; e.g. Johnson *et al.* 2012). Recently, researchers have attempted to reduce the uncertainty around flight durations (and hence calculated travel speeds) by using the wet-dry data that some loggers also record. In the words of Minton *et al.* (2011): "*To estimate the time of departure and arrival for each leg of migration we used the conductivity output of the geolocators – which effectively provides a record of whether the bird is in contact with seawater every 10 minutes. We made the well-founded assumption that if a bird was in contact with seawater it was not flying and either had not departed or had already arrived; we also made the not-quite-so-well-founded assumption that when a bird was continuously out of contact with seawater it was flying. The conductivity record therefore provides a measure of the maximum possible flight time which for birds that use salt water habitats at both ends of a flight might be actual flight time.*" This suggestion has been adopted by other researchers (e.g. Niles *et al.* 2012, Tomkovich *et al.* 2013). However, we are unaware of any explicit tests of these assumptions using independent observations of logger-equipped birds.

We are in a unique position to be able to test the assumption that a sustained drop in conductivity by a logger when becoming dry represents a departure on a migratory flight. At our main study site, the Manawatu River Estuary in New Zealand, individually-marked Bar-tailed Godwits *Limosa lapponica* and Red Knots *Calidris canutus* have been monitored on a daily basis during the northward migration period (March–early April) since 2008 (godwits) and 2013 (knots). Daily roll-calls enable the departure dates of most godwits to be determined, but many marked birds (in some years most) are directly observed setting off on migration (Conklin & Battley 2011). Our ability to determine exact departures of knots is slightly lower, but for both species a number of geolocator-tracked birds were observed at the time of departure, enabling us to compare true and inferred departure times. In this paper we compare actual and conductivity-estimated departure times of godwits and knots, to evaluate the accuracy and precision of the estimated departure times.

METHODS

Godwits and knots were studied at the Manawatu River Estuary, southern North Island, New Zealand (40.47°S, 175.22°E). This is a small estuary with small populations of birds (usually <250 godwits and <130 knots) that typically roost in just one or two easily observed spots. At this site, approximately 30–35% of each species are individually marked with colour-bands or field-readable engraved flags. Intensive fieldwork (all by JRC) during March–early April each year recorded marked individual godwits on a near-daily basis. Due to the conspicuous premigratory behaviour shown by godwits (vocalisations, bathing, group formation, and low circling flights), groups of prospective migrants could be checked on the ground for marked birds, with confirmation of individual departures being possible through photography of birds taking off or through subsequent ground checks (Conklin & Battley 2011). Knots are more itinerant than godwits and more prone to unexplained absences, so the certainty of departure date is slightly lower for that species. In some cases a bird was assumed to have departed in a specific flock, despite not having been directly observed, if the daily records indicated it had left and only one flock of birds was documented having departed.

Geolocators were deployed on godwits in 2008–2009 and 2013–2014, and on knots in 2013 (see Table 1 for details). Units were mounted on the tibia, on either colour-bands (godwits; Conklin & Battley 2010) or flags (knots; see Fig. 2). British Antarctic Survey (BAS, UK) and Biotrack (UK) loggers are essentially similar units, which recorded salt water contact every 10 minutes (on a 0–200 scale based on the total number of wets recorded every 3 sec during the 10-min period). Migrate Technology (UK) loggers additionally differentiated between salt and fresh water, but summarised data less frequently depending on recording mode settings (one or four hours): when set to record every four hours, wetness values were recorded every half-minute and summed over the whole period (maximum 480, so the total wet count represents how many half-mins

Table 1. Details of loggers used on Bar-tailed Godwits and Red Knots at the Manawatu River Estuary.

Species	Manufacturer	Model	Wet/dry sensor	Recording frequency	No. retrieved	No. with NZ departure information
Godwit	BAS	MK14	Conductivity (salt water only)	10 min	30	26
	Biotrack	MK4093[1]	Conductivity (salt water only)	10 min	4	3
	Migratech	Initgeo-C65K	Wetness+conductivity (salt+fresh water)	60 or 240 min	21	21 (9 x 60-min, 12 x 240-min)
Knot	Biotrack	MK5093	Conductivity (salt water only)	10 min	8	7

[1]Formerly BAS Mk10b.

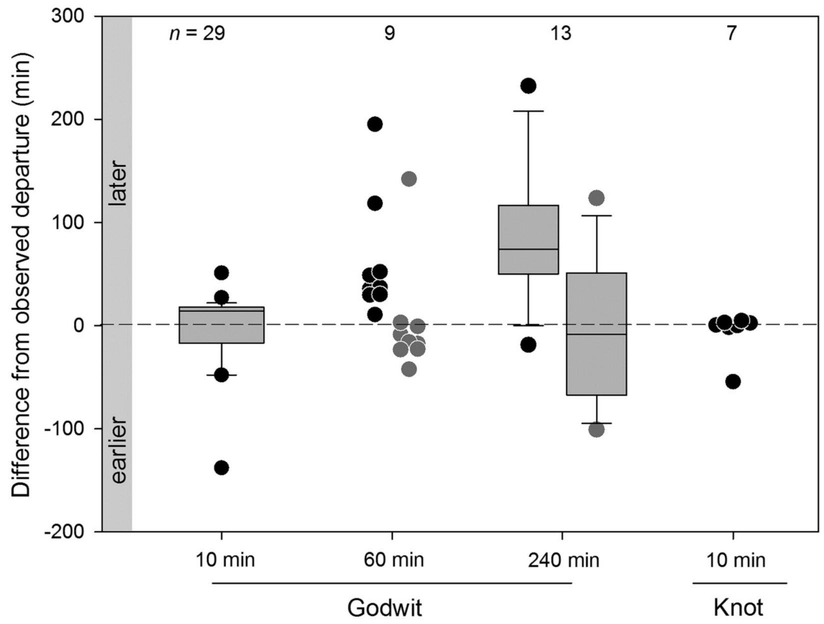

Fig. 1. Differences between inferred and actual departure times for Bar-tailed Godwits and Red Knots at the Manawatu River Estuary. Inferred departure times are based on geolocator conductivity measurements, and birds are grouped by the interval over which wetness values were recorded (*y*-axis), with sample size given above. For 60-min and 240-min loggers, values or plots on the left (with black circles) represent times taken as the end of the last wet interval; those on the right (with grey circles) are adjusted by the wet counts from the start of the interval. For boxplots, the boxes show the median and 25th to 75th percentiles, whiskers the 10th and 90th percentiles, and filled points the outliers; for dot plots all points are shown, offset where necessary for clarity.

over that 4-hr period the logger was wet); when set to record hourly they were capped at 14 counts (half-mins, so a maximum 7 min of wetness could be recorded) per interval. In both cases a maximum conductivity value for the recording time interval was also recorded on an arbitrary 0–127 scale, in which a value of 63 is recommended as a general cutoff between brackish and fresh water (James Fox pers. comm.). Hourly wetness summaries for loggers on hourly recording mode are given relative to the end of the 4-hr interval (which is denoted as 'T'), so 'T–3hr' refers to the first hour in the 4-hr interval, 'T–2hr' the second, and 'T–1hr' the third. We used the wetness and/or conductivity data to infer when birds departed on migration. For BAS and Biotrack loggers this meant the last wet interval before a prolonged dry period. For Migrate Technology loggers this meant the last wet interval that showed a marine conductivity signal.

The Migrate Technology loggers had coarser time resolution than the BAS and Biotrack units (recording only hourly or 4-hourly) but they also had counts of wet signals within intervals, which could be used to further refine the estimated departure time. Instead of taking the end of a time interval as the estimated departure time (as above), we considered instead the start of that interval and added the number of wet counts (in min) to estimate the earliest that the bird might have departed. This is likely to underestimate the departure time in the 60-min loggers, as their wet counts were capped at 14 (i.e. 7 min), whereas the bird could have departed at any time during that interval. For the 240-min loggers, while the wet count should be accurate, the assumption that all the wet counts occurred continuously from the start of the interval is likely to be false (as not all 'wet' intervals are wet for the entire time). Nevertheless, comparing results from using the end of the interval and using the start+wet counts reveals which method incurs greater error. We do not have observational data on arrivals after migratory flight, but designated the end of a flight as the time when marine or wet signals resumed after prolonged dryness. For arrivals inferred from Migrate Technology loggers, we analysed the end time of the interval in which wet counts first occurred, as well as by subtracting the wet counts from the end of the interval.

In total we recovered loggers from 41 godwits and eight knots, with multiple years for 15 godwits (14 with two years and one with three years), resulting in 57 departures from New Zealand for godwits and eight for knots. Of those we had corresponding visual departure information for 51 godwit departures and seven knot departures. Forty-two godwit departures were confirmed directly (the bird was conclusively identified in the flock that departed) and nine were deduced (generally through a marked bird being identified as a likely migrant in a flock and not resighted after the flock departed). For knots only three departures were confirmed directly, with the remainder (four) presumed to have departed in a single flock of 21 birds on 23 March 2013.

RESULTS

Conductivity data from loggers usually gave a clear indication that birds had departed on migration. Biotrack and BAS loggers had a single conductivity value, which typically dropped to zero when a bird departed, and remained so until the bird arrived at its destination. For example, data from the Red Knot CEU (Table 2) show the last wet 10-min interval ending at 5:05 (Greenwich Mean Time, GMT) on 21 March 2013. Migrate Technology Intigeo loggers had either a single wetness and a single conductivity value (240-min mode), or multiple wetness columns and a single conductivity value (60-min mode). In the 60-min example in Table 2 (Godwit 6RWBB) the last wet interval was the first of the 4-hr block measured, with the conductivity showing a marine signal. The bird presumably departed between 3:18 (end of the previous interval) and 4:18 (end of the last wet/marine interval) GMT on 23 March 2014, which can be further refined by the 14 wet counts (totalling 7 min) narrowing the period to 3:25–4:18. In the 240-min example (godwit 6RWWY), conductivity and wetness were both high up to the interval ending at 7:19 but both were zero in the next interval. Subsequent wetness counts were associated with low conductivity and presumably represented cloud moisture or rain. The 178 wet counts (totalling 89 min) imply that the bird likely did not depart until at least the second hour of that interval.

All loggers correctly recorded the observed day of departure. Loggers recording conductivity every 10 min went dry on average only 2 min before true departure for godwits and 7 min before departure for knots, although there was substantial variation among individuals (Fig. 1, Table 3). Loggers recording over longer time intervals tended to record later departure times if the end of the interval was used (means of 62 and 87 min later for 60-min and 240-min loggers, respectively) but were much closer if the time was adjusted by the wet counts (means of +1 and –4 min, respectively). The median values were remarkably close to actual departure times for the 10-min loggers (knots = 1 min later; godwits = 14 min later) and the wets-adjusted 60-min and 240-min loggers (16 min and 8 min earlier, respectively), and were still reasonable when considering only the end of the interval (i.e. not adjusted) for the 60-min and 240-min loggers (37 and 74 min later, respectively).

The godwits and knots tracked from New Zealand were all expected to land in coastal habitats, and all showed a clear apparent arrival in a marine habitat (based on the conductivity and wetness records) at the end of that flight (Table 2). Our data included some birds with 10-min loggers that departed from New Zealand in the same flock and whose loggers went wet within a few minutes of each other's upon arrival in Asia, suggesting that they had travelled together, landed at the same destination, and become wet around the same time. These included six godwits from one flock, two of which went wet three min apart (after 170 hr of flight), with the other four going wet within 16 min of each other eight hr later, evidently having travelled to a different destination. Of the Red Knots, two birds from one pair went wet within five min of each other, while three of four birds from a second flock went wet within 16 min of each other. We had similar results from godwits with other logger types. Three godwits from one flock went wet within 18 min of each other (even though one was a Biotrack 10-min logger and the others were Migrate Technology 240-min loggers, adjusted for wets), while two with 240-min loggers (adjusted) from another flock went wet within 21 min of each other.

DISCUSSION

Our analysis confirms that wet-dry data can provide quite accurate estimates of departure timing in waders that frequent intertidal areas. It is perhaps not surprising that conductivity sensors on loggers on knots work well, as the birds are not particularly long-legged and a tibia-mounted logger is only a few centimetres above the ground or water surface (mean tarsus length of knots in New Zealand = 31 mm, range 28–35 mm, n = 286; PFB unpubl. data; Fig. 2d) or underwater for wading birds. Godwit loggers were also mounted on the tibia (Fig. 2a–c), yet these also gave good data on wetness. Godwits often waded in water when feeding or when pre-roosting on the rising tide, so even a tibia-mounted logger 5–7 cm above the ground (mean tarsus length of godwits in New Zealand = 58 mm, range 50–69 mm, n = 372; PFB unpubl. data) may become immersed in water. When preparing to migrate, both species also bathed frequently in the 1–5 h before departure (PFB & JRC pers. obs.), increasing the likelihood that a bird about to migrate would have a wet logger not long before departure. Loggers that went dry before the bird departed were potentially on birds with longer legs, standing on drier terrain, that were not bathing, or whose loggers were perhaps less sensitive.

There were, however, some substantial differences between inferred and real departure times for godwits, with 10-min loggers going dry from over two hours before to almost one hour after migration started. The 4-hourly loggers varied by almost four hours, even after refinement by using the wet counts (while the median difference was only eight min before true departure, the range was still from over one and a half hr before to two hr after departure). Such variation is not unexpected, as birds are not necessarily on wet tidal flats at the point of departure, which can lead to a logger going dry well before departure, and if using raw values, any wetness recorded at the start of a 4-hour interval would cause the whole interval to be treated as wet.

The differences between estimates from the 'raw' Migrate Technology intervals and those adjusted by the wet counts confirm the expected biases. The 60-min loggers with wets capped at seven min inevitably gave earlier estimates of departures than the end-of-interval method and tended to underestimate departure time, though the median and mean were both within 20 min of the true departure time. As the cap on the wet counts will in most cases lead

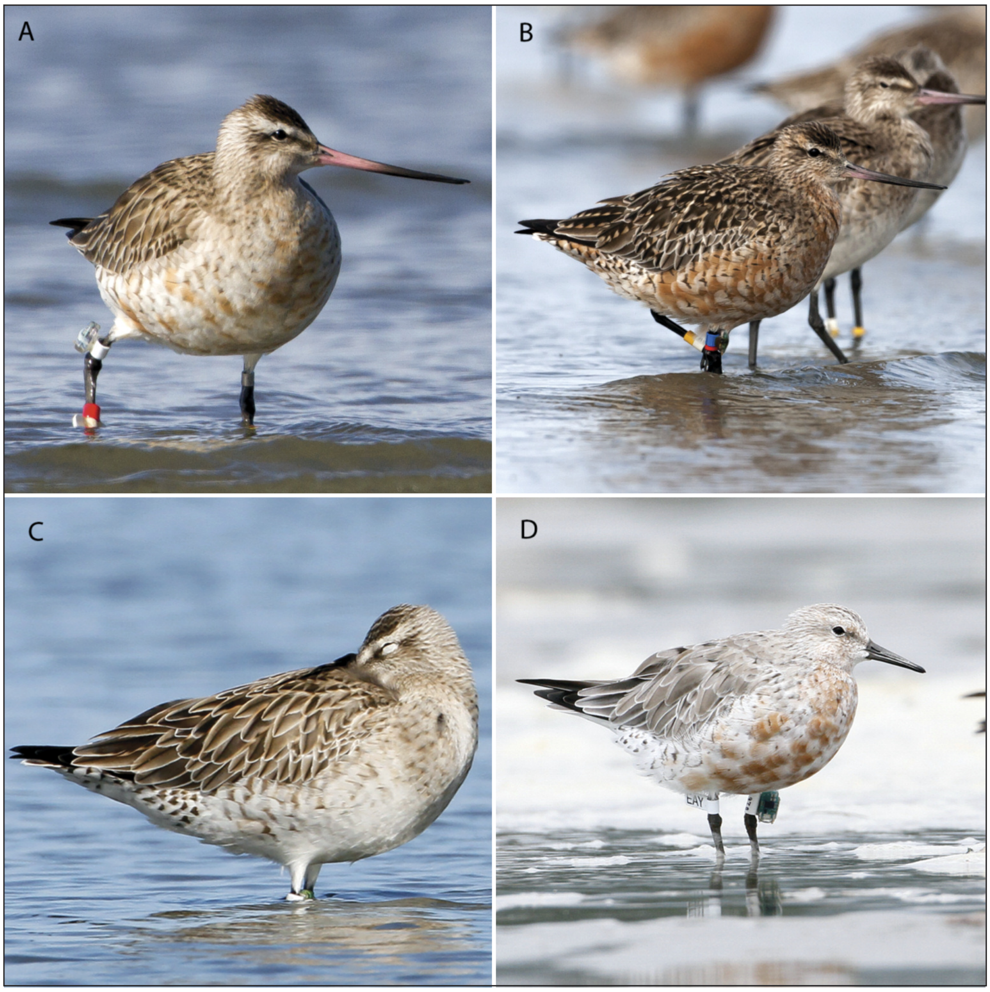

Fig. 2. Bar-tailed Godwits (A–C) and Red Knot (D) with tibia-mounted loggers in or near the water surface, Manawatu Estuary, New Zealand. Photos: Phil Battley.

to an underestimate of the departure time, the fact that the estimates were fairly close to the true departure times suggests that there may be two errors partly cancelling each other. It is possible that the loggers continue to record wetness even after a bird has departed, but this is countered by a systematic underestimate of the departure time through the use of capped counts. For the 240-min loggers, the wets-adjusted estimated departure times were evenly spread before and after the true departure, but they still varied by almost four hours between birds. We know that the assumption that all wet counts occur at the start of the last interval is likely to be untrue, but adjusting the departure times in this way did improve the overall fit of the estimates to the observed departure timings.

In addition to initial errors at departure, the time of arrival may also have errors for loggers with longer recording intervals, leading to overestimates of flight duration. However, while a small number of loggers went dry considerably before departure, it is unlikely that a logger on an arriving bird would show a wet signal before the bird actually landed. Field observations also show that newly arrived birds in intertidal areas may drink, feed, preen and bathe even at high tide while other birds are roosting (PFB pers. obs.). So it is unlikely that a logger will remain dry for a long period after arrival from a migratory flight, if the bird has landed near a tidal flat. The fact that some 240-min loggers recorded birds from a flock flying for the same duration and landing within a few minutes of each other supports using the wet counts to estimate arrival times.

The implications of these deviations from true departure times are in general minimal for the purposes of delineating long migratory flights. All of the loggers correctly identified the day of migration, and all but one of the 10-min units were accurate to within an hour. Migrate Technology loggers with 1-hr intervals were mostly accurate to within an hour, and even the 4-hr units were generally accurate to within 1–2 hr. For species making long migratory flights any such errors will make little difference to calculated flight durations (and therefore estimated speeds). Departure time differences were on average just 0.44% of the estimated flight durations for godwits (mean = 190 hr) and the 'worst' difference was still only 2.1%. For knots, initial errors were on average 0.20% of the mean estimated flight duration of 87.7 hr.

Table 2. Examples of conductivity data used to determine the start and end of migratory flights. Intervals at which the wetness or conductivity indicated the bird departed or arrived are shown in grey. Dates and times are GMT.

Biotrack MK5093 10-min Knot CEU		Migratech Intigeo-C65K 60-min Godwit 6RWBB						Migratech Intigeo-C65K 240-min Godwit 6RWWY		
	Conductivity		Wets (0–14)				Conductivity		Wets	Conductivity
Date and time	(0–200)	Date and time	T–3hr	T–2hr	T–1hr	T	(0–27)	Date and time	(0–480)	(0–127)
Departure										
21/03/13 04:25	65	22/03/14 15:18	0	0	5	14	110	15/03/13 15:19	480	115
21/03/13 04:35	0	22/03/14 19:18	14	14	14	8	116	15/03/13 19:19	480	114
21/03/13 04:45	0	22/03/14 23:18	14	7	14	14	114	15/03/13 23:19	388	115
21/03/13 04:55	63	23/03/14 03:18	14	14	14	14	116	16/03/13 03:19	211	115
21/03/13 05:05	103	23/03/14 07:18	14	0	0	0	116	16/03/13 07:19	178	115
21/03/13 05:15	0	23/03/14 11:18	0	0	0	0	1	16/03/13 11:19	0	0
21/03/13 05:25	0	23/03/14 15:18	0	0	0	0	0	16/03/13 15:19	88	26
21/03/13 05:35	0	23/03/14 19:18	0	0	0	0	0	16/03/13 19:19	0	1
21/03/13 05:45	0	23/03/14 23:18	0	0	0	0	0	16/03/13 23:19	37	7
21/03/13 05:55	0	24/03/14 03:18	0	0	0	0	0	17/03/13 03:19	38	2
Arrival										
24/03/13 02:35	0	30/03/14 11:18	0	0	0	0	0	23/03/13 07:19	0	0
24/03/13 02:45	0	30/03/14 15:18	0	0	0	0	0	23/03/13 11:19	0	0
24/03/13 02:55	0	30/03/14 19:18	0	0	0	0	0	23/03/13 15:19	0	0
24/03/13 03:05	0	30/03/14 23:18	0	0	0	0	0	23/03/13 19:19	0	0
24/03/13 03:15	0	31/03/14 03:18	0	0	0	0	0	23/03/13 23:19	0	0
24/03/13 03:25	17	31/03/14 07:18	8	0	0	0	87	24/03/13 03:19	327	112
24/03/13 03:35	2	31/03/14 11:18	14	14	14	14	117	24/03/13 07:19	465	114
24/03/13 03:45	0	31/03/14 15:18	14	14	14	14	117	24/03/13 11:19	429	114
24/03/13 03:55	0	31/03/14 19:18	14	14	14	14	117	24/03/13 15:19	171	114

Godwits from New Zealand have also been satellite-tracked migrating to Asia (Battley *et al.* 2012), and flight durations were estimated for nine birds making that flight. Flight durations estimated from the satellite-tagged birds were, perhaps surprisingly, significantly shorter than estimated from geolocators from the Manawatu Estuary (*t*-test for unequal variances, $t_{13,66} = 3.9$, $P < 0.001$), with means of 172.2 ± 12.3 hr for satellite-tagged and 190.5 ± 16.5 hr for all geolocator-tagged birds. This is a fairly large difference, part of which may stem from the duty cycles of the satellite tags, which were on a cycle of six hr on and 36 hr off. This meant that the timing of any departures or arrivals that did not occur during a transmitting cycle had to be estimated from subsequent or previous estimated flight speeds. The distance from the Manawatu River Estuary to the entry of the Yellow Sea is only slightly longer than from the departure sites of the satellite-tagged birds (Miranda, North Island, 280 km; Golden Bay, South Island, 120 km), which would equate to flight times of about 2–4.7 hr if flying at 60 km hr^{-1}. This still leaves a difference of approximately 14–16 hr in the estimated flight durations. Such disparity does not seem to be a result of flight conditions differing between the study periods, as there was one year (2008) in which godwits were tracked with both satellite-tags and geolocators, and the difference in flight durations was still present (176.3 ± 13.4 hr and 193.9 ± 9.2 hr for three satellite-tagged birds and 13 geolocator-tagged birds, respectively). The suggestion from this finding is that the flight durations of the satellite-tagged birds may have been underestimated, leading to the unexpected notion that geolocators might actually be more accurate than satellite-tags for documenting some flight durations.

Our observations confirm that for Bar-tailed Godwits and Red Knots in intertidal habitats, the conductivity loggers in geolocators can give good estimates of the departure time and presumably also the arrival time from migratory flights. In general, this ought to be true for other shorebirds with similar habits and habitats, but there are some caveats. One is that if birds depart from a high-tide roost following some hours of dryness, the actual departure time would be unclear. It is also possible that if individuals migrate at sea level they might have marine signals during flight that would obscure the flight details. Clearly, wetness measures will be lacking in birds migrating from dry habitats (e.g. Pacific Golden-Plovers *Pluvialis fulva* on Pacific islands, or pasture-feeding shorebirds), but the ability of Migrate Technology loggers to discriminate between marine and freshwater signals means that they might be useful for studying shorebirds that use freshwater wetlands.

If birds are tracked to their breeding grounds, whether or not an arrival will be detectable will depend on what habitat the bird lands in. For our godwits, all but one bird had a clear wet signal upon arrival in Alaska. In contrast, five of six knots with working loggers showed no wet signal at all when arriving in the Arctic from eastern Asia, and the sixth was only wet two days after its likely arrival, as determined by light-level geolocation.

Even though methods to analyse geolocator data are improving (e.g. Rakhimberdiev *et al.* 2015, 2016, Lisovski *et al.* 2016), supplementary confirmation of migratory flights from conductivity data will continue to be useful and in some cases may be essential for determining the migration timing. In additional to incidental problems such as geolocator shading on the departure or arrival day that may result in critical data being missing during analysis, migrations that occur around the equinox or that are heading due north or south may be challenging to analyse and interpret. Godwits migrating between New Zealand and Alaska, for instance, migrate around both equinoxes (Conklin & Battley 2011, Battley *et al.* 2012, Gill *et al.* 2014) and two of their major migratory flights have a predominant N–S axis (particularly on arrival in Asia and departure from Alaska), meaning that light-based analyses may struggle to determine actual migration times. Including birds that were not directly observed departing (so were not included in the earlier analyses) we have 68 records of geolocator-tracked godwits or knots arriving on their northbound stopovers. In 58 cases there was agreement between light data and conductivity regarding the day of arrival (with light data evaluated by obvious positional shifts when analysed in BAStrack or Intiproc, or from stabilising of the raw light

Table 3. Differences between inferred (logger) and actual (observed) departure times of Bar-tailed Godwits and Red Knots at the Manawatu River Estuary. For the 60-min and 240-min loggers, the 'raw' values refer to the end of the last wet interval while the 'adjusted' values are corrected by the wet counts in the interval.

Species	Logger duration	Mean ± SD	Median	Range
Godwit	10-min	–2 ± 38 min	+14 min	–148 to +52 min
	60-min (raw)	+62 ± 58 min	+37 min	+11 to +195 min
	60-min (adjusted)	+1 ± 54 min	–16 min	–42 to +142 min
	240-min (raw)	+87 ± 64 min	+74 min	–19 to +232 min
	240-min (adjusted)	–4 ± 69 min	–8 min	–101 to +124 min
Knot	10-min	–7 ± 21 min	+1 min	–55 to +5 min

data). For the remaining 10, most of the dates indicated from light data were within one day of the conductivity-derived date but were potentially one and a half or two days out (e.g. light data suggested 19–20 March while conductivity indicated 21 March). In these cases, the conductivity data are arguably far superior to light data for delineating actual migratory flight timings. Conductivity data can also reveal whether birds made short stops *en route* along a migration (even of just a few hours' duration), which can be useful when birds are migrating along coastal routes (e.g. Tomkovich *et al.* 2013), and identify whether possible local shifts are associated with habitat changes (Porter & Smith 2013).

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