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Articles

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Migrating birds make the longest non-stop endurance flights in the animal kingdom. Satellite technology is now providing direct evidence on the lengths and durations of these flights and associated staging episodes for individual birds. Using this technology, we compared the migration performance of two subspecies of bar-tailed godwit *Limosa lapponica* travelling between non-breeding grounds in New Zealand (subspecies *baueri*) and northwest Australia (subspecies *menzbieri*) and breeding grounds in Alaska and eastern Russia, respectively. Individuals of both subspecies made long, usually non-stop, flights from non-breeding grounds to coastal staging grounds in the Yellow Sea region of East Asia (average $10\,060 \pm$ SD 290 km for *baueri* and 5860 ± 240 km for *menzbieri*). After an average stay of 41.2 ± 4.8 d, *baueri* flew over the North Pacific Ocean before heading northeast to the Alaskan breeding grounds (6770 ± 800 km). *Menzbieri* staged for 38.4 ± 2.5 d, and flew over land and sea northeast to high arctic Russia (4170 ± 370 km). The post-breeding journey for *baueri* involved several weeks of staging in southwest Alaska followed by non-stop flights across the Pacific Ocean to New Zealand ($11\,690$ km in a complete track) or stopovers on islands in the southwestern Pacific en route to New Zealand and eastern Australia. By contrast, *menzbieri* returned to Australia via stopovers in the New Siberian Islands, Russia, and back at the Yellow Sea; birds travelled on average 4510 ± 360 km from Russia to the Yellow Sea, staged there for 40.8 ± 5.6 d, and then flew another 5680–7180 km to Australia ($10\,820 \pm 300$ km in total). Overall, the entire migration of the single *baueri* godwit with a fully completed return track totalled $29\,280$ km and involved 20 d of major migratory flight over a round-trip journey of 174 d. The entire migrations of *menzbieri* averaged $21\,940 \pm 570$ km, including 14 d of major migratory flights out of 154 d total. Godwits of both populations exhibit extreme flight performance, and *baueri* makes the longest (southbound) and second-longest (northbound) non-stop migratory flights documented for any bird. Both subspecies essentially make single stops when moving between non-breeding and breeding sites in opposite hemispheres. This reinforces the critical importance of the intertidal habitats used by fuelling godwits in Australasia, the Yellow Sea, and Alaska.

Evidence that migrating birds may fly distances of up to 5000 km non-stop has existed for some time (Johnson et al. 1989, Williams and Williams 1990), but recent satellite telemetry data on migrating birds reveal that distances more than twice as far are routine in some species (Gill et al. 2009). Not only are the distances flown enormous, but the relative amounts of fuel stored and the duration of high levels of exercise activity remain unsurpassed in vertebrates (Piersma and Gill 1998, Piersma 2011).

Migrations involving such massive flights require extensive fuelling periods, both before birds embark on migration and, usually, en route as well. This necessitates the use of a network of sites along a flyway. At these sites, birds stay for hours, days, or weeks, resting, moulting and refuelling for upcoming flights. Some sites may function as short-term stopover sites where birds prepare for relatively short subsequent flights (Warnock and Bishop 1998) and others as longer-term staging sites where birds prepare for long flights, often over large barriers such as oceans (Warnock 2010). The degree of connectedness between sites and populations can affect the conservation implications of habitat loss at these sites (Dolman and Sutherland 1995, Taylor and Norris

2010), but specific studies into the pathways used by different populations, and the scheduling of these migrations, are few for long-distance migrants. Within the shorebirds, so far only the migrations of red knots *Calidris canutus* have been documented and compared in considerable detail (Piersma et al. 2004, Piersma 2007, Buehler and Piersma 2008). Such comparisons may help us judge the degree to which these migrants are constrained in their migratory options, by time or the availability of suitable habitats.

Bar-tailed godwits *Limosa lapponica* represent an extreme among shorebird migrants. The Alaskan-breeding subspecies (*baueri*) makes the longest recorded non-stop migratory flight, across the Pacific Ocean from Alaska to New Zealand (Gill et al. 2005, 2009). However, details of their northwards migration and use of refuelling areas along the East Asian-Australasian Flyway have been lacking, beyond band records showing the population's presence on the coasts of China, South Korea, and Japan (McCaffery and Gill 2001, Battley and Schuckard unpubl.). It is unclear whether godwits from New Zealand fly non-stop to eastern Asia and what routes they take to Alaska. Likewise, knowledge of the migrations of the subspecies *L. l. menzbieri* (both hereafter referenced by subspecies name only) between northern Australia and arctic eastern Russia (Higgins and Davies 1996) is largely inferred from resightings or specimens across the species' range (Wilson et al. 2007). This lack of knowledge about migration patterns and pathways is of real concern given the global pressures on tidal flat habitats, particularly in Asia (Moores et al. 2008, Amano et al. 2010, Rogers et al. 2010, van de Kam et al. 2010, Yang et al. 2011). In other flyways, red knot populations declined precipitously as food at principal staging sites were reduced through human activity (Baker et al. 2004, Kraan et al. 2009).

Here we describe the timing, routes, flight lengths, and flight durations of the entire migratory paths of the two subspecies of bar-tailed godwits inhabiting the Pacific Basin. We compare their trans-hemispheric migrations and describe the relative proportions of time spent by each subspecies on active migration throughout an annual cycle. We also discuss the godwits' dependence on a limited number of staging sites during their migrations, focusing on sites in East Asia.

Methods

We present data on 30 adult godwits tagged between 2006 and 2010 as they prepared for migration in New Zealand

(12 birds) or northwest Australia (13 birds) or when breeding in Alaska (5 birds) (Table 1; Fig. 1 and 2 for all locations). In New Zealand, birds were caught at the Firth of Thames, North Island (37°11'S, 175°19'E) and Golden Bay, South Island (40°38'S, 172°40'E), and in Western Australia at Roebuck Bay (17°58'S, 122°19'E). In Alaska, *baueri* were caught on breeding grounds on the Yukon-Kuskokwim Delta (YKD, 61°25'N, 165°27'W), or North Slope (70°04'N, 151°30'W). An implantable satellite transmitter (PTT-100, Microwave Telemetry) was surgically inserted into anaesthetised godwits into space within the right coelomic air sac with the aerial emerging horizontally on the right side of the bird's tail (Mulcahy et al. 2011). As it was not clear at the start of the study how well birds of differing sizes would tolerate the ca 25-g transmitters, we preferentially tagged female godwits (27 birds), which are substantially larger than males (McCaffery and Gill 2001, Battley and Piersma 2005). In 2008, to confirm whether males were capable of equivalent flights to those of females, single males from New Zealand and Australia were tracked with implanted transmitters. In 2010, we implanted a smaller version (ca 19 g) of the implantable PTT-100 in a single female.

Transmitters deployed on godwits in Australasia were programmed with a duty-cycle that turned the PTT on for 6 h then off for 36 h to conserve battery life and enable tracking through the northward migration. Such programming and unanticipated long battery life enabled us to track many of these individuals during their return trips, and thus entire migrations were documented for both subspecies. The duty-cycle schedule for Alaskan-tagged birds during migration was 8 h on: 24 h off. The PTT transmissions were acquired via the Argos data collection system and processed by CLS (< www.clsamerica.com >). Each location estimate was assigned to one of 7 accuracy classes by CLS, broadly described as standard locations (classes 3, 2, and 1) and auxiliary locations (classes 0, A, B, and Z). Standard-class locations have 1-sigma errors < 1500 m, while accuracies of auxiliary locations are highly variable and unspecified by CLS (< www.clsamerica.com/argos-system/faq.html >). We used a systematic filtering algorithm (< http://alaska.usgs.gov/science/biology/spatial/douglas.html >) to assess plausibility of the auxiliary locations based on movement rates, turning angles, and spatial redundancy. Our filtering methods are described more fully in Gill et al. (2009). We assumed travel routes between consecutive locations followed Great Circle (orthodrome) paths, so our calculated flight distances necessarily underestimate the true distances travelled. Departure

Table 1. Deployment details of satellite-transmitters implanted into bar-tailed godwits (*Limosa lapponica baueri* in New Zealand and *L. l. menzbieri* in Australia). NZ = New Zealand, YKD = Yukon-Kuskokwim Delta, FOT = Firth of Thames, GB = Golden Bay, and RB = Roebuck Bay. See text and Fig. 1 for site locations.

| Month-year	Country	Capture site	No. tagged	Sex	Mean body mass (range)	Mean transmitter as % of body mass (max)	No. birds died en route
Jun-06	USA	YKD, Alaska	4	female	351 (325–384)	7.0 (7.5)	1
Feb-07	NZ	FOT, North Island	4	female	490 (434–532)	5.3 (6.0)	
Feb-07	NZ	GB, South Island	3	female	499 (482–514)	5.1 (5.3)	
Feb-08	NZ	FOT, North Island	4	female	471 (450–487)	5.4 (5.6)	1
Feb-08	NZ	FOT, North Island	1	male	426	6.0	
Feb-08	Australia	RB, Western Aust.	12	female	369 (335–407)	6.8 (7.5)	3
Feb-08	Australia	RB, Western Aust.	1	male	325	7.7	
Jul-10	USA	North Slope, Alaska	1	female	345	5.4	
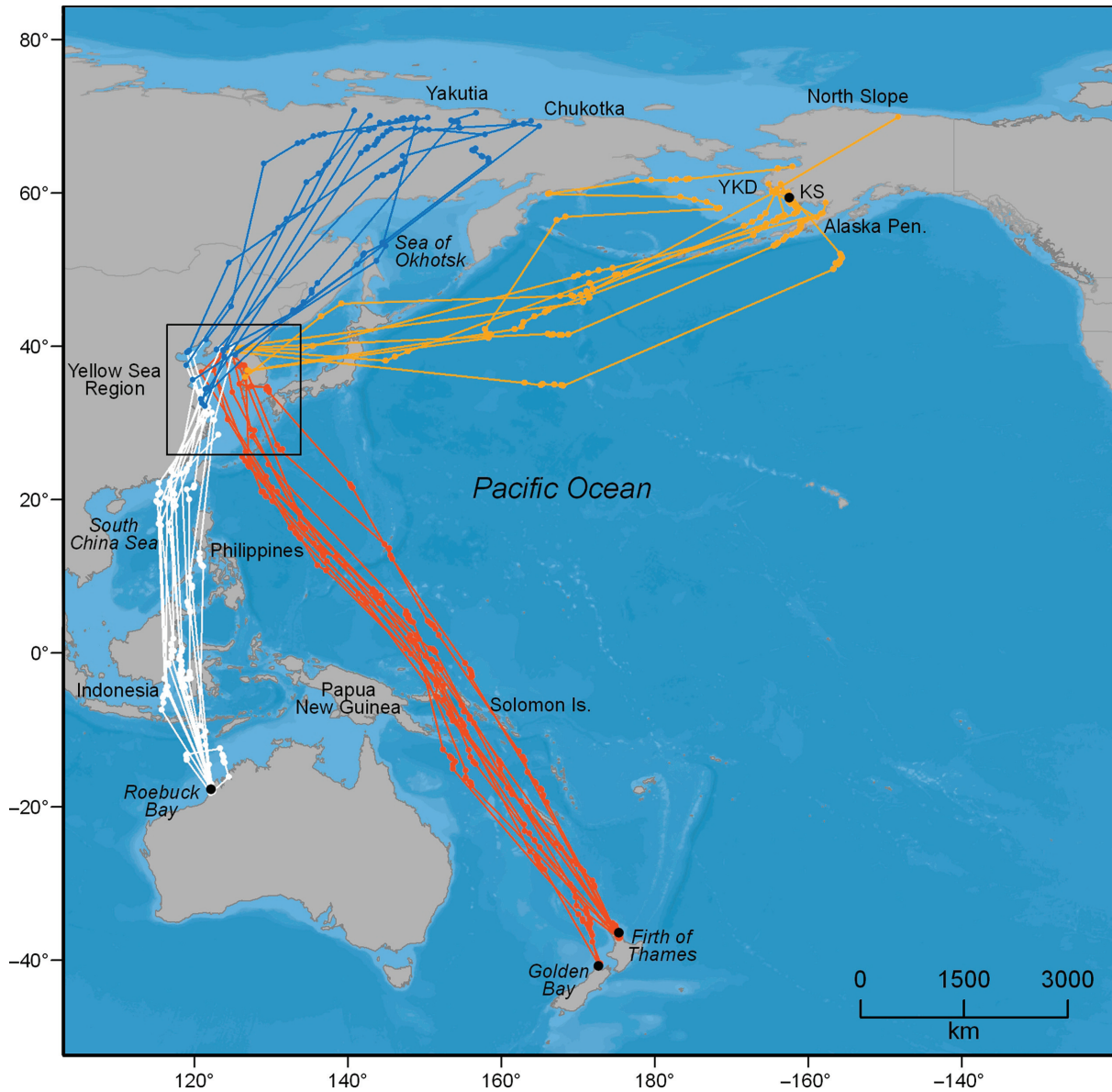
Figure 1. Tracks of satellite-tagged bar-tailed godwits on northward migration, with place names mentioned in the text. White/blue tracks represent *L. l. menzbieri* (white = northwest Australia to the Yellow Sea region; blue = Yellow Sea region to the breeding grounds in Siberia); red/gold tracks represent *L. l. baueri* (red = New Zealand to the Yellow Sea region; gold = Yellow Sea region to Alaska). Small circles along track lines represent positions calculated from Argos data. YKD = Yukon-Kuskokwim Delta, KS = Kuskokwim Shoals. Map is a Plate Carrée projection.

and arrival times that were outside a transmitter's duty-cycle on-period were estimated by extrapolating the subsequent or previous travel speed over the intervening travel distance. Transmitters also reported temperature, which for implanted PTTs is effectively the body temperature of the bird. Mortalities were readily identified when temperature fell below 38°C, and in all five cases were corroborated by lack of subsequent movements.

Sample sizes decreased during the course of study due not only to bird deaths but also to battery failure. We categorised flights based on the extent of tracking: the term 'complete' refers to tracks that reached land, the term 'incomplete' to tracks where transmitter signals were lost during flight but where birds were subsequently known to have survived based on visual sightings. In four such cases of incomplete tracking, distances of the untracked portions of flights have been

included in predicted flight distances reported here. Mean values for most summaries are presented, with full descriptive statistics in tables; where values are not summarised in tables, means ± SD are given in the text.

We describe two components of movement for migrating godwits. 'Flight distances' (and durations and ground speeds) refer to major non-stop migratory flights, defined as departure to first landfall in the destination region. 'Travel distances' consist of the non-stop flights plus any subsequent segments leading to the eventual destination (thus, for birds that flew directly to their final destination, flight and travel distances are the same). We did not attempt to incorporate small-scale, local movements into these totals. We also investigate migration speeds that include the estimated time spent fuelling before departure from the non-breeding grounds (Alerstam and Lindström 1990).
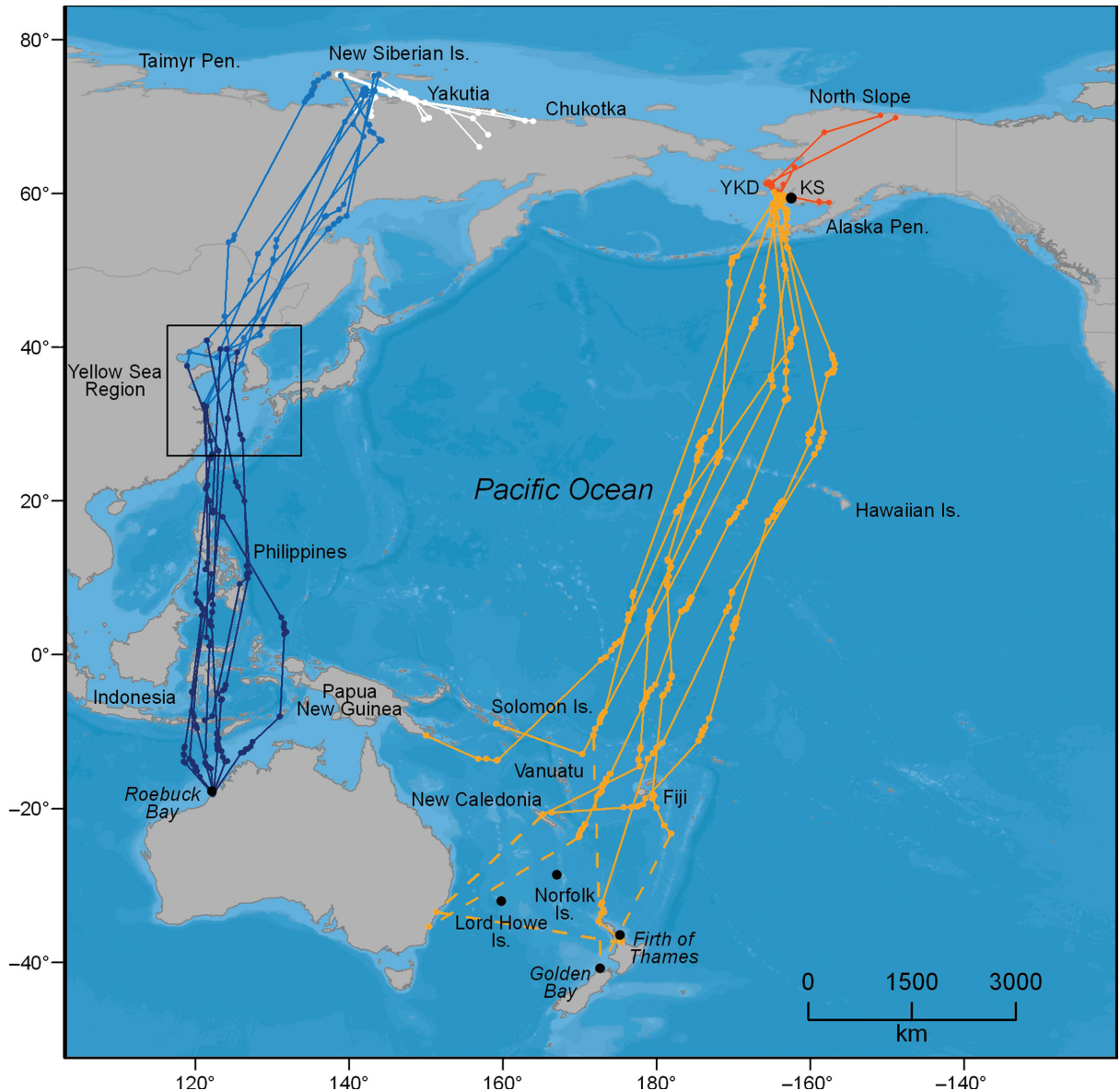
Figure 2. Tracks of satellite-tagged bar-tailed godwits on southward migration, with place names mentioned in the text. White/blue tracks represent *L. l. menzbieri* (white = breeding grounds to staging areas about the New Siberian Islands; light blue = staging grounds back to the Yellow Sea region; dark blue = Yellow Sea region to northwest Australia); red/gold tracks represent *L. l. baueri* (red = intra-Alaska movements; gold = the main leg from the Yukon-Kuskokwim Delta staging grounds to Australasia). Small circles along track lines represent positions calculated from Argos data. Dashed lines for *baueri* denote movements interpolated from resightings subsequent to transmitters going off air. YKD = Yukon-Kuskokwim Delta, KS = Kuskokwim Shoals. Map is a Plate Carrée projection.

To ascertain whether birds could have successfully bred, we assumed that breeding takes around 7 weeks or more (1 week for egg laying, at least 3 weeks for incubation and 3 weeks for chick rearing: McCaffery and Gill 2001, McCaffery et al. 2010).

Results

Migrations of *L. l. baueri*

Twelve *baueri* godwits departed New Zealand from 15 March–2 April and migrated along a ca 550- to 1000-km-wide corridor, passing between the eastern islands of Papua New Guinea and the eastern Solomon Islands, then north-west across the western Pacific Ocean to eastern Asia and the Yellow Sea region (Fig. 1). One bird died after flying 8800 km to Okinawa, Japan, and two birds went off air after flying >8700 km. The flights of all others exceeded 9380 km and averaged 10 060 ± 290 km over 7.2 ± 0.5 d (Table 2, Fig. 1; Fig. 4 for cumulative distances for individuals over all migration legs). Most birds made landfall in the eastern and central Yellow Sea region, from Yalu Jiang National Nature Reserve, China (39°48′N, 124°08′E) eastwards. Three birds that landed in the western Yellow Sea moved to Yalu Jiang within 7–9 d; three others made movements from North or South Korea to Yalu Jiang, or from Japan to South Korea (Fig. 3). Total travel distances to final refuelling sites averaged 10 280 km in 13.1 d.

Migration leg		baueri distance (km)	baueri duration (d)	menzbieri distance (km)	menzbieri duration (d)
NB–YS	flight	10060 ± 290 (9380–10270, n=9)	7.2 ± 0.5 (6.4–7.9, n=9)	5860 ± 240 (5620–6410, n=11)	4.1 ± 0.5 (3.3–4.7, n=11)
	travel	10280 ± 300 (9850–10600, n=9)	13.1 ± 9.0 (6.4–34.8, n=9)	6350 ± 380 (5720–6780, n=11)	8.3 ± 4.6 (4.0–18.0, n=11)
YS–breed	flight	6770 ± 800 (6150–8520, n=8)	4.6 ± 0.8 (3.5–6.0, n=8)	4170 ± 370 (3690–4800, n=11)	2.4 ± 0.5 (1.6–3.3, n=11)
	travel	7280 ± 1050 (6240–9010, n=8)	8.9 ± 6.1 (3.6–18.2, n=8)	4210 ± 410 (3690–4900, n=11)	2.5 ± 0.6 (1.6–3.6, n=11)
Alaska–NZ	flight	11690 (n=1)	8.1 (n=1)		
Alaska–Pacific islands	flight	10410 ± 440 (10030–10940, n=4)	8.5 ± 1.0 (7.3–9.4, n=4)		
Alaska–NB (estimated)	flight	11820 ± 450 (11440–12320, n=3)	n/a		
NSI–YS	flight			4070 ± 220 (3580–4280, n=8)	3.0 ± 0.6 (2.2–3.6, n=8)
	travel			4510 ± 360 (4040–4930, n=8)	6.3 ± 3.5 (2.2–11.6, n=8)
YS–AUS	flight			6100 ± 390 (5740–6560, n=4)	4.5 ± 0.8 (3.6–5.3, n=4)
	travel			same as flight	same
YS–island stop–AUS	flight			5340 ± 780 (4170–5780, n=4)	4.6 ± 0.8 (3.4–5.2, n=4)
	travel			6510 ± 760 (5680–7180, n=3)	16.9 ± 10.5 (5.2–30.4, n=3)

Most birds staged in eastern Asia for 41.2 d (Table 3); one staged for 62 d and departed Asia unusually late (8 June, 15 d later than all others; this is not included in Table 3). Birds departed for Alaska from 1 May to 8 June, most heading across Japan and out over the North Pacific Ocean, before making marked northward course changes towards Alaska (Fig. 1). One migrant made slow progress when 'blocked' by a low pressure zone and associated headwinds in the northwest Pacific. It diverted when about 450 km from the YKD, Alaska, and flew about 1300 km to Russia. It resumed migration to Alaska 9 d later and covered 8910 km total en route to Alaska (in 7.0 d flying). Excluding this bird, average flight distance to Alaska was 6770 km and flight time 4.6 d (Table 2).

Eight *baueri* arrived in Alaska with functioning transmitters and, including local movements, they travelled 7280 km in 8.9 d from Asia to their eventual destinations (Table 2). Two birds stayed on the coast of the YKD and apparently did not attempt to breed. Of the six birds that seemingly did attempt to breed, two appeared to fail (present at site < 45 d), three potentially bred successfully (present 49, 55, and 64 d), and one stopped reporting during breeding. All failed breeders, non-breeders, and breeders including the five birds tagged in Alaska subsequently moved to the Kuskokwim Shoals (59°50′N, 164°08′W), a traditional staging region for godwits on the south YKD (Fig. 2: Gill and McCaffery 1999), between 11 June and 17 July. Four birds made trips (two twice) to estuaries on the Alaska Peninsula, ~400 km away. Four *baueri* tracked for the entire northern summer spent on average 121.4 d in Alaska (Table 3); of that, 72 ± 27% of the time was spent at the Kuskokwim Shoals (38 and 65% for the two birds that attempted to breed, and 84 and 100% for the two that did not).

A total of eight birds transmitting during the southward migration period departed Alaska 30 August–7 October and headed south across the Pacific Ocean through a corridor approximately 1500 km wide (Fig. 2). The easternmost bird passed within 200 km of the main Hawaiian Islands. Only one bird (E7) was tracked completely back to New Zealand, flying 11 690 km in 8.1 d (Table 2, Fig. 5). Four birds flew for 10 410 km (in 8.5 d) before landing on islands in the southern Pacific. Transmitters of three birds stopped reporting in flight after the birds had flown 9260 ± 1010 km, but the birds were seen in Australia and/or New Zealand 5 d to 5 months later. The estimated total flight distance for them, assuming no detours for the remainder of their routes, was 11 820 km.

E7, the single *baueri* for which the entire migration was tracked, travelled 29 280 km over a 174-d period. One other bird was tracked for most of a round-trip (E5); she travelled at least 30 000 km during the year (track distance of 26 170 km plus Great Circle distances between her stopover site in New Caledonia and re-sighting sites in Australia and New Zealand).

Migrations of *L. l. menzbieri*

Godwits marked at Roebuck Bay, Australia, departed northbound from 6 to 16 April, about 3 weeks later than *baueri* from New Zealand. *Menzbieri* made non-stop flights to the
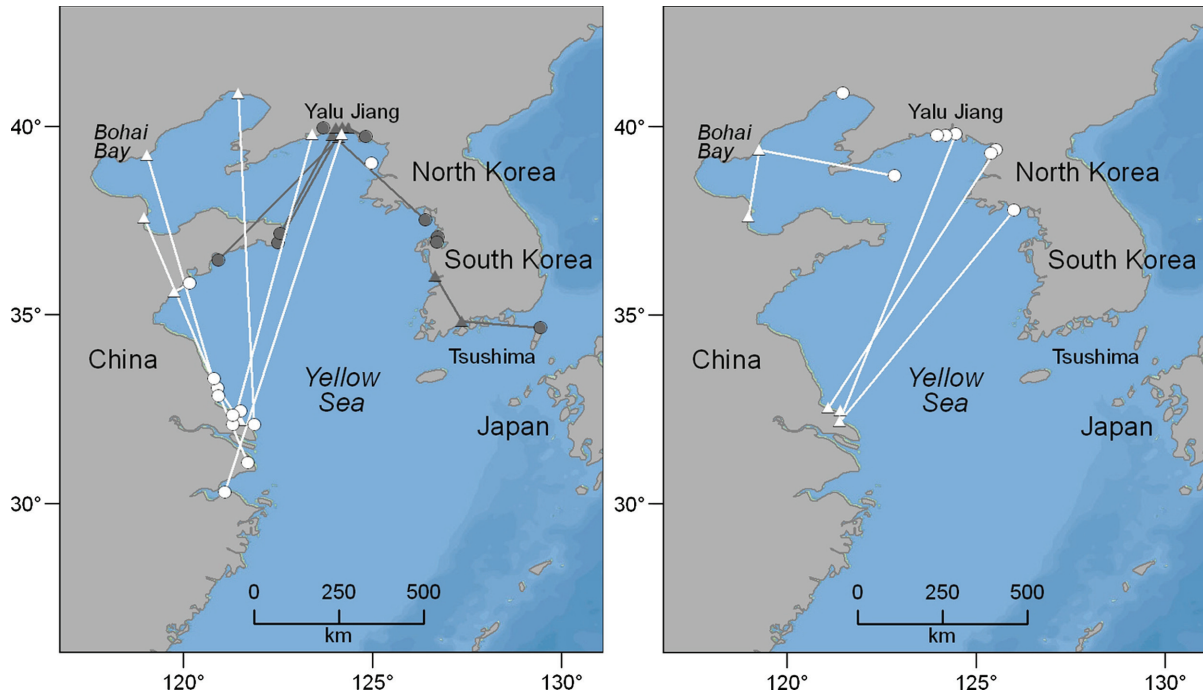
Figure 3. Site use of satellite-tagged bar-tailed godwits in the Yellow Sea region on northward (left) and southward (right) migration. Circles denote initial landfalls; triangles show subsequent locations for birds that moved to a different staging site. Subspecies *L. l. menzbieri* is shown in white, *L. l. baueri* in grey. Note that only *menzbieri* uses the Yellow Sea on southward migration.

Yellow Sea region that averaged 4.1 d and 5860 km (Table 2, Fig. 1). Initially, all birds flew generally northwest, passing over eastern Indonesia and then north in a 600-km-wide corridor over the East China Sea and western Philippines before making landfall along the western shores of the Yellow Sea and estuaries immediately south (Fig. 1). Four birds flew directly to their final destination; the other seven travelled 95–1100 km more within the Yellow Sea region to their eventual fuelling site (Fig. 3). Overall travel distances averaged 6350 km in 8.3 d.

Menzbieri spent an average of 38.4 d staging in the Yellow Sea (Table 3). They left Asia from 18 to 27 May and migrated north across eastern Russia, northern Japan, and the Sea of Okhotsk, flying 4170 km in 2.4 d to breeding sites spanning 800 km of eastern Siberia (northern Yakutia) and northwest Chukotka (Table 2, Fig. 1). Two birds moved short distances within Russia (200 and 240 km), and travel distances were similar overall to flight distances (Table 2). Birds arrived on the breeding grounds from 20 to 29 May but, based on durations spent at their presumed nesting sites (22–31 d), no birds bred successfully. Two birds died from 9 to 11 June during a period of widespread harsh weather (Soloviev and Tomkovich 2009: see Discussion). The remaining nine birds

left their breeding grounds from 15 to 28 June and moved 280 ± 180 km to tundra habitat along the coast of the East Siberian Sea, where they spent 3–7 d before moving northward another 290 ± 130 km to stage for 16–26 d on the New Siberian Islands (Fig 2; total distances travelled ranged from 140 to 1010 km). Birds spent 55.1 ± 4.3 d in total in Russia, including 26.1 ± 3.9 d (range 21–34 d) staging before starting southward migration.

All eight *menzbieri* that survived the summer with functional transmitters were tracked to the Yellow Sea on southward migration (Fig. 2), arriving between 13 and 29 July after flying 4070 km in 3.0 d (Table 2). Four birds moved an additional 880 ± 350 km within the Yellow Sea region thereby increasing the average overall travel distance to post-breeding staging grounds for all *menzbieri* to 4510 km in 6.3 d. Birds remained in the Yellow Sea for 40.8 d (Table 3) before continuing migration from 20 August to 7 September. Southbound tracks tended to be farther east than northbound ones with birds flying in a 700-km-wide corridor spanning the Philippines (Fig. 2).

Four birds flew non-stop back to Roebuck Bay from the Yellow Sea (6100 km in 4.5 d; Table 2). Three stopped en route for 8–24 d before continuing on to Roebuck

Table 3. Length of stay or residence (d) during migration and breeding of satellite-tagged bar-tailed godwits. Values given are means ± SD (range, n).

Period	baueri	menzbieri
Northbound staging Asia	41.2 ± 4.8 (36–49, n = 7)*	38.4 ± 2.5 (34–43, n = 11)
Total duration in Alaska or Russia	121.4 ± 17.6 (100–140, n = 4)	55.1 ± 4.3 (46–61, n = 8)
Post-breeding staging Alaska or Russia	44 and 91 (n = 2)	26.1 ± 3.9 (21–34, n = 8)
Southbound staging Asia		40.8 ± 5.7 (35–50, n = 8)

*Excludes one bird with a 62-d staging period.

Bay, including a bird that flew 4170 km to Sulawesi and two birds that flew 5710 and 5780 km, respectively, to sites in Indonesia (Table 2). A fourth bird also travelled 5700 km to a site in Indonesia, but died there shortly thereafter.

Entire migrations were documented for seven Australian-tagged godwits. They travelled $21\,940 \pm 620$ km in 154 ± 14 d.

Based on cumulative distances flown over time (Fig. 4) there are three key differences in timing and flights between *baueri* and *menzbieri*. First, *baueri* precede *menzbieri* temporally on northward migration but *menzbieri* precede *baueri* on the way back. Second, *menzbieri* use an intermediate staging area on southward migration whereas *baueri* do not. The third difference between the subspecies is in distances migrated: the total distance to the breeding grounds for *menzbieri* is about the same as the length of just the first flight of *baueri*, from New Zealand to Asia.

Ground speeds, migration speeds, and overall time-budgets

Ground speeds during the major non-stop flights did not differ significantly among the three major migration legs for *baueri* with means of 58.7 ± 4.6 km h^{-1} (New Zealand–Asia, $n = 10$), 63.3 ± 11.3 km h^{-1} (Asia–Alaska, $n = 8$) and 53.3 ± 6.4 km h^{-1} (Alaska south, $n = 5$) (ANOVA, $F_{2,22} = 2.46$, $p = 0.11$). In contrast, ground speeds of *menzbieri* flying from Asia to the breeding grounds were greater than on all other flights (ANOVA, $F_{3,34} = 7.94$,

$p < 0.001$, Tukey Post-hoc test): 59.8 ± 5.6 km h^{-1} Australia–Asia ($n = 11$), 76.3 ± 15.9 km h^{-1} Asia–Russia ($n = 11$), 58.2 ± 11.7 km h^{-1} Russia–Asia ($n = 8$), and 53.1 ± 8.7 km h^{-1} Asia south ($n = 8$).

Migration speed (total time for the migration, including initial fuelling: Hedenström and Alerstam 1998, Alerstam 2003) was estimated for a single *baueri* (E7) tracked over its entire migration. This bird was tracked for $29\,280$ km over a 174-d period, and spent 20 d in major migratory flights (27 d if local movements in Alaska are included). The entire migration lasted 249 d if initial fuelling is assumed to have begun on 1 January (based on a capture mass on 6 February of 532 g, well above a predicted non-breeding mass based on size of 347 g; J. R. Conklin pers. comm.). The daily rate for the total migration, including initial fuelling, to the breeding grounds was 132 km d^{-1} (125 km d^{-1} for the leg to Asia, 144 km d^{-1} for the leg to Alaska); the rate for the return trip (upon leaving the breeding grounds on 17 July and arriving in New Zealand on 7 September) was 68% higher at 223 km d^{-1}. Overall, 11.5% of the time away from New Zealand was spent in major flights; the bird spent 36.9% of its time on the breeding grounds and 47.5% on staging grounds (the remainder consisted of smaller movements that were not readily identified as periods of travel or not, given the transmission schedules).

Menzbieri's schedules were complicated by harsh weather leading to breeding failures, which likely affected their time-tables and the proportion of time spent at staging grounds
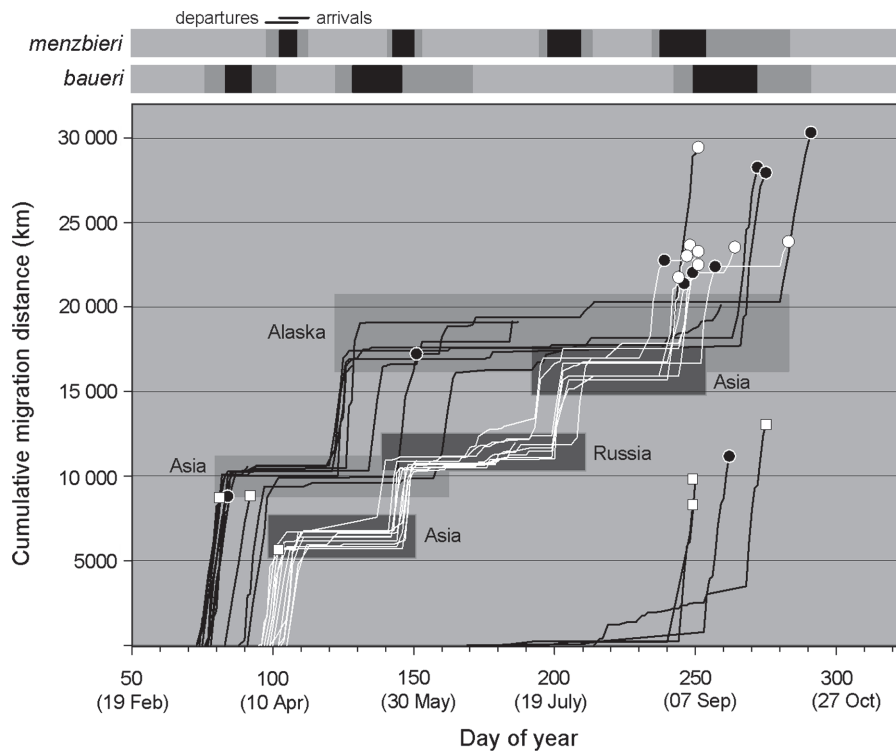

Figure 4. Cumulative track distances for satellite-tagged bar-tailed godwits tagged in New Zealand (*L. l. baueri*, black lines) and northwest Australia (*L. l. menzbieri*, white lines). Shaded blocks represent the spans of staging periods in the Yellow Sea region (medium grey for *baueri* and dark grey for *menzbieri*). Symbols denote the end-points of tracking (hollow circles = back on non-breeding grounds, filled circles = tracked to an island stopover, open squares = off air in flight). Tracks for four *baueri* tagged in Alaska (lower right-hand corner of plot) represent distances tracked before and during southward migration only. The bars above the plot denote the periods during which birds were departing from a fuelling site or arriving at a destination. Note that tracking of *menzbieri* is from a single year whereas *baueri* represent two years.

on southward migration. Birds were away from Australia for 153.6 ± 15 d ($n = 7$) and made migratory flights on 14.4 ± 1.0 d. Assuming fuelling started on 5 January (Wilson et al. 2007), the total migration lasted on average 249 ± 14 d. Migration speeds for *menzbieri* averaged 75 ± 3 km d^{-1} for the journey to the breeding grounds (58 ± 3 km d^{-1} Australia–Asia; 115 ± 12 km d^{-1} Asia–Russia) and were 91% higher on the return (142 ± 20 km d^{-1} overall: 187 ± 25 km d^{-1} Russia–Asia; 107 ± 28 km d^{-1} Asia–Australia). Away from Australia, $9.4 \pm 0.4\%$ of the time was spent in major flights, $19.0 \pm 2.8\%$ of the time was spent on the breeding grounds (in a year of unsuccessful breeding), and $69.5 \pm 4.2\%$ was spent clearly at staging grounds.

Discussion

Flight routes, flight lengths, and use of staging sites

Our data confirm that *baueri* godwits make one of the most epic movements in the animal kingdom. Their southward migration from Alaska to New Zealand or eastern Australia entails the longest known non-stop flight of any landbird (Gill et al. 2009) and their 10 000 km northward flight is the second-longest known. Both flights take a week or more of non-stop flying. Previously, the longest tracked flight had been from Australia to China for an eastern curlew *Numenius madagascariensis* (possibly 7000 km: Driscoll and Ueta 2002), though it is now known from remote tracking that Hudsonian godwits *L. haemastica*, bristle-thighed curlews *N. tahitiensis*, whimbrels *N. phaeopus* (Gill and N. Senner et al. unpubl.), ruddy turnstones *Arenaria interpres* (Minton et al. 2010), and red knots (Niles et al. 2010) are capable of longer flights than had been proposed for eastern curlews. The maximum flight length we recorded is by no means the longest flight expected. About 25 000–30 000 godwits winter up to 1000 km farther south than E7, the *baueri* that flew 11 690 km. The *baueri* tagged in Alaska and recorded in Australia after transmitter failure likely flew > 12 300 km.

Baueri from New Zealand were highly conservative in their use of staging sites, and most stopped in just one or two countries when migrating north through Asia. E7 completed a 29 000-km-long circuit during which she landed in just three regions: the Firth of Thames, New Zealand; Yalu Jiang, China; and the YKD and Alaska Peninsula, Alaska (Fig. 5).

Several *baueri* stopped on a range of islands in the southwest Pacific Ocean during southbound migration (Gill et al. 2009). One of these was subsequently seen in Australia before returning to its non-breeding site in New Zealand. Such stopovers on southward migration are also known from birds not carrying transmitters. Colour-banded godwits from New Zealand are recorded annually on the east coast of Australia on southward migration (Battley and Schuckard unpubl.), and one bird tracked via a geolocator apparently made a short stop, probably in New Caledonia, before continuing to New Zealand (Conklin and Battley unpubl.). We interpret these diverted courses as being adaptive responses to the risks of continued flight over open oceans in adverse wind conditions (Gill et al. 2009, Shamoun-Baranes et al. 2010). All four cases of landfall of satellite-tagged birds coincided with

Figure 5. Round-trip migrations of individual bar-tailed godwits of the *L. l. baueri* and *L. l. menzbieri* subspecies. The *baueri* individual (leg-flagged 'E7', orange track) was tracked for 29 280 km including three main migratory flights, of 10 270 km (in 7.0 d) between New Zealand and the Yellow Sea (China), 6510 km (4.9 d) between the Yellow Sea and Alaska (USA), and 11 690 km (8.1 d) between Alaska and New Zealand. The *menzbieri* ('C7', blue track) was tracked for 21 210 km, including four main migratory flights, of 5620 km (4.2 d) between Australia and the Yellow Sea, 3990 km (2.1 d) between the Yellow Sea and Siberia (Russia), 4090 km (2.6 d) between Siberia and the Yellow Sea, and 6270 km (5.3 d) between the Yellow Sea and Australia.

previous passage, or continued flight, through adverse winds (Gill et al. 2009). There are no major island groups in the 1800 km between Fiji (18°S) and northern New Zealand, or in the 1300 km between New Caledonia (21°S) and northeast Australia, so these islands represent final stopover opportunities for southward trans-Pacific migrating godwits. It is not clear whether birds stopping on islands in the southwest Pacific before continuing to Australia and/or New Zealand do so for the same reasons (e.g. low on energy stores or facing adverse winds). It is also not clear whether visiting Australia is part of the regular migration strategy for some individual *baueri* that eventually winter in New Zealand.

When *menzbieri* left Roebuck Bay, they travelled in a roughly northwest direction, but tracks were essentially northwards by the time birds passed northern Indonesia. This accords well with visual and radar work in Roebuck Bay (Lane and Jessop 1985, Tulp et al. 1994), which found that flocks of waders departed in NW-NNW directions. The northbound tracks over southeast Asia of the satellite-tagged godwits lay several degrees of longitude to the west of the departure site. At its most westerly, one *menzbieri* was about 750 km from the direct Great Circle route from Roebuck Bay to the Yellow Sea.

Menzbieri godwits also used few staging areas. The tracking confirmed the major non-stop flights suggested previously for *menzbieri* (Wilson et al. 2007): non-stop flights

from Western Australia to the Yellow Sea in the first half of April, an overland flight to Russian breeding grounds, and a non-stop, overland flight on southward migration to the Yellow Sea followed by a final leg to Australia. During migration most birds were recorded in just three countries (China, Russia, and occasionally North Korea, although some birds made stops in Indonesia or Sulawesi on the final journey back to Australia).

Interestingly, our work revealed a previously undocumented movement of all tagged *menzbieri* northward from the breeding grounds to the New Siberian Islands (as far as 75°N). The timing of this mid-season move was evidently in response to unusually cold and snowy conditions on the breeding grounds in June 2008 (Soloviev and Tomkovich 2009). Similar northward movements by godwits on the Taimyr Peninsula are thought to entail mostly non-breeding adults (Rogacheva 1992); however, we do not know if this northward movement is representative of failed breeders, post-breeding birds, or both, because of the apparent nesting failure of our marked birds in 2008. Occasional observations of foraging godwits at the Indirgka Delta and New Siberian Islands before southward migration, and the lack of intertidal flats near the inland breeding grounds of *menzbieri*, suggest that the movements we tracked are part of a regular phenomenon (P. S. Tomkovich pers. comm.).

An intriguing contrast is that *baueri* make a non-stop flight back to the non-breeding grounds, whereas *menzbieri* stage in the Yellow Sea on the way south. The total distances travelled on southward migration are similar, and it is not clear why *menzbieri* flights are not of similar magnitude to *baueri* flights given similarities in morphology (the main difference being that *menzbieri* are slightly longer-billed for their body size than are *baueri:* Wilson et al. 2007, Conklin et al. 2011) and flight speeds. Perhaps this difference reveals the superior fuelling potential of rich YKD mudflats compared with Siberian tundra, allowing only *baueri* to store enough fuel for flights > 10 000 km (Gill et al. 2009). However, theory suggests that due to the diminishing return of flight distance with fuel stores, migrants should make several short trips rather than one long one (Alerstam 1979). Given that the migrations of *menzbieri* are essentially along a north-south axis with a central fuelling locus, there might be no benefit to attempting a longer flight south, particularly if fuelling rates on tundra are indeed slower than on mudflats.

Bar-tailed godwits essentially migrated along corridors approximating Great Circle routes, with the exception of *baueri* flying from Asia to Alaska and to a lesser extent from Alaska back to Australasia (Battley et al. unpubl.). Between Asia and Alaska most birds headed eastwards immediately upon departure from the Yellow Sea area (Fig. 1) before making major course changes of at least 20–50° towards Alaska while crossing the North Pacific. Previously we reported on the association between winds and the southward flight of *baueri* from Alaska to Australasia (Gill et al. 2005, 2009). The eastbound routes shown here by godwits flying between the Yellow Sea and Alaska also appear to be related to wind (Gill unpubl.; detailed meteorological analyses of the timing and paths of flights will be discussed in future papers). Birds flying from Asia to Alaska in spring cross one of the most atmospherically dynamic regions on Earth, where intense and frequent storms develop and track east across the North Pacific

(Overland et al. 2002, Rodionov et al. 2005, Pickart et al. 2009). This same 'storm factory' and associated winds are used by godwits in their southward migration to Australasia, so it is reasonable to expect that the same individuals use winds to assist other flights throughout their annual cycle.

The cumulative distances flown over time (Fig. 4) show that *baueri* migrated earlier than *menzbieri* on the way north but later on the way back. This is not surprising, as *baueri* have much farther to travel, but nevertheless breed in areas that thaw earlier. As no *menzbieri* in our sample bred successfully, it is not clear if the timing of their southward movements is typical, or whether the southward migration would be later for birds that spent longer on the breeding grounds. The distribution of satellite-tagged godwits in Asia on northwards migration suggests that *menzbieri* predominantly use the western parts of the Yellow Sea, whereas *baueri* mostly use the eastern parts. This is supported by resightings of individually-marked birds tagged in New Zealand and northwest Australia (Battley, Riegen and Hassell unpubl.), which shown a similar pattern. It is possible that the early arrival of *baueri* enables them to secure the highest quality refuelling sites, which happen to be present in the more easterly sites; however, each subspecies in essence uses the coastline nearest to the direction of arrival and subsequent departure, so there may be no need to invoke any hypotheses about competition to explain their distributions.

Round-trip time budgets

The complete round-trips recorded for both subspecies provide the first accurate information on how the annual migrations are apportioned into flight, staging, breeding, and migration components in an extreme long-distance migrant shorebird. For both subspecies, the strategy of having just a few, sustained multi-day flights and extended staging periods resulted in flight being only a small component of the time spent on migration. Daily movement rates were high when flying, e.g. 1410 ± 110 km d^{-1} and 1430 ± 140 km d^{-1} for *baueri* and *menzbieri*, respectively, on the northbound legs from Australasia to the Yellow Sea region. While these are not the highest short-duration travel rates detected among migrants (Stahl and Sagar 2000, Klaassen et al. 2011), the fact they are sustained for up to or over a week of flight makes for exceptionally fast movements across the globe during the flight periods of migration. These major flights by godwits occurred on only ~9–12% of the total period individuals were away from the non-breeding grounds. A large proportion of the time spent away from the non-breeding grounds was spent staging (almost half of the time for one *baueri* and over two-thirds for *menzbieri*). Overall, ca 60–80% of the total time away from the non-breeding grounds was associated with migration rather than breeding.

Differences in migration speeds between migrations towards or away from the breeding grounds have been established in a number of species, though generally with fairly small samples. Including fuelling time, red-backed shrikes *Lanius collurio* travelled 88% faster on spring migration than autumn migration (Tøttrup et al. 2011). Ospreys *Pandion haliaetus* migrating between Africa and Sweden travelled 31% faster overall on spring than autumn migration (Alerstam et al. 2006). Two female hoopoes *Upopa epops* travelled

38 and 51% faster on spring migration than autumn (active travel times only) (Bächler et al. 2010). Peregrine falcons *Falco peregrinus* travelled 15% faster on northward than southward migration (Fuller et al. 1998). This is generally consistent with the idea that selective time pressures are higher travelling to versus from the breeding grounds, but differences in wind assistance may also correspond with faster ground speeds on spring migration (Kemp et al. 2010). Both *baueri* and *menzbieri* showed the opposite pattern, travelling faster on southward than northward migration. For *baueri*, this difference relates to both the shorter distance travelled on southward migration (11 690 km direct rather than 17 590 km via Asia) and the longer initial fuelling period (estimated at 75 d in New Zealand and 44 d in Alaska). *Menzbieri* also have a long initial fuelling period that, together with a comparatively long staging period in Asia, contributes to a slow migration speed on northward migration. Whether this slow initial fuelling on the non-breeding grounds reflects constraints on fuelling (in NWA, as has been suggested for tropical-wintering red knots: Piersma et al. 2004) or an opportunity enabled by a lack of avian predators (as in New Zealand, so hence no mass-dependent predation risk, Kullberg et al. 1996) is unclear.

Conservation implications

Australasian bar-tailed godwits exemplify the migration strategy of relying on only a few sites to refuel and making remarkable movements that cover 10 000 km and span hemispheres. The persistence of such extreme flights (Gill et al. 2009, Piersma 2011) relies on the continued presence and productivity of these important staging sites (Warnock 2010).

Human impacts on the sites used by godwits vary greatly. The breeding grounds in Alaska and Siberia and the non-breeding grounds in Australia and New Zealand are generally subject to low levels of modifications on tidal flats, although high-tide roosts on non-breeding grounds are increasingly disturbed by human recreation. In contrast, the tidal flats of the Yellow Sea region are arguably the most threatened in the world. Almost 1.4 billion people live in the three countries surrounding the Yellow Sea, which all actively claim tidal flats for industrial and other developments (Moores et al. 2008, Birds Korea 2010). Recent analyses by Amano et al. (2010) suggest that tidal reclamation is having a negative population-level effect on a number of shorebird species that use the Yellow Sea, including the bar-tailed godwit. The scale of development in this region is massive. In South Korea, the Saemangeum project involves a 33-km-long seawall enclosing over 30 000 ha of tidal flats known to formerly host more than a half a million shorebirds (Moores et al. 2008, Birds Korea 2010). In Bohai Bay, development threatens virtually all of the tidal flats recently discovered to hold much of the East Asian-Australasian Flyway's red knot populations on northward migration (Rogers et al. 2010, Yang et al. 2011). In addition to the dire immediate concerns prompted by these massive reclamation projects, future climate change threatens to inundate critical non-breeding and staging areas through rising sea levels (Galbraith et al. 2002), modify habitat of high-latitude breeding grounds (Hinzman et al. 2005, Meltofte et al. 2007) and potentially affect global wind patterns on which godwits rely for migration (Gill et al. 2009).

Our study confirmed the critical importance of three key staging sites to migrating bar-tailed godwits – Yalu Jiang, China, the Kuskokwim Shoals, Alaska, and the New Siberian Islands, Russia. Yalu Jiang is well known for its importance to godwits (Barter et al. 2000, Barter 2002), and the most recent survey there (April 2010) recorded 85 000 godwits (Riegen unpubl.). Six of the nine satellite tagged *baueri* used Yalu Jiang on northward migration; three *menzbieri* staged at Yalu Jiang on northward migration, and four of eight *menzbieri* passed through or staged at Yalu Jiang on the way south.

In Alaska, Kuskokwim Shoals is a region of coastline on the southwest YKD (Fig. 2) where a series of sandy barrier islands provides safe roosting habitat adjacent to rich, pristine tidal flats upon which birds feed. All satellite-tagged *baueri* in this study used the ~80-km-long stretch of coast centered on the Kuskokwim Shoals when fuelling for southward migration, as did all 16 birds from New Zealand tracked via geolocators in a separate study (Conklin and Battley unpubl.). It is clear from these efforts and previous studies (Gill and Handel 1990) that the central and southern YKD is of paramount importance to autumn staging godwits. An unexpected finding from our work was the link shown between the YKD and Alaska Peninsula estuaries. The latter are known to support populations of godwits throughout the staging period and godwits have been observed departing on their southward migration from these sites (Piersma and Gill 1998, McCaffery and Gill 2001). The satellite-tagged godwits revealed a number of flights between the Kuskokwim Shoals and Alaska Peninsula estuaries over the course of a few weeks or even days (even including multiple flights by individuals). The function of these site-exchanges remains unclear.

Every *menzbieri* that we tracked headed to the New Siberian Islands to stage before migrating southward back to the Yellow Sea. As none of our tracked birds bred successfully we have no data on whether this movement occurs in all birds. The lack of rich tidal habitats (such as the YKD provides for *baueri*) near the breeding grounds of *menzbieri* (P. S. Tomkovich pers. comm.) means that fuelling for the southward migration for this subspecies occurs on tundra rather than on mudflats and raises the possibility that the New Siberian Islands region is as important to *menzbieri* as the YKD is to *baueri*.

Overall, the results of this study reveal the bar-tailed godwit's extreme reliance on a few staging sites for a migration that can encompass > 30 000 km and take half a year. These staging sites have the capacity to act as population bottlenecks for godwits (Taylor and Norris 2010) and degradation of these sites appears to already be impacting on bar-tailed godwit populations (Amano et al. 2010). Bar-tailed godwits are highly site-faithful throughout their annual cycle (McCaffery and Gill 2001, Battley et al. in press, Battley and Conklin unpubl.). Such site-fidelity could limit birds' knowledge of and ability to move to alternative sites if development compromises traditionally used staging sites, or it may also indicate a real absence of suitable alternatives. Although the most critical conservation threats to bar-tailed godwits exist in the Yellow Sea region, effective conservation of these populations requires multinational efforts to protect shared resources. Especially for sites within the Yellow

Sea, means are needed to ensure there is adequate protection of the habitats used by godwits to perpetuate the greatest known avian endurance migration.

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