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Consistent annual schedules in a migratory shorebird

Phil F. Battley*,†

Department of Mathematics and Statistics, Otago University, PO Box 56, Dunedin, New Zealand
**philbattley@quicksilver.net.nz*
†*Present address: School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand*

Many migratory birds start prebreeding moult and premigratory fuelling some months before the breeding season and face severe time constraints, while travelling up to 15 000 km between non-breeding and breeding grounds. Shorebirds typically leave Southern Hemisphere non-breeding areas over a 3–4 week period, but whether they benefit from interannually consistent timing of departure is unknown. Here, I show that individual bar-tailed godwits (*Limosa limosa baueri*) from New Zealand are highly consistent in their migratory scheduling. Most birds left within the same week each year (between-year repeatability, *r*, of 0.83) and adult males, which moult into a bright breeding plumage, were also highly repeatable in the extent of their prebreeding moult ($r=0.86$). This is consistent with the hypothesis that birds have individually optimized migration schedules. Within adult males, but not females, smaller birds tended to migrate earlier than large birds. Whether this reflects differences in size-related migration speed, optimal breeding time at different sites or size-related natural or sexual selection pressures, remains unknown.

Keywords: migration; timing; repeatability; plumage; shorebird; age differences

1. INTRODUCTION

The timing of arrival on the breeding grounds can be a critical element in the fitness of migratory birds (Both & Visser 2001), and migration is often portrayed as being a period of severe time constraints; but while there are ample examples of the benefits of early nesting (such as increased reproductive output and subsequent recruitment of young, e.g. Møller 1994*a*), little is known about how individuals schedule their entire migrations (Drent *et al.* 2003).

It is clear that there can be both extrinsic and intrinsic influences on the timing of migration. Habitat quality, for instance, can affect fuelling rates and consequently when individuals depart from non-breeding grounds (Marra *et al.* 1998) and arrive on the breeding grounds (Gill *et al.* 2001; Norris *et al.* 2004). Individual variation also exists, with early arrival on the breeding grounds being related to the quality in barn swallows (*Hirundo rustica*; Møller 1994*b*), but to body size in dusky warblers (*Phylloscopus fuscatus*; Forstmeier 2002). Whether individuals show interannually consistent migratory schedules is less known, though repeatabilities of arrival date on the breeding grounds of 0.18–0.51 have been reported for barn swallows (Møller 2001), dusky warblers (Forstmeier 2002) and black-tailed godwits (*Limosa limosa islandica*; Gunnarsson *et al.* 2006). These suggest that individual timetables may exist.

Here, I assess whether individual bar-tailed godwits (*Limosa lapponica baueri*) show year-to-year consistency in the timing of migration from a Southern Hemisphere non-breeding site and in the extent of their prebreeding moult (which is often interpreted as a signal of quality; Piersma & Jukema 1993), as is expected if birds migrate according to regular individual schedules. By studying birds at a single non-breeding site, confounding factors such as different habitat qualities and environmental conditions experienced by birds could be avoided. I tested whether individuals: (i) departed on a 15 000 km northward migration from New Zealand at the same time in different years, having (ii) undergone the same amount of prebreeding moult, as is expected if migration is internally rather than externally controlled.

2. MATERIAL AND METHODS

Bar-tailed godwits of the subspecies *baueri* breed in Alaska and ‘winter’ in Australia and New Zealand, making the longest migrations of any bar-tailed godwit population and possibly the longest single migratory flight of any bird (Gill *et al.* 2005). Returning to the breeding grounds, birds depart New Zealand from the second week of March to the first week of April (Battley 1997; P. F. Batley 2003–2006, unpublished data) and make a long flight towards eastern Asia (Battley & Piersma 2005). After refuelling in the Yellow Sea region of China and the Korean Peninsula, birds fly another 5000 km from late April/early May to the breeding grounds (McCaffery & Gill 2001).

Godwits were caught from 2004 to 2006 in the western Firth of Thames, North Island, New Zealand (37°11′ S, 175°19′ E), measured and individually colour banded. Birds were sexed on bill length (Battley & Piersma 2005) and aged on wing moult and contour feather appearance and wear. Intensive (near daily) resighting efforts were made at roosts in the western Firth of Thames in March 2004–2006 to determine when individual birds left on migration and what stage of prebreeding moult they were in. Whenever possible, banded birds were sexed visually on the basis of body size, bill length and breeding plumage (only males moult into an extensively red plumage; Higgins & Davies 1996). Breeding plumage was scored on a 1–7 scale (including half scores where necessary) for males (from non-breeding to complete breeding plumage; Piersma & Jukema 1993) and on a 1–4 scale for females (which do not develop much red plumage). Plumage scores assigned in the field proved to be highly consistent. The repeatability (discussed later) of plumage score based on 671 consecutive resightings not more than 7 days apart in March (so that differences in plumage score probably arose from scoring differences rather than from moult) involving 106 birds was 0.96 ($F_{670,671}=43.851$, $p<0.001$). Frequent resightings of site-faithful birds allowed estimation of the date of departure for some individuals (the date of the last sighting). Dates of last sighting are given as ‘March days’, starting on March 1. They were standardized to account for 2004 being a leap year and are referred to as ‘apparent departure dates’. Late-departing birds tend to be resighted more often than early-departing birds (number of records in March was positively correlated with date; Pearson’s $r=0.55$) as they were ‘available’ for longer, and the declining number of birds present through the departure period probably also caused detection rates to be higher late in the season. The number of resightings per bird was positively correlated between years (Pearson’s $r=0.68$), so the relative accuracy of last dates should not systematically differ between years. As dates of last sightings and plumage do not score exact measures, reduced major axis (RMA) regressions are used to explore their consistency among years. Individual apparent departure dates were treated as independent in each year. Birds aged as immature (2 or 3 years old) and adult are separated in analyses. Repeatabilities (the intraclass correlation coefficient) of

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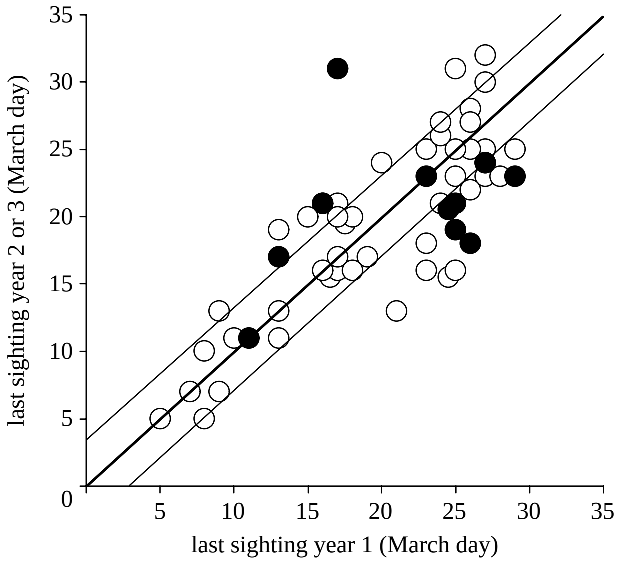

Figure 1. Apparent departure dates of bar-tailed godwits from the Firth of Thames, New Zealand, in successive years from 2004 to 2006. Adults are shown by hollow symbols, immatures by filled ones. The bold reference line shows a 1 : 1 relationship; thin reference lines demarcate the period of 3 days on either side of that. Some overlapping points have been offset for clarity.

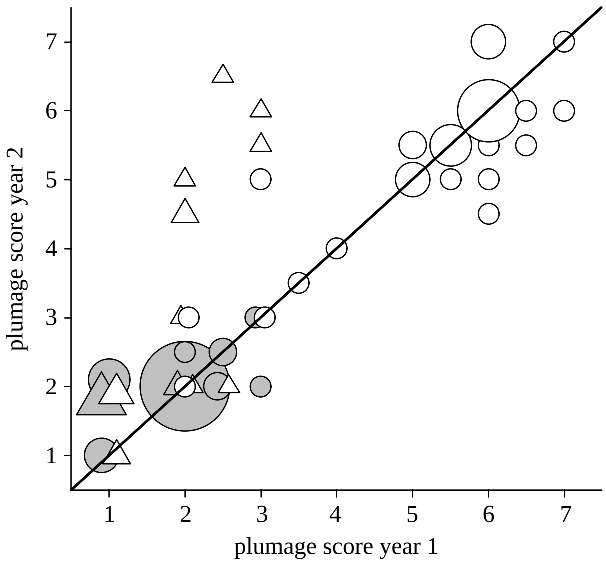

Figure 2. Plumage scores of bar-tailed godwits in different years before migration from the Firth of Thames, New Zealand, in 2004–2006. Circles, adults; triangles, immatures; filled symbols, females. Symbols are scaled relative to the number of records of birds in those plumages. The reference line shows a 1 : 1 relationship. Some overlapping points have been offset for clarity.

departure date and plumage score were calculated according to Lessells & Boag (1987).

3. RESULTS

Departure dates were estimated for 41 birds in 2 years and eight birds in 3 years, giving a total of 57 comparisons. The date of the last sighting in 1 year was strongly correlated with the last date in the previous year (figure 1). The slope of the RMA relationship between departure dates in different years was 1.02 (±s.e. 0.08, 95% CI$=$0.85–1.19, $R^2=0.60$), which was not significantly different from a 1 : 1 relationship. However, variation was present, with some birds differing by up to 14 days. Some of this variation appears to be age-related; of the birds whose last records varied by more than 3 days between years (reference lines in figure 1), immatures were disproportionately represented. Of 11 immatures, 8 (73%) were recorded outside the ±3 day window, compared with 17 of 46 adults (37%; Fisher's exact test, $p<0.05$). Generally, the majority of birds (32 of 57 comparisons) left in the same week each year, despite migration occurring over a four-week period in total.

Some individuals were remarkably consistent in their timing. For 23 comparisons, birds were recorded last within 2 days of their previous last record, and five birds were consistent to within 3 days over all 3 years. Overall repeatability (r) of the apparent departure date was 0.77 ($F_{48,57}=8.144$, $p<0.001$), but if immatures (which had poorer repeatability; $r=0.38$, $F_{10,11}=2.233$, $p>0.1$) are excluded, repeatability becomes 0.83 ($F_{37,46}=1.958$, $p<0.001$).

The extent of prebreeding moult done before departure was also highly consistent among years for adults (figure 2; RMA slope of 1.05±0.04, 95% CI$=$0.98–1.12, $R^2=0.91$, did not differ from one). Between-year repeatability of plumages for adult males was 0.86 ($F_{26,33}=14.773$, $p<0.001$). As breeding plumage is age related in young birds and some birds increased their breeding plumage scores across years, repeatability for immature males was much lower, ($r=0.21$, $F_{13,15}=1.551$, $p>0.2$). Repeatability of adult female breeding plumage scores was lower than for males ($r=0.61$, $F_{22,25}=4.279$, $p>0.001$).

For adult males, apparent departure date was unaffected by breeding plumage score (multiple regression using mean plumages and departure dates for 20 males recorded in more than 1 year and seven males recorded in 1 year; plumage standard coefficient$=-0.060$, $t=-0.345$, $p=0.7$), but it was by body size: smaller males left earlier than larger males (total head length standard coefficient$=-0.576$, $t=-3.296$, $p=0.003$; overall $R^2=0.313$; the same relationship held for other morphological measures). Neither plumage score nor total head length influenced departure date in females ($n=28$, $p>0.6$ for both variables).

4. DISCUSSION

Adult bar-tailed godwits migrating north from New Zealand are highly consistent, in when they leave on migration and in what plumage they depart in. Even allowing for year-to-year variation in weather conditions that doubtlessly affected whether birds departed on a given day (Battley 1997; Green 2004), the repeatabilities of apparent departure date (0.83) and the extent of breeding plumage of adults (0.86) imply that birds have quite strict individual 'schedules' for physical appearance and timing of migration. The repeatabilities of migration timing for godwits are considerably higher than those for male barn swallows (arrival date $r=0.51$; Møller 2001), dusky warblers (arrival date $r=0.34$; Forstmeier 2002), black-tailed godwits (arrival date $r=0.18$; Gunnarsson *et al.* 2006) and Bewick's swans (*Cygnus columbianus bewickii*; r_{approx} of Lessells & Boag (1987) is 0.15 for arrival at and 0.06 for departure from the non-breeding grounds, calculated from Rees 1989). This suggests that the individual optimization of departure schedules in bar-tailed godwits is especially strong.

While the control of migration is at least partially genetic (Berthold 1996), the greater variation in migration timing of immatures than adults implies that behavioural refinement with experience may be involved in determining the optimal departure date. For plumage, the consistent appearance of adult males suggests that differences between individuals have a genetic basis. Photographs of males in different years reveal them to be qualitatively identical in terms of where on the body retained non-breeding plumage is (unpublished data), indicating a high level of control of the moulting process. The lower repeatability of plumage score for females probably reflects the limited number of categories used and the small differences between them.

The breeding plumage of godwits has been suggested to be a reliable indicator of individual quality (Piersma & Jukema 1993), yet in my study, it had no influence on the timing of migration. Instead, there was a size gradient in departure dates, with smaller males migrating before larger ones. This gradient is unlikely to be a function of absolute size *per se*, because females are larger than all males yet overlapped completely with them in the timing of migration. Whether it reflects natural or sexual selection pressures is not clear: small males could migrate slower, breed earlier (e.g. in lower latitudes or altitudes) or need to arrive earlier for competitive reasons than large males, but there is no direct evidence on any of these possibilities. Predicted flight ranges of New Zealand godwits do not vary with body size (Battley & Piersma 2005), suggesting that a systematic size-related difference in flight length and number of stopovers is unlikely. However, there are no data on actual departure masses of birds in this study.

Gunnarsson *et al.* (2004) found that black-tailed godwits breeding in Iceland showed remarkable synchrony in the arrival of mates despite birds having wintered up to 1900 km apart. One suggestion for how such synchrony was maintained is that pairs independently synchronize their arrival to the optimal time for each specific breeding location. If, as I suggest here, birds do have strong individual timetables for migration, then synchronous arrival on the breeding grounds is a likely consequence. In fact, given how short the window of opportunity for pair formation seems to be in black-tailed godwits (the two divorces in 10 pairs were both in pairs where mates arrived 8 days or more apart; Gunnarsson *et al.* 2004), it could be argued that mate retention is simply a by-product of strong individual migration schedules that happened to coincide and allow pair formation in the first place.

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