

Plumage and timing of migration in bar-tailed godwits: a comment on Drent et al. (2003)

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Rudi Drent and co-workers presented data on the plumage and apparent quality of bar-tailed godwits (*Limosa lapponica*) migrating northwards through the Netherlands en route from Africa to Siberia (Drent et al. 2003). They identified two groups of males in their samples based on the extent of the prebreeding moult – birds with extensive red breeding plumage ('dark' birds) and birds with little red plumage ('pale' birds). The pale birds were considered to be low quality individuals, which showed a higher incidence of cestode infestation (32.4% of individuals c.f. 12.2%) and, while the dataset was very small, lower subsequent survival (no pale birds were recaptured in later years whereas 11 red males were). They radio-tracked birds to determine the migration date of pale and dark birds towards the breeding grounds and were surprised to find that, contrary to expectation, the pale birds left on migration earlier than the dark birds. Noting that there was no evidence for any age-related changes in the breeding plumage score of male godwits (though their Fig. 7 indicates they never recaptured any pale birds so could not test this), Drent et al. erected a hypothesis to explain the unexpected finding. The pale birds were suggested to be 'desperates', birds of low quality whose only chance of successful breeding was to arrive early on the breeding grounds and achieve the benefits of prior occupancy on good territories. Given that it is generally high-quality individuals that can afford the risks of early arrival on the breeding grounds (Møller 1994), the lower apparent survival of these pale godwits reflected the costs associated with this strategy.

Appealing as this idea may be, data collected on the non-breeding grounds of a more accessible population of godwits show that most pale birds in Drent et al.'s study are almost certainly immature birds, potentially on their first migration. Together with colleagues from

the Ornithological Society of New Zealand, I have individually colour-banded godwits (subspecies *baueri*) in New Zealand since 2004 and aged these birds at capture. Godwits show delayed maturity and young birds remain on the non-breeding grounds for up to 3–4 years before migrating northward (McCaffery and Gill 2001). Where possible birds were aged as 1 (in the 1st year of life), 2 or 3+, though at some times of year birds could simply be designated as immature (age 2/3). Ageing was by plumage (juveniles have distinctive upperpart contour feathers that are retained until birds reach the non-breeding grounds), timing of wing moult (adults start wing moult only after arrival on the non-breeding grounds in September–October, whereas immatures that did not migrate to the breeding grounds start earlier; juveniles may undergo partial wing moult in the southern autumn) and feather condition (juvenile primaries become highly abraded by the time of the southern winter; adult breeding plumage contour feathers and tertials become very worn during the breeding season). Checks were then made at high-tide roosts to determine the presence of colour-banded birds and, when practical, the breeding plumage of males was scored on the same scale as used by Drent et al. (where 1 = complete non-breeding plumage, 2 = a trace of breeding plumage, 3 = 25% breeding plumage, 4 = 50% breeding plumage, 5 = 75% breeding plumage, 6 = only a trace of non-breeding plumage remains, and 7 = complete breeding plumage).

Resightings of marked birds in New Zealand show that the breeding plumage grown by male godwits is strongly age-related (Fig. 1). Across all birds, most age 1 and 2 godwits had very little breeding plumage, whereas many 3rd-year and most 'adult' godwits had substantial breeding plumage scores (Fig. 1, upper). The pattern of

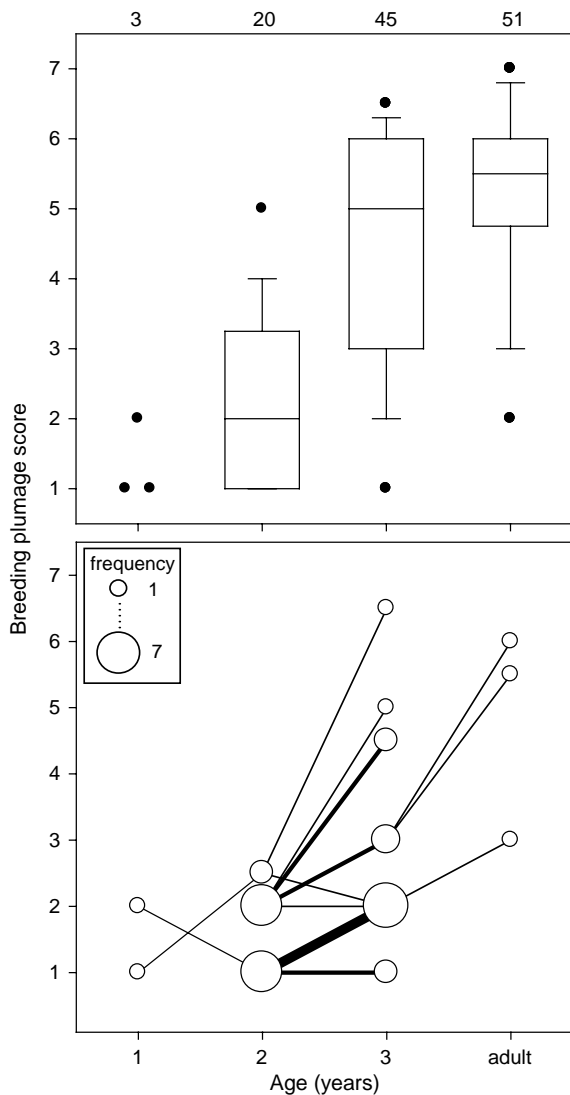


Fig. 1. Plumage scores of male bar-tailed godwits in the Firth of Thames, New Zealand. Scores represent the maximum plumage score recorded for birds before migration (which occurs in March) or, in the case of non-migrating immatures, over the northern summer period when adults are on the breeding grounds. Upper plot: plumages of males of different ages. Boxes enclose the 25th, 50th and 75th percentiles, whiskers the 5th and 95th, and outliers are shown as dots. Sample sizes are shown above the plot. Lower plot: changes in breeding plumage of individuals over time. Point areas are proportional to sample size. Lines join plumages of individuals seen in different years (thin line = 1 individual with that plumage change, medium line = 2 individuals, thick line = 4 individuals).

increasing breeding plumage with age is confirmed by resightings of individuals in consecutive years (Fig. 1, lower): scores increased for most birds as they got older, and the only birds that did not were recorded as having

a trace of breeding in one year and not the next and score 2–3 in one year and 2 the next. While there is variation between individuals of the same age, most pale birds are young birds.

Once adult, however, plumage scores of adults are highly repeatable between years ($r=0.86$, $F_{26,33} = 14.773$, $p < 0.001$; Battley 2006; repeatabilities calculated according to Lessells and Boag 1987). In contrast, repeatability of plumage scores of birds aged as immatures (age 2 or 3) when banded is much lower ($r=0.21$, $F_{13,15} = 1.551$, $p > 0.2$), as young birds increased their breeding plumage scores as they got older.

The age of first migration of godwits is difficult to ascertain fully, as the figures in the literature (not until nearly 4 years old in *baueri*; McCaffery and Gill 2001) are based on the presence of birds of these ages on the nonbreeding grounds during the breeding season. This can only determine the age that some birds do not migrate until – it does not prove that no younger birds have migrated. Five sightings of colour-banded birds from New Zealand on migration have confirmed that not all godwits delay migration until they are what would be considered adult. Two birds banded as juveniles in December 2004 were seen on migration in South Korea and China in 2006, making them 2nd-years when migrating (the official birth-day for northern hemisphere breeding shorebirds is 1 August; these birds would have been around 21 months old when they started their first northward migration). Three birds banded as probable 2nd-years have been seen on migration, one while still two years old, two while probably three years old. The probable 2nd-year was photographed in Japan in April 2005 (Fig. 2) and in appearance is virtually identical to the pale birds shown in Drent et al. (2003, their Fig. 6). A further bird was banded as a juvenile on the staging grounds in Alaska in September 2004 and resighted there in September 2006, also having migrated as a 2nd-year (R.E. Gill and M. Green, pers. comm.).

Together, these data from colour-banded birds in New Zealand establish (a) that immature godwits have low breeding plumage scores that tally with the pale birds recorded on migration by Drent et al., (b) adult godwits mostly have the higher breeding plumage scores taken to represent the 'good quality' Dutch birds, (c) once adult there is little if any plumage change between years, and (d) young pale birds can migrate towards the breeding grounds earlier than hitherto recognised. Because there would be little difference between immatures and true adults on migration apart from the extent of breeding plumage (primary feather wear would only be subtly different), it is not surprising that Drent et al. treated all their pale and dark birds as adults.



Fig. 2. Immature male bar-tailed godwit on migration in Japan, April 2005. This bird was banded in New Zealand on 31 October 2004 as a probable 2-year old, seen leaving its non-breeding site in a flock on migration on 17 March 2005 and photographed in Japan on 2 April 2005. Photo: Kouji Takenaka.

So what do these findings mean for the hypothesis of risky deserters of Drent et al. (2003) Instead of representing a state-dependent behavioural strategy adopted by low-quality or poor condition birds, these birds should probably be considered naïve first-time migrants with no prior experience of final flight duration, spring conditions and the optimal arrival date on the breeding grounds. Young migrants can only have a basic genetic program of where and when to migrate (though they might travel in flocks with adults), whereas adults have the benefit of fine-tuning their migrations based on experience. Suboptimal decisions on when to migrate are therefore expected in immatures more than adults. Supporting this idea, immature godwits in New Zealand changed their departure dates in subsequent years more than adults did (Bartley 2006). The tendency for these birds, however, was to advance their departure date, as they left on average slightly later than adults did (but not significantly; mean of 23 March for nine probable first-time migrants versus 20 March for average departure dates of 41 adults recorded in 2 or 3 years; T-test assuming unequal variances, $T_{12,7} = 1.434$, $p > 0.1$; note that the departure span for adults completely encompassed the dates for immatures).

With the small sample size of pale godwits radio-tracked by Drent et al. it is difficult to know how real the earlier departures of pale (young) birds are. If they are real, the question becomes why immatures would consistently migrate to the breeding grounds earlier than adults, particularly if there was selection against this (as suggested by the absence of pale birds in recaptures between years in the Netherlands; this could also be

explained by lower site-fidelity of immatures rather than lower survival). Perhaps the timing of migration of immatures represents the genetic breadth of the population, which includes early departures that are cropped by mortality in some years but could allow early breeding in others (when conditions are amenable). Such early arrival by naïve youngsters could provide a mechanism by which the population as a whole could adjust the timing of breeding towards an increasingly early optimal breeding date (Both and Visser 2001). Alternatively, immatures could migrate in shorter flights than adults, refuelling en route at sites that thaw earlier than the actual breeding grounds that later adults fly directly to, or some pale birds could even be very old, experienced individuals that no longer undergo a full moult. It is all too easy to speculate on such topics; it is probably wiser to refrain until stronger datasets exist.

High parasite loads in young birds are not unusual (Borgsteede et al. 1988), and there is not necessarily any direct functional link between parasite loads and extent of moult in either male (Drent et al. 2003) or female (Piersma et al. 2001) bar-tailed godwits. Such analyses in the future will need to explicitly account for age effects.

The logistics of studying trans-hemispheric migrants will always be challenging, but a full understanding of how individuals schedule their migrations demands such large-scale approaches (Marra et al. 1998, Norris et al. 2004, Gunnarsson et al. 2005). Inferences about migrants from stop-over sites in the absence of information from the initial fuelling sites can lead to dubious conclusions. While 'risky deserters' may exist in migratory bird populations, there is as yet no evidence for their existence in bar-tailed godwits. And if the pale birds recorded on migration are indeed young birds, then conclusions based on the assumption that all birds on migration are adult (implicit in Piersma and Jukema 1993) may need revisiting.

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