

barred) predispose a bird to feather-pecking and the way in which this is influenced by the social environment through frequency-dependent effects.

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Pair bonds

Arrival synchrony in migratory birds

Synchronous arrival of pairs of migratory birds at their breeding grounds is important for maintaining pair bonds and is achieved by pairs that remain together all year round. Here we show that arrival is also synchronized in paired individuals of a migratory shorebird, the black-tailed godwit (*Limosa limosa islandica*), even though they winter hundreds of kilometres apart and do not migrate together. The mechanisms required to achieve this synchrony and prevent 'divorce' illustrate the complexity of migratory systems.

Long-lived migratory birds generally show high degrees of mate fidelity, and divorce is often followed by a decrease in reproductive success¹. Synchrony in timing of arrival on the breeding grounds is thought to be crucial for retaining a mate from the

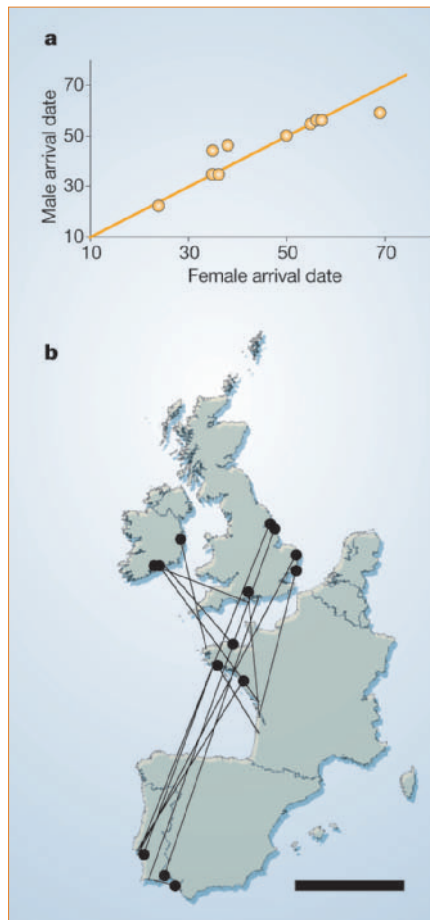


Figure 1 Paired black-tailed godwits arrive at their breeding sites synchronously but winter separately. **a**, The arrival dates (days from 31 March) of paired males and females were highly correlated ($r=0.97$, $P<0.001$); the regression line indicates identical arrival times for males and females. For each pair, data are for one year only. **b**, Wintering locations of pairs of godwits. Each line links a pair and the circle indicates the female's location. Locations of 12 of the 14 pairs are known in the same winter. Godwits show a very high degree of between-year philopatry in winter.

previous year and avoiding a costly divorce^{2,3}. In a few species¹, pairs both migrate and winter together, so synchronous arrival in spring is inevitable. In many others, one sex departs from the breeding grounds ahead of the other and so the pair migrate separately⁴; however, their arrival could still be synchronous if they wintered together or were reunited during the spring migration.

The Icelandic black-tailed godwit winters between Britain and Iberia and breeds almost exclusively in Iceland⁵. About 1.5% of the population is currently individually colour-marked⁵, and the winter destinations of 55% of these birds have been identified using a large network of volunteer observers. To investigate the arrival patterns of pairs of godwits, we located individuals that had been colour-marked as breeding birds in previous years by twice-weekly searches of 14 study plots on the breeding grounds in southern Iceland, in 2002 and 2003.

Breeding godwits arrived over a one-month period between mid-April and the

middle of May. Previously paired males and females arrived within 3.1 (± 1.3 s.e., $n=10$) days of one another (Fig. 1a). These remarkably synchronous arrival times are not achieved through pairs wintering in the same area and therefore departing together: paired male and female godwits winter, on average, 955 km apart (± 165 s.e., $n=14$; range, 49–1,946 km; Fig. 1b).

Neither do the pairs meet during migration: during 1999–2004, we studied migratory flocks upon their arrival in Iceland (before they moved on to the breeding grounds)^{5,6} and never encountered paired birds in the same flocks, despite locating 15 marked individuals whose mates were known. Arrival synchrony seems to be related to mate retention, however, as the only divorces occurred in two of the three pairs that arrived more than eight days apart (Fig. 1a).

How is this degree of synchrony maintained between pairs when they winter so far apart and the environmental conditions for migration are likely to differ locally? It is possible that pairs of birds may winter in areas of similar quality (despite their geographic separation) and so be in a similar condition to arrive at specific times in spring; or they may share some genetic or physiological determinant of timing of migration; or they may independently synchronize their arrival to the optimal time for each specific breeding location (for example, to exploit peaks in resource abundance). As individuals often use a series of passage sites during spring migration, they may refine these timings as they approach their breeding grounds. Identifying which of these mechanisms is operating is likely to be key to understanding how synchrony is achieved and divorce avoided in migratory species.

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