Feather-pecking and victim pigmentation

A genetic factor that encourages this form of farmyard bullying has been identified.

Feather-pecking in domestic birds is associated with cannibalism and severe welfare problems[1]. It is a dramatic example of a spiteful behaviour in which the victim's fitness is reduced for no immediate direct benefit to the perpetrator[2] and its evolution is unexplained. Here we show that the plumage pigmentation of a chicken may predispose it to become a victim: birds suffer more drastic feather-pecking when the colour of their plumage is due to the expression of a wild recessive allele at *PMEL17*, a gene that controls plumage melanization[3], and when these birds are relatively common in a flock. These findings, obtained using an intercross between a domestic fowl and its wild ancestor, have implications for the welfare of domestic species and offer insight into the genetic changes associated with the evolution of feather-pecking during the early stages of domestication.

To investigate whether there could be a genetic basis for a chicken becoming a target of feather-pecking, we analysed the variance in feather damage due to feather-pecking suffered by individual birds (Fig. 1a; for methods, see supplementary information). These birds were from the second generation of a large-scale intercross between a line of white leghorn domestic fowl (*Gallus gallus domesticus*) and its wild ancestor, the red junglefowl *G. gallus*. We found that feather-pecking damage had a highly significant quantitative trait locus (QTL; residual variance explained, 14.9%) that coincided perfectly with the dominant white locus in the chicken genome[4] (31 compared with 32 centimorgans; Fig. 1b).

The domestic fowl's dominant white allele (*I*) at this locus inhibits feather pigmentation, whereas birds homozygous for the wild-type allele (*i*) show a variety of pigmented (non-white) plumage. We found that these pigmented birds were significantly more vulnerable to feather-pecking than the white birds; a significant dominance effect revealed that heterozygous birds (*I/i*) that were white, or white with some minor pigmentation, were almost as well protected from feather-pecking as the *I/I* homozygotes (Fig. 1b, legend).

We showed previously that the dominant white colour is caused by a 9-base-pair insertion in exon 10 of the *PMEL17* gene, which encodes a melanocyte-specific protein that is essential for the normal development of eumelanosomes[3]. The fact that the QTL effect on feather-pecking and the *PMEL17* effect on pigmentation show the same mode of inheritance (the allele from the domestic chicken is almost completely dominant) indicates that *PMEL17* is likely to be the causative gene for this QTL. We conclude that the victim's phenotype is critical for stimulating this spiteful behaviour.

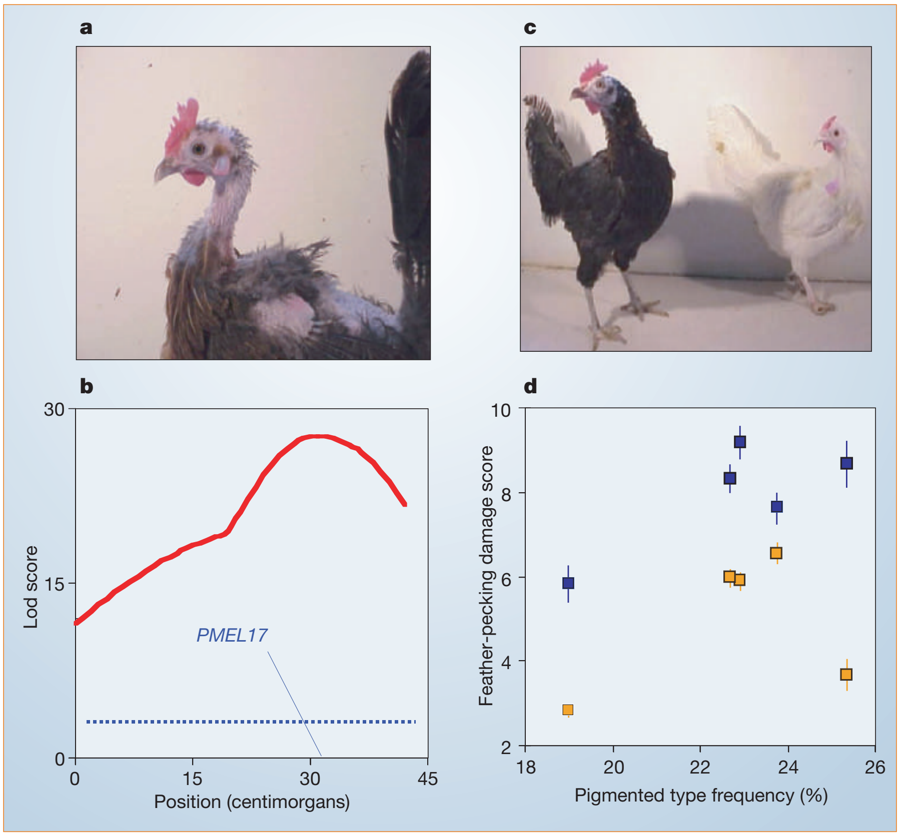

Figure 1 Chicken vulnerability to feather-pecking. **a,** Bird with feather damage due to feather-pecking by other birds. **b,** Lod scores for quantitative trait locus (QTL) on chromosome E22C19W28 associated with feather damage. The identified QTL coincides with the plumage-colour gene *PMEL17* and is significant at the genome-wide level (lod score, 26.3; $P < 0.0001$; dotted line: $P = 0.05$). Additive (1.67 ± 0.18) and dominance (−1.25 ± 0.29) effects (± s.e.) show that feather damage is 2.92 and 3.34 times higher in *i/i* than in *I/i* and in *I/I* birds, respectively: the tendency for *I/i* to suffer more feather damage than *I/I* birds was not significant. **c,** *PMEL17* plumage phenotypes: domestic, white type (*I/I*, right) and wild, pigmented type (*i/i*, left). **d,** Mean feather damage in pigmented (*i/i;* blue) and white (*I/i* and *I/I*; orange) birds in relation to the frequency of pigmented birds in a cohort; bars indicate standard error.

Social transmission[5] may contribute to the spread of feather-pecking when genetically predisposed victims are relatively common. We find an environmental effect that contributes to feather-pecking damage and is associated with the frequency of the two *PMEL17* plumage phenotypes (pigmented and white; Fig. 1c) in a cohort: pigmented birds are more vulnerable to feather-pecking than white birds when they are relatively common (Fig. 1d). Vulnerability to feather-pecking may therefore also be influenced by the relative frequency of the two *PMEL17* phenotypes, directly and through interaction with a bird's phenotype (cohort: $\chi^2_{4,720} = 122.52$, $P < 0.0001$; phenotype: $\chi^2_{1,720} = 112.79$, $P < 0.0001$; cohort × phenotype: $\chi^2_{4,720}$11.91, $P = 0.018$; Fig. 1d). In addition, the light-coloured wood-shavings that are used as floor litter may be more conspicuous when deposited on pigmented rather than on white birds[6] and so may act as a pecking stimulus.

The propensity to peck feathers is independent of the assailant's plumage genotype in the intercross studied here[7]. Some genetic variation associated with becoming a victim of feather-pecking has been found among other domestic lines[8–10]. The propensity to perpetrate or to become a victim of feather-pecking therefore seems to be genetically independent.

We have discovered a strong genetic effect that is mediated by plumage phenotype. Our findings illustrate the importance of a victim's phenotype in the evolution of spiteful behaviours such as feather-pecking and have crucial implications for the welfare of domestic species. Key issues still to be addressed are the extent to which differently pigmented plumage phenotypes (for example, black or 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 success[1]. Synchrony in timing of arrival on the breeding grounds is thought to be crucial for retaining a mate from the previous year and avoiding a costly divorce[2,3]. In a few species[1], 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 separately[4]; however, their arrival could still be synchronous if they wintered together or were reunited during the spring migration.

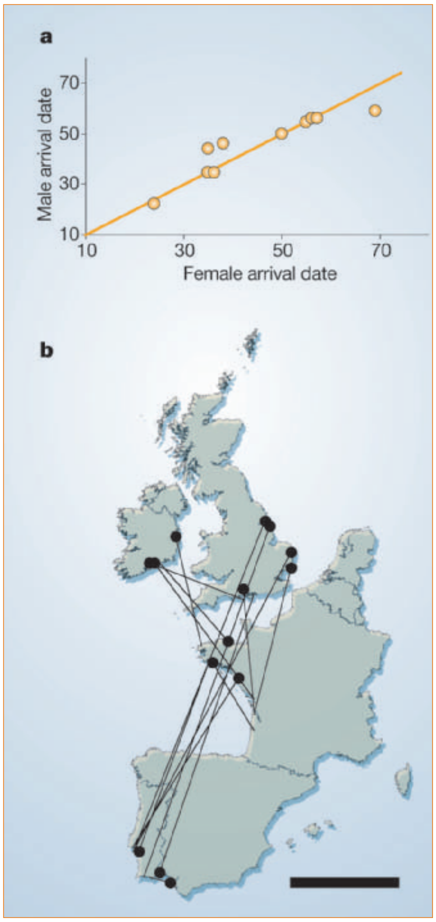

Figure 1 Paired black-tailed godwits arrive at their breeding sites synchronously but winter separately. **a,** The arrival dates (days from 31 March) of paired males and females were highly correlated ($r=0.97$, $P<0.001$); the regression line indicates identical arrival times for males and females. 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.

The Icelandic black-tailed godwit winters between Britain and Iberia and breeds almost exclusively in Iceland[5]. About 1.5% of the population is currently individually colour-marked[5], 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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