

Birds of a feather lek together

Paul W. Sherman

A lek looks like a winner-takes-all competition between males to attract females. But appearances could be deceptive, and the males might be a family group cooperating to their mutual evolutionary advantage.

The lek is nature's version of a singles bar. A group of males aggregates at a traditional site, where they perform intricate vocal, visual or chemical displays to attract receptive females. Lekking arenas contain no resources valuable to females and males give no parental care, so females choose mates by comparing males' physiques and displays, or copying choosy females. On most leks only a few, extremely attractive males do nearly all of the mating — so why do subordinates bother joining them? Two studies, one of black grouse in Finland, published in *Proceedings of the Royal Society*¹, and the other of free-ranging peacocks at Whipsnade Park in the United Kingdom, on page 155 of this issue², reveal that males lek with their kin. Males that are apparently unsuccessful may gain an evolutionary advantage by boosting the mating success of family members. Petrie *et al.* also show that peacocks recognize brothers by 'phenotype matching' — comparing other males with themselves.

Lekking is rare but taxonomically widespread, occurring mainly in insects and birds (about 200 species), but also in some mammals, amphibians and fishes³. Three hypotheses have been proposed to explain why males aggregate: the hotspot model (clusters form near places females frequently visit), the hotshot model (individuals cluster around attractive males to increase their chances of being noticed), and the female-preference model (males cluster because females like to visit groups, where they can choose a mate quickly and safely). Tests of each hypothesis have found support in some species, but not others³.

All three hypotheses predict that males should join leks to increase their mating opportunities. Indeed, in some species larger leks do attract proportionally more females. However, in many species mating success per male declines as lek size increases^{4,5}, raising the question of why males keep joining up. Either they have no better options, or they are gaining reproductive benefits in some other way.

For example, if larger, cooperatively displaying groups make leks more attractive, subordinate males might increase their inclusive fitness — the number of additional genes their behaviour enables kin to pass to the next generation — by joining leks dominated by their relatives^{6,7}. For example, when subordinates are brothers or sons of the

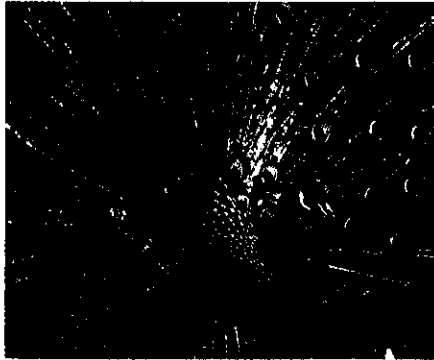


Figure 1 Display of unity? Petrie *et al.*² found that male peacocks choose related birds as lek mates. What's more, it seems that males don't need to learn who their relatives are to be able to recognize them.

alpha male, his matings will conceive their nieces and nephews or full- and half-siblings, respectively. The benefits of helping closely related dominants to attract more females may outweigh the subordinate males' own meagre mating opportunities.

A critical prediction of this kin-selection hypothesis is that males will be more related within than among leks. The first species tested was the long-tailed manakin, a bird that lives in Central American rainforests⁸. Males display cooperatively in pairs, but the dominant of the two wins 99% of the copulations. However, analyses of DNA microsatellites revealed that displaying pairs were no more likely to be related than any two randomly chosen birds. (Molecular techniques, such as DNA fingerprinting and microsatellite analysis, have been a godsend for behavioural ecologists, as they allow levels of relatedness to be measured directly — information that field observations alone cannot reveal.)

But the new studies^{1,2} have revived the kin-selection hypothesis. In the grouse, Höglund *et al.*¹ used DNA microsatellites to infer the existence of significant genetic differentiation among five winter flocks of males (but not females), and among 15 leks composed of males from the same and different winter flocks — in other words, males associate with family members. In the peacocks, Petrie *et al.*² used DNA fingerprinting to infer that relatedness was significantly higher within each of four leks than between them; average relatednesses for lek-mates approximated those of half-brothers. In both

black grouse and peacocks, larger leks — consisting of up to 20 males — attract more females and male mating success is skewed.

So, how did related males end up on the same arena? For the grouse, genetic structuring of winter flocks and leks was attributed to natal philopatry — the tendency for individuals to remain in the area where they grew up — although differentiation among leks from the same winter flock "suggests that some active kin-recognition mechanism may be at work"¹.

For the peacocks, the serendipitous extension of a sexual-selection experiment⁹ revealed that natal philopatry cannot be the explanation. In 1991, Petrie and her colleagues removed eight breeding peacocks that differed in their attractiveness to females from Whipsnade Park and moved them to Norfolk, over 100 km away. Each was penned with four randomly chosen peahens. Their eggs were collected daily, and the chicks hatched in isolation in an incubator. Chicks were ringed and reared in groups from the same and different pens. Presumably, therefore, they could not learn from their social environment who their relatives were. Early in 1992, 96 yearlings (three from each female) were released in Whipsnade Park.

In 1995, when the 19 surviving four-year-old males established permanent display sites, their territories were mapped by observers who were unaware of the birds' relatednesses. Surprisingly, there were highly significant tendencies for (full- or half-) brothers to display closer to each other than to non-relatives. Brothers were also nearest display-neighbours far more often than would be expected from chance.

There are three ways that the peacocks could have recognized their siblings¹⁰. First, related birds might prefer similar micro-environments, even in the homogeneous, non-native parkland. But the released males did not display near their fathers' ex-display sites, as would be expected if such a preference were heritable. Second, birds might learn to recognize the young they grew up with (normally their siblings), and later use this mental image to match the birds they encountered. But males that were reared together did not lek together. Third, males might learn their own physical features and later associate with phenotypically similar birds. Such self-referent phenotype matching¹¹, which Dawkins¹² dubbed the 'arm-pit



100 YEARS AGO

Many observers in different countries, noticing the fact that malaria is most prevalent at the most active period of mosquito life, have attributed malaria to the agency of this insect. Dr. Patrick Manson, in 1894, first brought the subject forward in England ... Bignami and Bastianelli, who had been trying unsuccessfully to infect a man by allowing mosquitoes to bite him, attributing their want of success to the use of the wrong kind of mosquito, and, acting on the observations of Grassi, tried again with some mosquitoes imported from the malarious district. This time they succeeded in infecting the man with malaria of the same type that prevailed in the district from which the mosquitoes came. ... Whether the *Anopheles* can be extirpated from a locality, and by what means, will be the problem for scientific workers resident abroad to settle; fortunately they seem to be confined to small areas, so the suggestion of Ross to draw off the water from stagnant pools may not be so hopeless a task as it would at first appear.

From *Nature* 7 September 1899.

50 YEARS AGO

For the woman, Dr. Turquet saw two possibilities fraught with anxiety and frustration and therefore likely to add to the sum of aggression in society. One is her entry into an occupational life in which her opportunities compare unfavourably with a man's. If, on the other hand, she prefers the older domestic role with its exemption from the need to compete on the male pattern, she then faces the anxiety of choosing and securing a husband, on whose adequacy her own social status will largely depend, and to whom she will lose some of her individual identity. In either case the woman meets an atmosphere of masculine superiority which contrasts sharply with her childhood experience of the mother's seeming superiority in the home. Aggression results from the inferiority which she feels in such an atmosphere. Hence, said Dr. Turquet, ambivalent feelings towards motherhood, the declining birthrate, and an unconscious desire to reject the more fundamental aspects of the feminine role.

From *Nature* 10 September 1949.

Many more extracts like these can be found in *A Beside Nature: Genius and Eccentricity in Science, 1867-1953*, a 266-page book edited by Walter Glazer and Constance O'Rourke. E-mail: Lor@uk.ac.uk

effect', could allow males with the same father to recognize one another, whether they were reared together or apart, as often occurs in species where males mate with many females.

I believe that this is the most likely explanation. However, confirmation requires identifying what heritable cues males use (for example, calls, plumage or odour), altering them experimentally, and observing whether manipulated males indeed prefer similar but unrelated lek-partners.

Petrie and colleagues' results² are important for several reasons. First, they (and Höglund *et al.*¹) suggest that lek-joining in some species is best analysed by considering inclusive fitness, not just male-male competition. Second, although phenotype matching has been observed in many invertebrates and vertebrates¹⁰ (most recently in chimpanzees¹³), this is the first report for a lekking species. Third, the likelihood of self-referencing in peacocks should galvanize studies of this intriguing, yet controversial^{10,11,14},

kin-recognition mechanism, particularly among species in which social learning is an inadequate or misleading guide to relatedness.

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Nanotechnology

Synthetic molecular motors

Anthony P. Davis

The construction of miniature, 'nanoscale' machines is a goal of modern science and technology, inspired by Richard Feynman's remark that "There's plenty of room at the bottom"¹. Chemists, by the nature of their discipline, are already at the bottom, manipulating the smallest entities that have complex shapes (molecules), and which can therefore be used as engineering components. While engineers and physicists explore the top-down approach to nanoscale engineering through lithography and scanning probe microscopy, chemists are well placed to pursue the bottom-up strategy, whereby molecular-scale components are created using chemical synthesis and then self-assembled into devices by pre-programmed intermolecular forces².

Among the more interesting challenges in this area is the design and synthesis of 'molecular actuators', molecules that can undergo changes in shape in response to external stimuli and thereby, in principle, perform mechanical work. To date, most research has concentrated on two-state systems, ranging from classical *cis-trans* isomerism to more elaborate 'rotaxanes' and 'catenanes' (Fig. 1)^{3,4}, and biomolecular constructs, such as a device based on the transition of right-handed to left-handed DNA⁵. These systems, in which movement is driven by chemical, electrochemical or photochemical forces, are best described as molecular

switches or shuttles, and they have great potential in, for example, molecular-scale information processing. However they are not capable of the continuous, unidirectional

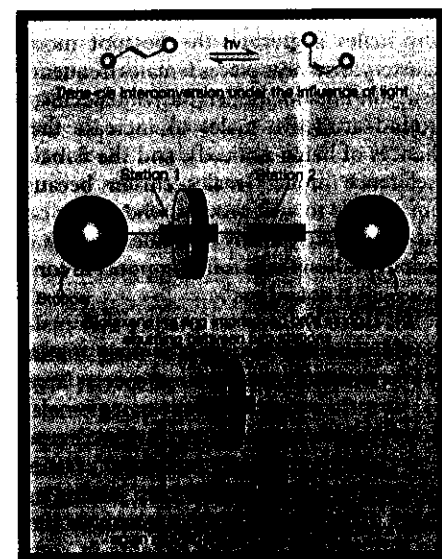


Figure 1 Two-state molecular systems. Established molecular actuators include systems capable of *cis-trans* isomerism, where groups lie on the same (*cis*) or opposite (*trans*) sides of a double bond, and more complex structures such as rotaxanes and catenanes. The rings in the rotaxanes and catenanes may be driven between stations by chemical, electrochemical or photochemical input.

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Acknowledgements

Financial support from the Netherlands Organisation for Scientific Research (NWO-STW) to B.L.F. is acknowledged.

Peacocks lek with relatives even in the absence of social and environmental cues

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Lek mating systems are characterized by males displaying in groups. The main benefit from group display is thought to be an increase in the number of females arriving per male. However, when mating success is highly skewed it is not clear why unsuccessful males participate in group display¹. In theory, all males on leks could obtain indirect fitness benefits if displaying groups consisted of related individuals². Here we present two independent sets of data that show that peacocks (*Pavo cristatus*) display close to their kin. DNA fingerprinting showed that males at Whipsnade Park were more closely related to males within the same lek than to males at other leks. Separately, we found that after an experimental release of a mixed group of related and unrelated males, brothers (paternal sibs or half-sibs) established permanent display sites very close together. This result is unex-

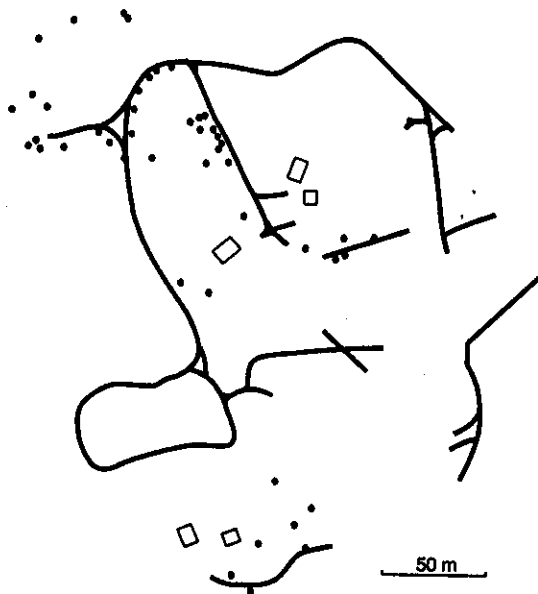


Figure 1 Distribution of 59 displaying male peacocks at Whipsnade Park in 1995 (excluding released males). Four leks (green, red, purple and yellow) were defined in the study area according to close visual contact between displaying males. Adjacent birds excluded from leks (blue) were obscured by topography, stands of trees or fencing.

pected, as the released birds could not become familiar with their brothers during their development. The released young were hatched from eggs that had been removed from their parents shortly after laying and mixed with the eggs of non-relatives. These data indicate that birds can evolve a means of kin association that does not involve learning the characteristics of relatives or the use of environmental cues. If social learning is not necessary for kin association then kin effects may be of more widespread importance in avian social interactions, and in particular in the evolution of lek mating, than previously appreciated.

Males in lek mating systems aggregate to display to attract females. Group display has been shown to increase the number of females arriving per male in several lekking species^{3,4}, but, as a result of the skew in mating success, this does not always increase the number of matings for all of the participants under all circumstances⁵. Unsuccessful males appear only to be increasing the mating success of their more successful neighbours. However, they may gain inclusive fitness benefits from their display if they lek in association with relatives, and lekking may therefore be promoted by kin selection². Here, we investigate whether peacock leks consist of relatives.

Peacocks were studied at Whipsnade Park, UK, where there is a population of around 200 free-ranging peafowl. Peacocks are a classic lekking species where groups of males aggregate at display sites and call together. Once females arrive on leks, males stop calling and display their upper tail coverts⁶; mating success is highly skewed, and most males on leks gain no matings. Peacocks establish permanent display sites in their fourth year. Males are present on their display sites for most of every day for the duration of the mating season, and return to the same site every year. Males can be as close as 2.5 m apart and, on one lek site in the park containing 10 individuals, males were on average 8.83 m (s.d. 6.50 m) apart⁶. We took blood samples from 21 displaying males distributed across four main lek sites (Fig. 1). We used multilocus fingerprinting to compare the genetic similarity (measured as the degree of band-sharing) within and between these lek sites. The degree of band-sharing within leks was significantly higher than that between leks (within leks mean $S = 0.816$, $n = 48$; between leks $S = 0.777$, $n = 162$; Mantel randomization test⁷, 100,000 randomizations, $P = 0.01$; Fig. 2). Assuming that birds in different leks are unrelated and the detected minisatellites segregate independently, the increased band sharing within leks is close to that expected for half-siblings (0.810)⁸.

How could peacocks come to display near to their close kin? Peacocks take no part in reproduction after mating and therefore young birds cannot learn the identity of their fathers. One possibility that could result in a tendency for related birds to display

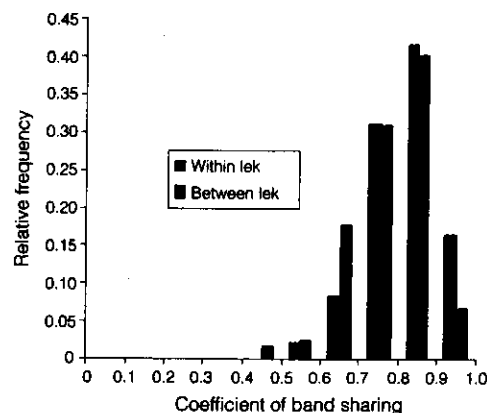


Figure 2 Comparison of band-sharing between individual multilocus minisatellite DNA profiles within (blue bars) and between (red bars) the display sites represented in Fig. 1. Peacocks displaying at the same lek ($n = 4, 6, 4$ and 7 , respectively) were significantly more genetically similar to one another than they were to birds at other leks ($P = 0.01$).

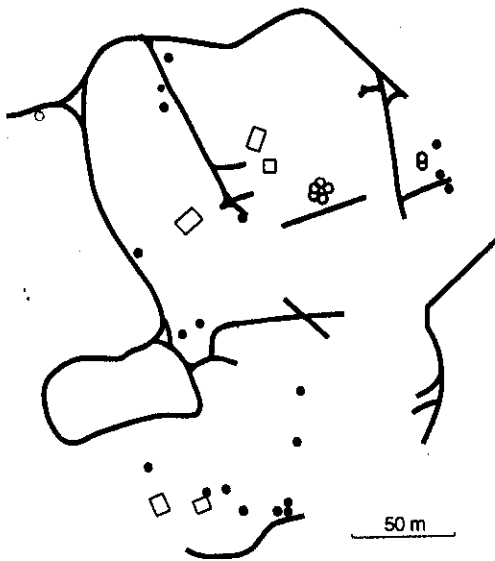


Figure 3 Permanent display sites established by all 19 peacocks of known paternity four years after their release into the study area (filled circles). Peacocks of the same paternity, and the ex-display site of each of their eight fathers (open circle) are represented in the same colour. On average, released birds of the same paternity established display sites that were significantly closer than those of different paternity ($P = 0.01$; Fig. 4), and became nearest neighbours far more often than expected by chance ($P = 0.0002$).

together is that there might be limited dispersal by males from their natal sites. We considered this possibility by testing whether it was necessary for peacocks to have been born in the park in order for them to display close to their relatives. We did this by plotting the display positions of a sample of young of mixed relatedness that were released into the park after being reared elsewhere. Our data allowed us to reject this possibility.

Figure 3 shows the positions of the display sites of 19 four-year-old males in 1995 (filled circles) that were released into Whipsnade Park as part of an experiment designed to look at the survivorship of the offspring of sires of differing attractiveness⁹. In 1991, eight full-trained displaying males of varying attractiveness were removed from Whipsnade Park (the open circles in Fig. 3 show the positions of the ex-display sites of these sires). These males were each allowed to breed with four females at a farm in Norfolk, UK. To control for rearing differences, eggs were removed from their parents, marked and incubated in groups of mixed relatedness. Individually marked young were kept in large mixed groups until they were old enough for a sample to be released into Whipsnade Park, early in 1992. The young of known paternity were released in batches of eight, each consisting of one offspring from each of the eight sires. After release, the young flocked and ranged together in large groups. Unexpectedly, given that the offspring could not be familiar with their relatives, when the birds established their permanent adult display sites several years after their release there was a clear tendency for known brothers or half-brothers to display close together (Fig. 3). Using a Mantel matrix randomization test, we found that the pairwise distances between relatives (paternal sibs/half-sibs) were significantly shorter than those between non-relatives (mean distance between pairs of paternal sibs/half sibs = 117 m, s.d. = 97 m, $n = 16$; mean distance between non-relatives = 183 m, s.d. = 99 m, $n = 137$; 100,000 randomizations, $P = 0.01$; Fig. 4). Although relatives were on average significantly closer than expected, the frequency of relatives that were nearest neighbours was particularly high. Considering just the display sites of the 19 birds released in the experiment, eight were closest to a paternal relative, when only 1.48 was expected ($P = 0.001$; Fig. 3). When the pre-existing displaying males (Fig. 1) were also included in the analysis, six of the released birds had paternal relatives as nearest

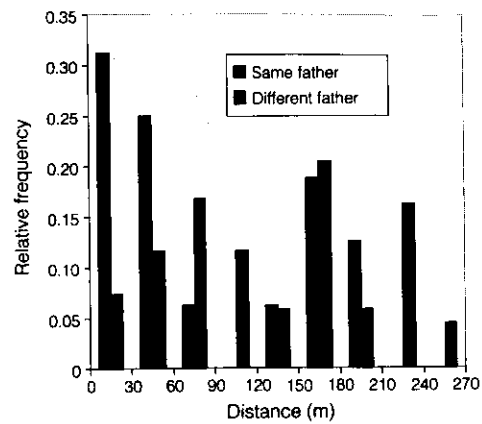


Figure 4 Comparison of distances between the permanent display sites of related (blue bars) and unrelated (red bars) experimentally released males (see Fig. 3; excludes the one male without a brother).

neighbours, when only 0.39 was expected ($P = 0.0002$).

It is possible that birds would be more familiar with the young that hatched in the same batch on the same day and this could influence their tendency to associate. However, there was no tendency for birds that were briefly reared together in the same batch to establish display sites close together (mean = 2.57 males per batch; Mantel test, 100,000 randomizations, $P = 0.59$).

One possible explanation for these data could be that the released brothers (full or half) tended to display close together because related individuals have the same genetic preference for particular environmental features. However, this seems unlikely on this small scale and in this homogeneous, non-native environment; moreover, it might then be expected that the offspring would also share such a genetic preference with their fathers. There is no obvious tendency for the released males to establish display sites near to their fathers' ex-display sites (birds are significantly closer to their nearest brother than to their father's ex-display site, $t = 2.44$, $P < 0.029$, $n = 18$).

These two independent sets of data show that peacocks display close to their kin. There is also evidence that male kin associate at leks in the black grouse, *Tetrao tetrix*, where it is suggested that this arises through limited natal dispersal by males¹⁰. In peafowl, our experimental release data show that lekking males will display next to their relatives even in the absence of any learnt social or environmental cues to their identity. They could use self-referent phenotype matching¹¹, where peacocks match heritable cues in their own phenotypes with those in other individuals. Evidence for kin discrimination in the absence of social learning has rarely been obtained¹²⁻¹⁸ and, to our knowledge, these data provide the first such evidence for birds^{18,19}. Although social learning is not apparently necessary for kin association, this does not necessarily mean that it is never used when available.

The results indicate that there could be advantages to displaying close to kin. It may be that the inclusive fitness benefits of cooperating with relatives to attract mates outweigh any costs of communal display. It is also possible that females prefer to choose mates from among a group of related individuals, and that the evolution of group displays by relatives is female-driven. Evidence for a purely genetic basis to kin association indicates that kin selection and inbreeding avoidance could be more important in the evolution of avian mating systems and other aspects of behaviour than has been previously appreciated. □

Methods

Multilocus DNA fingerprints were prepared from blood samples as described²⁰. Genomic DNA samples were digested with *MboI* (Applied Biotechnologies), run on 1% agarose gels, blotted onto Magna Charge (Micon Separations) nylon membranes and probed with Jeffreys' minisatellite probe 33.6 using a stringency of $1 \times \text{SSC}0.1\%$ SDS at 65 °C. There

was a high degree of band-sharing between individuals, probably due to past inbreeding in this population. The large number of monomorphic and common bands provided a reference ladder that allowed 28 apparently homologous polymorphic minisatellite fragments in the size range 4.0–23.0 kilobases (kb) to be identified between fingerprints, thus enabling the ready comparison of all individuals. The order of the samples was randomized within and between gels, and the band patterns were scored by an assistant who had no knowledge of the lek sites of the individual birds.

Eight free-ranging full-trained displaying lek males whose mating success varied were removed from Whipsnade Park during February 1991 and transferred to a peacock farm in Norfolk, UK. The peacocks were housed in separate pens and four naive adult peahens, known to be at least 2 years old, provided by the farm, were measured and randomly assigned to each pen on 14 March. Pens were checked daily for eggs (it was not possible to know which of the four hens laid which egg unless egg laying was observed) and any eggs found were labelled and removed. Groups of eggs originating from several different pens over several dates were mixed and placed under broody domestic chickens for incubation. Eggs were removed from the hens after 26 days and placed in a hatcher in batches, where each egg had its own compartment; each of the hatched chicks was given an individual colour ring combination. Each batch of eggs was incubated and hatched separately at approximately weekly intervals from May to August. Each batch of chicks was provided with a heat lamp and food and water *ad libitum*; batches were subsequently pooled and reared together. Females produced 519 eggs and the growth of the surviving 349 offspring was monitored. In January and February 1992, 12 offspring (7 males and 5 females) from each of the 8 males (3 from each of the 4 females per male) were introduced into Whipsnade Park. A matched sample of young was chosen from each pen so that there were no overall significant differences in hatching dates or weights of the offspring between fathers (at day 84, $F_{7,95} = 0.838$, $P = 0.559$; at introduction, $F_{7,95} = 0.358$, $P = 0.924$). Care was taken to release the offspring in batches of eight, consisting of one young of the same sex from each pen. The fate of the offspring was recorded by a field assistant who had no knowledge of the relatedness of any of the individuals, and the birds were observed every spring until they established permanent display sites in 1995 (aged 4). Of the introduced males, 19 were observed to have established permanent display sites in 1995 (Fig. 3).

Mantel tests⁷ that randomized the pairwise physical distances or band-sharing values, respectively, were performed on square-root transformed distances using the program RT v2.1 (ref. 21). We analysed nearest-neighbour associations using a program that randomized (100,000 times) the positions of relatives and non-relatives, as appropriate, and counted the number of occasions on which nearest neighbours were relatives.

Received 11 March; accepted 2 July 1999.

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Acknowledgements

This study was initiated while M.P. was at the Department of Zoology, University of Oxford and A.K. and T.B. were at the Department of Biology, University of Leicester. We thank the Zoological Society of London for permission to study the peafowl at Whipsnade

Wild Animal Park; L. Lovett for help at Whipsnade; Q. Spratt for allowing M.P. To work at his peacock farm; A. Williams for help at the farm; P. Carpenter for help in scoring gels; E. Bell and A. Askew for writing computer programs; J. Brookfield for advice; J. Futer for help with producing Figures; B. Hatchwell, M. Young, G. Roberts, F. Ratnieks and P. Watt for comments on the manuscript; and the NERC and the BBSRC for financial support.

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An epigenetic mutation responsible for natural variation in floral symmetry

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Although there have been many molecular studies of morphological mutants generated in the laboratory, it is unclear how these are related to mutants in natural populations, where the constraints of natural selection and breeding structure are quite different. Here we characterize a naturally occurring mutant of *Linaria vulgaris*, originally described more than 250 years ago by Linnaeus^{1–3}, in which the fundamental symmetry of the flower is changed from bilateral to radial. We show that the mutant carries a defect in *Lcyc*, a homologue of the *cycloidea* gene which controls dorsoventral asymmetry in *Antirrhinum*⁴. The *Lcyc* gene is extensively methylated and transcriptionally silent in the mutant. This modification is heritable and co-segregates with the mutant phenotype. Occasionally the mutant reverts phenotypically during somatic development, correlating with demethylation of *Lcyc* and restoration of gene expression. It is surprising that the first natural morphological mutant to be characterized should trace to methylation, given the rarity of this mutational mechanism in the laboratory. This indicates that epigenetic mutations may play a more significant role in evolution than has hitherto been suspected.

Mature wild-type flowers of *Linaria vulgaris* (toadflax) have five petals that are united for part of their length to form a corolla tube ending in five separate lobes (Fig. 1c, d). Dorsoventral asymmetry is clearly evident in the shape and colour of the petals. The two dorsal (adaxial) petals have relatively long strap-shaped lobes; the two lateral petals have wider lobes with a partially orange lip; and the ventral (abaxial) petal has a small lobe with an orange lip, and a spur-shaped nectary at its base. Dorsoventral asymmetry is also evident in the stamens: the dorsal stamen is arrested early in development to give a sterile staminode (Fig. 1d), and the two lateral stamens are shorter and less hairy than the two ventral stamens.

Flowers of naturally occurring peloric mutants in *Linaria* are radially symmetrical (Fig. 1a–d). All five petals resemble the ventral petal of wild type, each having a small lobe with an orange lip, and a spur at their base. Similarly, there are five stamens, all of which closely resemble the ventral stamens of wild type in length and hairiness. In being fully ventralized, these mutant *Linaria* flowers resemble peloric mutants of *Antirrhinum* which lack the activity of two related genes, *cycloidea* (*cyc*) and *dichotoma*^{4,5}. The peloric mutation in *Linaria* is recessive, as crosses to wild type yielded essentially wild-type F₁ progeny. Only one of the F₁ individuals occasionally gave one or two extra spurs.

We compared the development of wild-type and peloric flowers of *Linaria* by scanning electron microscopy. No differences were

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