

teaching. This interpretation fits neatly with broader definitions of teaching by animals, in which teaching is seen to be widespread in the animal kingdom, including examples in social insects, birds and carnivores, for example⁷. One definition of ‘active teaching’ suggests that the tutor must modify the behaviour of naïve observers at a cost to the teacher⁸, and these criteria nonetheless also appear to be fulfilled here. The behaviour comes at considerable energetic cost to the mother, as the pups may weigh up to 41% of their mother’s body mass, hence increasing flight costs and affecting flight performance by probably reducing flight speed and manoeuvrability⁹. Considerable fitness benefits must arise in the longer-term from the mother’s behaviour, for example by increasing the survival prospects of their offspring. Such a high level of maternal investment is important given that bats typically produce single offspring.

How might the young bats learn routes and remember the trees they were parked in? Any odour cues left on the trees may only be detectable over short distances so are unlikely to be important. Although Egyptian fruit bats echolocate by tongue-clicking^{10,11}, they do this mainly to orientate in cave roosts or near trees, and echolocation operates over short distances because the high frequencies used attenuate rapidly in air. Goldshtein *et al.*² suggest that the bats retain memories of their environment by using vision, as vision is given preference over echolocation when the bats decide where to fly¹². Although they are carried upside down by their mothers (Figure 1), the pups appear to keep their eyes open at least some of the time, and can form spatial orientations of their environment even when upside down¹³. Repeated exposure to flight routes when attached to their mothers and repeated parking at trees may also perhaps reinforce spatio-temporal memory in a cognitive map via a magnetic compass¹⁴.

It remains unclear how widespread parking pups at drop-off points is in bats. Mothers in many bat species carry infants for short periods of time, for example when moving roost sites, but the constant attachment of young over the first three weeks of life may be unusual. Nevertheless, the Egyptian fruit bats provide a remarkable example of

maternal care that has previously been overlooked, by leading pups to bases where they can develop their skills in exploration and navigation. The Goldshtein *et al.*² study also raises wider issues about the importance of maternal tuition during the challenging times when young animals become independent from their parents.

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Evolutionary genetics: Inversions — Do not quail but go big!

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<https://doi.org/10.1016/j.cub.2021.12.016>

How local phenotypic variation is maintained in highly mobile organisms, like birds, is an open question. A new study shows that a massive chromosomal inversion underlies a polymorphism in common quail.

Local phenotypic variation, from light- and dark-coloured pocket mice living on rock and lava¹ to local ecotypes of sunflowers^{2,3}, has long fascinated ecologists and evolutionary biologists.

Spatially structured phenotypes in these and some other cases are typically maintained by variation in fitness across local niches⁴. Mechanisms underlying spatial distribution of phenotypes have

been also studied at wider geographic scales, exemplified with distinct warning wing patterns of geographic morphs of the iconic Amazonian *Heliconius* butterfly, where clines between morphs are sustained by frequency-dependent selection⁵. Characterising the genetic basis of geographically restricted behavioural phenotypes that affect movement and spatial distribution of animals, such as seasonal migration, has proved to be quite tricky. In a new study in this issue of *Current Biology*⁶, Ines Sanchez-Donoso, Carles Vilà and colleagues tackle this challenge by investigating the genomic basis of geographically restricted migratory phenotypes in a highly motile bird, the common quail (*Coturnix coturnix*).

In contrast to domesticated and resident Japanese quail, wild common quail across most of their breeding distribution in the western Palearctic migrate between their breeding sites and wintering grounds in Africa and southern India. The exceptions are populations of common quail breeding in the southern Iberian Peninsula and northern Africa — these are resident. Besides variation in migratory behaviour, they also exhibit geographic variation in weight and throat pigmentation: southern quail are heavier and have darker throats. The common quail system thus represents geographically restricted behavioural and morphological variation. Previous studies revealed that male quail are highly mobile within the breeding season in search for additional mating opportunities and better environmental conditions^{7,8}. Females can lay multiple clutches in different locations within a single breeding season⁹. This high motility in common quail potentially leads to erosion of geographically structured phenotypes due to interbreeding.

To characterise population structure among quail across the breeding distribution, Sanchez-Donoso and colleagues⁶ sequenced genomes of common quail, including both migrants and residents from seven different locations across continental Europe, the Macronesian islands and northern Africa. They found elevated differentiation among populations in one large block located on chromosome 1, contrasting the otherwise very low genome-wide differentiation. This chromosomal region

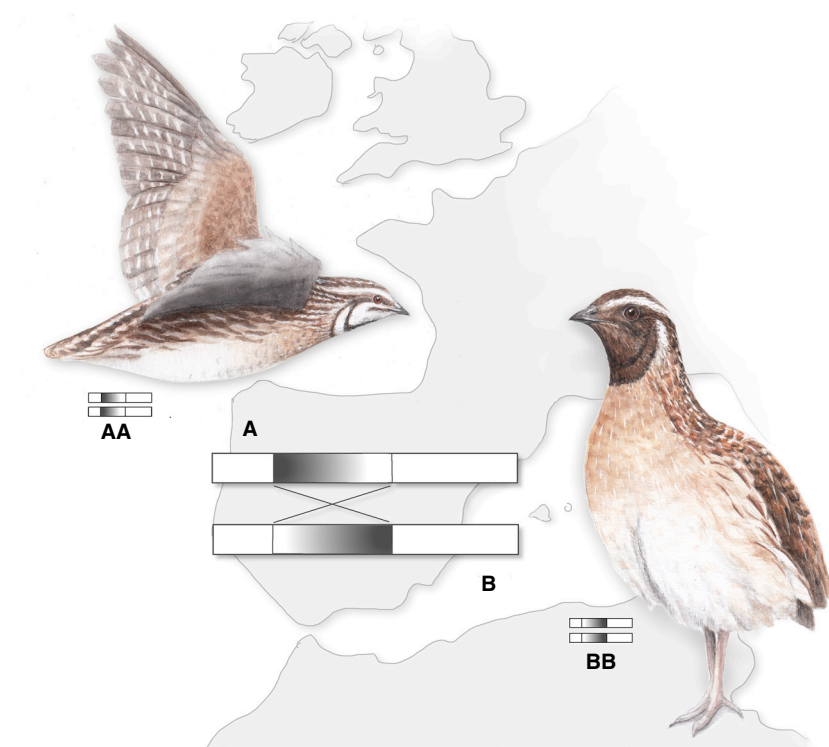


Figure 1. A polymorphic inversion is associated with geographically structured traits in common quail.

Sanchez-Donoso and colleagues⁶ identified a large polymorphic inversion on quail chromosome 1, which covers genes associated with migration, throat pigmentation, and body weight. A and B represent two arrangements of the inversion. The AA genotype dominates in the north where the migratory behaviour occurs, illustrated by the flying quail, while residency occurs in the southern distribution range around the Mediterranean Sea. (Illustration by Corinna Langebrake.)

harboured three genotypes (AA, AB, and BB) with two distinct chromosomal haplotypes (A and B), based on the pattern of relatedness as well as ancestry assignment. Distribution of differentiation along the chromosome between the two haplotypes indicated they represent the normal and inverted arrangements of a polymorphic inversion, which was further confirmed by cytogenetics with fluorescent *in situ* hybridisation. The characterised inversion is over 115 Mb in length, or roughly 12% of the entire genome, and contains 7,000 genes.

Polymorphic inversions can affect multiple traits by coadapted linked mutations within the inversion locus¹⁰. Sanchez-Donoso and colleagues⁶ asked whether the identified polymorphic inversion in the common quail could explain some of the geographically structured migratory phenotypes. Wing shape (pointiness) and size of the pectoral lipid band were used as indirect proxies for migratory phenotypes. As a more

direct measure of seasonal migration, the authors analysed stable isotopes in feathers. Frequencies of isotopes differ across locations; thus, isotopic signals in feathers grown in their breeding and wintering ranges differ in migrants but not in residents. Quail with haplotype B (BB and AB) show rounder wings and smaller pectoral lipid bands, indicative for resident phenotype, in line with the limited occurrence of haplotype B in southern populations which are assumed to be resident. Only AA quail with the pointiest wings and the largest pectoral lipid bands, indicative for a migratory lifestyle, show different levels of the isotopic signals, suggesting that AA quail are migratory (Figure 1). In addition to migratory phenotypes, the identified inversion was also associated with variation in throat colour (Figure 1) and body weight. These results highlight the correlated geographic distribution of migratory phenotypes, pigmentation and body weight with the inversion frequency,

demonstrating linked phenotypic effects of the polymorphic inversion on geographically restricted phenotypes of multiple traits.

Where did this chromosomal inversion come from? Sanchez-Donoso and colleagues⁶ claim that introgression is one possibility. In other words, the inverted haplotype may have originated from another species and was introduced into the common quail genome through a historical hybridisation event. Examples for introgression of an inverted haplotype causing distinct phenotypes are known from other systems, such as distinct polymorphisms in plumage, physiology and behaviour of the white-throated sparrow¹¹, as well as wing patterns of the Amazonian butterfly *Heliconius numata*¹². However, confirming the extrinsic origin of the common quail inversion with phylogenomic approaches is difficult in the common quail because sympatric sister species are now extinct. An alternative scenario could be that an old polymorphic inversion was maintained until today through frequency-dependent selection or a heterozygote advantage as has been shown for sperm competition in the zebra finch^{13,14} and lekking of male ruffs^{15,16}, though fitness effects of the common quail inversion are not known.

How does the geographically restricted inversion affect traits? Normal and inverted haplotypes of a polymorphic inversion often accumulate tightly linked mutations causing polymorphisms in multiple traits, due to suppressed recombination between the two arrangements¹⁰. Two genes with known effect on pigmentation in birds (RAB-38 and TYR) were located within the common quail inversion locus. Non-synonymous substitutions in these genes between the two haplotypes indicate they may be involved in the variation in throat pigmentation. For migration, the current study did not pinpoint specific candidate genes out of the 7,000 genes located within the inversion locus. However, this new finding in the common quail that inversion genotypes are associated with migratory phenotypes parallels studies independently revealing polymorphic inversions associated with migratory phenotypes in other animals such as willow warbler¹⁷, Atlantic cod¹⁸ and rainbow trout¹⁹. It remains to be shown how general the involvement of

polymorphic inversions is in variation of migratory phenotypes within species. At a mechanistic level, genes within an inversion locus can have differential allelic expression at particular tissues due to differential gene regulation between arrangements, thereby affecting morphology, physiology and behaviour among genotypes²⁰. We are curious to see if additional studies will be able to identify overlap in genes and epigenetic regulations in chromosomal inversions associated with geographic variation in migratory behaviour of different animals including common quail.

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