Sex differences in vocal learning in birds

Young females pick up songs much faster than males but are not so versatile later on.

A young songbird develops its songs by imitating adults[1], just as human infants acquire speech, listening to and memorizing adult songs during an early sensitive phase and then practising its vocalizations until they match the memory formed earlier[2]. Here I investigate whether patterns of song learning differ between the sexes among northern cardinals (*Cardinalis cardinalis*), one of a few temperate species in which both sexes sing, rather than just the males. I find that females learn the same number of songs as males but in less than one-third of the time; however, auditory experience is not essential for males to develop their songs, whereas it is necessary for females to do so.

To determine the sensitive learning phase of male and female cardinals, nestlings (15 females, 11 males) were raised individually in an acoustically controlled environment and tutored daily by using tape-recorded cardinal songs over a period of 1 year. Each pupil was tutored daily with four tutor-song types which were changed regularly; in total, all pupils heard between 40 and 44 tutor-song types. At 1 year of age, a pupil's song was shown to be an imitation of a tutor-song type by their close spectrographic resemblance (Fig. 1a). Because tutor songs were played to the birds in a scheduled sequence throughout the year, identification of the copied tutor model allowed me to pinpoint when the bird memorized each song. The sensitive phase for each bird was defined as the entire period during which the bird heard tutor-song types that it later copied.

The sensitive learning phase was significantly shorter in females than in males: it started at a similar age in both sexes (males, 27.8 ± 2.80 days; females, 22.4 ± 2.06 days; Mann–Whitney test, $U = 43.5$, $P = 0.12$), but lasted more than three times as long in males as in females (males, 187.1 ± 33.4 days; females, 48.7 ± 9.8 days; $U = 11.0$, $P < 0.001$) and thus ended much later (males, 214.9 ± 35.3 days; females, 71.1 ± 10.5 days; $U = 17.0$, $P < 0.01$; Fig. 1b). The weighted mean age of song acquisition[3], a measure that takes the number as well as the timing of songs acquired into account, was significantly younger in females than in males, with an average difference of 51 days (females, 40.1 ± 4.0 days; males, 91.5 ± 13.3 days; $U = 16.0$, $P < 0.01$; Fig. 1b).

The sex difference in the length of the sensitive phase cannot be attributed to exposure to an insufficient variety of tutor models, a factor known to delay the closure of the sensitive phase in other species[4],
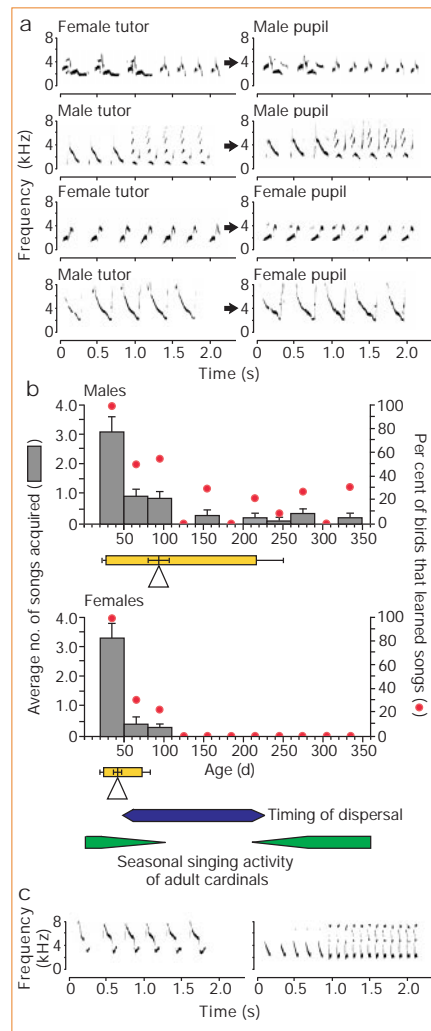

Figure 1 Gender differences in vocal learning in female songbirds. **a,** Sound spectrograms of tutor and pupil songs. Left, songs of male and female tutors: four song types with distinct acoustic profiles are shown. Right, attempted imitation of tutoring songs by male and female pupils. All the song components included in the pupils' songs closely resemble those of the tutor song types and are repeated in the same order as in the tutor songs. Male and female pupils imitated male and female tutor songs equally well. **b,** Timing of the sensitive phase for song memorization in male and female cardinals (15 females, 11 males). Bar charts show the mean and standard error of the number of songs acquired during each 30-day time bin by males (top) and females (bottom). Red points indicate the percentage of males and females that acquired songs during each 30-day period. Yellow bars indicate the average range of the sensitive phase (with standard error); triangles indicate weighted mean age of song acquisition. Blue bar, timing of dispersal in wild juvenile cardinals; green bars, seasonal singing activity of adult cardinals, indicating the availability of tutor models in the wild. **c,** Sound spectrograms of songs of two acoustically isolated males. Improvised songs developed by isolated male birds are composed of repeated song components that are characteristic of normal cardinal songs.

because males and females were exposed to the same variety of tutor models. Furthermore, when a subset of pupils was exposed to a richer variety of song types early in life (20 tutor-song types by 70 days of age for 2 males and 9 females), I found that the timing of their sensitive phases was still sex-specific and no different from that of pupils exposed to a regular variety of tutor songs (8 tutor-song types by 70 days of age for 8 males and 5 females; end of sensitive phase: U, 8.0 and 14.0, respectively; P, 0.99 and 0.26, respectively; weighted mean age: U, 5.0 and 10.0, respectively; P, 0.433 and 0.095, respectively).

Despite the difference in the length of the sensitive phase, the number of song types imitated was similar in both sexes (male, 5.2 ± 0.76 songs; female, 3.7 ± 0.45 songs; $U = 40.5$, $P = 0.08$). Although males acquired, on average, 1.5 more songs than females, the difference does not account for the threefold increase in the length of the

sensitive phase in males. In addition, although songs of male and female cardinal adults have subtle and consistent differences in acoustic morphology[5], pupils did not show any preference for learning either male or female tutor songs: when exposed to both types (25% female songs, 75% male songs) during the sensitive phase, male and female pupils imitated songs of males and females equally well (sign test with predicted chance expectancy of 25%: females, $P = 0.227$; males, $P = 0.508$).

I also raised cardinals (2 females, 3 males) in acoustic isolation in order to determine whether a lack of tutor models could have sex-specific effects on song development. I found that isolated males developed improvised song types (5.0 ± 1.0 types) similar to normal cardinal songs (Fig. 1c). In contrast, isolated females sang only rarely, and when they did, their songs were of poor acoustic quality, indicating that auditory exposure to adult songs early

in life may be necessary to produce songs in females, but not in males. In summary, male and female cardinals differed markedly in when they acquired songs, but were similar in what they acquired. The sensitive phase estimated by using tape tutoring generally agrees with that measured using live tutoring[6] and is likely to guide song acquisition in wild birds; the sensitive phase of wild male cardinals is entirely consistent with my results[7].

The different sensitive phases for the sexes may be an adaptation to meet the functional requirements of songs. Juvenile cardinals disperse from their parents' territory to establish their own territory between the time they become independent from their parents (about 45 days of age) and the start of the first breeding season (when they are about 8.5 to 11 months old; Fig. 1b)[8]. My results show that, although both sexes start learning songs in their natal territory, the females lose the ability to acquire new songs soon after independence and males continue to learn songs until after dispersal is complete.

Songs of adult cardinals form 'dialects' in different geographical regions, so dispersing juveniles may settle into a population with a foreign dialect. The male-typical sensitive phase therefore allows him to match his song types with those of his neighbours, even when he settles into a new population, whereas the female-typical sensitive phase preserves her natal dialect. Song matching may be important for male cardinals in the context of establishing territories, as in other species[9], but evidently is not for females, for reasons yet to be identified. These findings parallel subtle but consistent gender differences in human speech acquisition[10] and offer an opportunity to study the biological basis of distinctions in male and female learning.

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Biogeochemistry

Phosphorus solubilization in rewetted soils

Biogeochemical cycles are shaped by events that follow soil drying and rewetting. Here we show that the process of drying and rapidly rewetting soil increases the amount of water-soluble phosphorus present and that this is predominantly in organic form after having been released from the soil microbial biomass. This effect could not only significantly affect phosphorus pollution of water-bodies but might also corrupt results from analyses involving water extraction of dried soils.

We investigated the effect of drying and rewetting soil on its content of soluble phosphorus by determining the amount of water-soluble phosphorus in 29 lowland permanent grassland soils from England and Wales. The total amounts of water-soluble phosphorus in moist soils were small, but increased after drying by 185–1,900%. Comparable amounts of phosphorus were solubilized when soils were dried at different temperatures, but solubilization occurred more rapidly at 30 °C (maximum phosphorus solubilization after 1–3 days) than at 15 °C (maximum solubilization after 7–10 days).
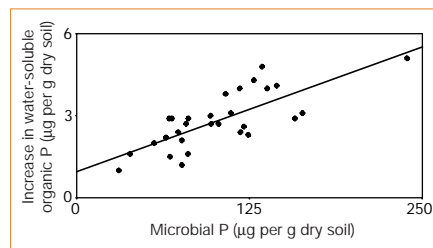
Most of the soluble phosphorus was pre-

Figure 1 Increase in water-soluble organic phosphorus after soil drying as a function of soil microbial phosphorus. Data are from 29 permanent grassland soils in England and Wales containing various amounts of phosphorus ($NaHCO_3$-extractable inorganic phosphorus was 9–48 mg kg^{-1}), total carbon (29–80 g kg^{-1}) and clay (22–68%). Increase in water-soluble organic phosphorus $= (0.95 \pm 0.33) + (0.018 \pm 0.003)$ (microbial phosphorus); $R^2 = 0.58$; $n = 29$; $P = 1.6 \times 10^{-6}$. The amount of water-soluble phosphorus was determined by extracting soils at field-moisture capacity (after drainage from saturation for 48 h) with water in a 4:1 water/soil ratio for 1 h. Subsamples were air-dried for 7 days at 30 °C and extracted in the same way. Extracts were filtered (pore size < 0.45 μm) and analysed for inorganic and organic phosphorus[2]. Phosphorus levels in soil microbial biomass were determined by measuring the phosphorus released by chloroform fumigation[6].

sent in an organic form, which accounted for 56–100% of the total phosphorus released by drying at 30 °C. The amount of solubilized organic phosphorus was positively related to the soil microbial phosphorus concentration ($P < 0.0001$; Fig. 1). We attributed this effect to direct release of phosphorus from the soil microbial bio-

mass, because microbes can be killed by osmotic shock and cell rupture when rapid rehydration follows a period of drying[1].

Phosphorous released from microbes after drying and rewetting the soil could contribute to the pollution of water bodies, because soil drying coincides with cracking, which enhances preferential movement of water and associated phosphorus through the soil. This may explain the increased concentrations of phosphorus found in drainage waters after periods of soil drying and rewetting[2]. The impact of this effect on water quality may be increased by irrigation practices and in regions where climate change causes longer dry periods or more frequent cycles of wetting and drying[3].

Our results also have implications for the usefulness of environmental soil-phosphorus tests that measure only inorganic phosphorus, rely on aqueous extraction, and take no account of soil moisture[4]. The effect shown here may also apply to other soil nutrients and could partially explain a similar phenomenon observed for nitrogen mineralization in tropical soils[5].

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Epidemiology

Foot-and-mouth disease under control in the UK

Following the first reported case on 20 February this year, foot-and-mouth disease spread to over 1,500 livestock farms in the United Kingdom by the end of April[1–3]. From late March, the Ministry of Agriculture, Fisheries and Food (MAFF) required livestock on infected farms to be culled within 24 hours of the disease being reported and those on neighbouring farms within 48 hours. Here we investigate whether progress towards meeting these targets[3] has had a detectable impact on the course of the epidemic in the United Kingdom. We conclude that it has now been brought under control, but it will be important to contain rapidly any new outbreaks