

- 26 Monteiro, A.F. *et al.* (1994) The evolutionary genetics and developmental basis of wing pattern variation in the butterfly *Bicyclus anynana*. *Evolution* 48, 1147–1157
- 27 Monteiro, A. *et al.* (1997) The genetics and development of an eyespot pattern in the butterfly *Bicyclus anynana*: response to selection for eyespot shape. *Genetics* 146, 287–294
- 28 Wagner, G. (1996) Homologues, natural kinds, and the evolution of modularity. *Am. Zool.* 36, 36–43
- 29 Sekimura, T. *et al.* (2000) A model for colour pattern formation in the butterfly *Papilio dardanus*. *Proc. R. Soc. London B Biol. Sci.* 267, 851–859
- 30 Carroll, S.B. (2000) Endless forms: the evolution of gene regulation and morphological diversity. *Cell* 101, 577–580
- 31 Entchev, E.V. *et al.* (2000) Gradient formation of the TGF- $\beta$  homolog *Dpp*. *Cell* 103, 981–991
- 32 Strigini, M. and Cohen, S.M. (2000) *Wingless* gradient formation in the *Drosophila* wing. *Curr. Biol.* 10, 293–300
- 33 Teleman, A.A. and Cohen, S.M. (2000) *Dpp* gradient formation in the *Drosophila* wing imaginal disc. *Cell* 103, 971–980
- 34 Keys, D.N. *et al.* (1999) Recruitment of a hedgehog regulatory circuit in butterfly eyespot evolution. *Science* 283, 532–534
- 35 Lawrence, P.A. (1992) *The Making of a Fly*, Blackwell Science
- 36 Biehs, B. *et al.* (1998) Boundaries in the *Drosophila* wing imaginal disc organize vein-specific genetic programs. *Development* 125, 4245–4257
- 37 Koch, P.B. *et al.* (2000) The molecular basis of melanism and mimicry in a swallowtail butterfly. *Curr. Biol.* 10, 591–594
- 38 Koch, P.B. *et al.* (2000) Insect pigmentation: activities of Beta-alanyldopamine synthase in wing color patterns of wild-type and melanic mutant swallowtail butterfly *Papilio glaucus*. *Plg. Cell Res.* 13 (Suppl. 8), 54–58
- 39 Koch, P.B. *et al.* (1998) Regulation of dopa decarboxylase expression during colour pattern formation in wild-type and melanic tiger swallowtail butterflies. *Development* 125, 2303–2313
- 40 Koch, P.B. *et al.* (2000) Butterfly wing pattern mutants: developmental heterochrony and co-ordinately regulated phenotypes. *Dev. Genes Evol.* 210, 536–544
- 41 Gilbert, L.E. *et al.* (1988) Correlations of ultrastructural and pigmentation suggest how genes control development of wing scales on *Heliconius* butterflies. *J. Res. Lepidop.* 26, 141–160
- 42 Nijhout, H.F. (1999) Control mechanisms of polyphenic development in insects. *BioScience* 49, 181–192
- 43 Monteiro, A. and Pierce, N.E. (2001) Phylogeny of *Bicyclus* (Lepidoptera: Nymphalidae) inferred from *COI*, *COII*, and *EF-1A* gene sequence. *Mol. Phylog. Evol.* 18, 264–281
- 44 Roskam, J.C. and Brakefield, P.M. (1996) A comparison of temperature-induced polyphenism in African *Bicyclus* butterflies from a savannah-rainforest ecotone. *Evolution* 50, 2360–2372
- 45 Joron, M. and Mallet, J. (1998) Diversity in mimicry: paradox or paradigm? *Trends Ecol. Evol.* 13, 461–466
- 46 Mallet, J. (1999 (2001)) Causes and consequences of a lack of coevolution in Müllerian mimicry. *Evol. Ecol.* 13, 777–806
- 47 Jiggins, C.D. and McMillan, W.O. (1997) The genetic basis of an adaptive radiation: warning colour in two *Heliconius* species. *Proc. R. Soc. London B Biol. Sci.* 246, 1167–1175
- 48 Brower, A.V.Z. and Egan, M.G. (1997) Cladistic analysis of *Heliconius* butterflies and relatives (Nymphalidae: Heliconiini): a revised phylogenetic position for *Eueides* based on sequences from mtDNA and a nuclear gene. *Proc. R. Soc. London B Biol. Sci.* 264, 969–977
- 49 Brower, A.V.Z. (1994) Rapid morphological radiation and convergence among races of the butterfly *Heliconius erato* inferred from patterns of mitochondrial DNA evolution. *Proc. Natl. Acad. Sci. U. S. A.* 91, 6491–6495
- 50 Brower, A.V.Z. (1996) Parallel race formation and the evolution of mimicry in *Heliconius* butterflies: a phylogenetic hypothesis from mitochondrial DNA sequences. *Evolution* 50, 195–221
- 51 Tamura, T. *et al.* (2000) Germ-line transformation of the silkworm *Bombyx mori* L. using a piggyBac transposon-derived vector. *Nat. Biotechnol.* 18, 81–84

# The honesty of bird song: multiple constraints for multiple traits

Diego Gil and Manfred Gahr

**The function of bird song is closely linked to sexual selection. A fundamental question regarding the evolution of sexually selected male signals is how their honesty is maintained. The neural space required for storing a large song repertoire size has traditionally been identified as a key constraint. However, it is often forgotten that bird song is a multifaceted behaviour, and that the different characters that comprise it have specific costs. Recent research has revealed the existence of new constraints, such as social aggression or learning opportunities, which limit the expression of several song characteristics. We review the existing evidence for each of these constraints, revealing some major gaps in our knowledge of this fascinating biological system.**

The two main functions of song in male birds are mate attraction and territory defence against other males [1]. Individual variation in song characteristics does affect reproductive success through mate choice and male–male competition, the two mechanisms of sexual selection [2]. Current theory predicts that when senders and receivers have different evolutionary interests, as in sexual selection, signals must be costly (i.e. subject to some constraint) to constitute stable, honest indicators of quality [3]. Individual variation in the expression of

these signals will therefore depend on the condition of the male [4]. Thus, differences in phenotypic or genetic quality between males would result in differences in song production. Evidence for condition dependency of song characteristics is, however, scant and often controversial [5]. A problematic feature of bird song is that it constitutes a set of characters rather than a simple trait, and each of these characters can be limited by specific constraints, a fact that is commonly ignored in the literature. Here, we consider which song characteristics are, or can be, sexually selected, and examine how different costs and constraints can limit the expression of each of these characteristics.

## Bird song: multiple sexually selected traits

Bird song encompasses multiple traits that can be sexually selected, but which are not equally important in all species. We expect that characteristics with the greatest individual variation and repeatability will be those that are most important in the context of sexual selection.

## Box 1. Bird song repertoires

In many bird species, males have several song variants (called a song repertoire), which are used interchangeably in the same context, and which are classic examples of redundancy in animal signals [a]. Questions about the evolution of song repertoires require comparative analyses to uncover general evolutionary patterns. Particularly exciting are the positive interspecific associations among song repertoire size and aspects of sexual selection, such as parasite burden [b] or the size of brain nuclei [c]. However, a difficulty these studies face is how to reduce the interspecific diversity of song organization patterns to a simple, common unit (the comparability problem) [a].

In some species, such as the great tit *Parus major*, the songs of a male can be classified into distinct categories (song types), characterized by unique sequences of elements. In other species, songs consist of sequences of randomly assembled elements, rarely repeated in the same order (e.g. the sedge warbler *Acrocephalus schoenobaenus*). In such cases, the total number of elements is used as a measure of repertoire size. Some species present intermediate styles, like the willow warbler *Phylloscopus trochilus* [d], whose song types are not homogeneous categories but share elements among them.

Most researchers avoid the comparability problem by acknowledging it and then ignoring it in their comparative analyses, in the hope that variance in measurement criteria will be random noise. In the most comprehensive comparative analysis of song repertoires, Read and Weary used two measures of repertoire size: number of song types and number of elements within each song [e]. Although a good compromise, this approach might not always be biologically relevant. For example, they assigned a repertoire size

of infinite to the sedge warbler, in virtue of its combinatory abilities, even though its repertoire comprises ~60 elements [f]. By contrast, the song sparrow *Melospiza melodia* has a repertoire size of 15 song types, each comprising five elements on average. The total amount of song material that these two species produce is remarkably similar, and the dramatic differences in song depend more on the organization of the song output.

A potential solution is repertoire length, a new measure adopted by Irwin [g], which corresponds to the sum in seconds of the duration of all different elements in a repertoire. Neuronal mechanisms for storing song repertoires are likely to be set by both the number and the length of song units. Therefore, although not perfect [h], repertoire length is probably the least biased measure that could be used in a comparative analysis of a wide range of species.

### References

- a Krebs, J.R. and Kroodsma, D.E. (1980) Repertoires and geographical variation in bird song. *Adv. Study Behav.* 11, 143–177
- b Hamilton, D.W. and Zuk, M. (1982) Heritable true fitness and bright birds: a role for parasites? *Science* 218, 384–387
- c Szekely, T. *et al.* (1996) Evolutionary changes in a song control area of the brain (HVC) are associated with evolutionary changes in song repertoire among European warblers (Sylviidae). *Proc. R. Soc. London B. Biol. Sci.* 263, 607–610
- d Gil, D. and Slater, P.J.B. (2000) Song organisation and singing patterns of the willow warbler *Phylloscopus trochilus*. *Behaviour* 137, 759–782
- e Read, A.F. and Weary, D.M. (1992) The evolution of bird song: comparative analyses. *Philos. Trans. R. Soc. London Ser. B* 338, 165–187
- f Catchpole, C.K. (1976) Temporal and sequential organisation of song in the sedge warbler (*Acrocephalus schoenobaenus*). *Behaviour* 59, 226–245
- g Irwin, D.E. (2000) Song variation in an avian ring species. *Evolution* 54, 998–1010
- h Yu, A.C. and Margoliash, D. (1996) Temporal hierarchical control of singing in birds. *Science* 273, 1871–1875

### Performance-related traits

Performance-related traits are characteristics of song that can be measured quantitatively irrespective of song content, for example, time spent singing, song rate, length or amplitude, etc., and field evidence shows that these characteristics are under positive sexual selection. For instance, individual song rate correlates with date of pairing in several species [6], even after controlling statistically for territory quality. Experimental increase of song rate in pied flycatchers *Ficedula hypoleuca* results in birds acquiring mates earlier in the breeding season [7]. In the laboratory, white-crowned sparrow *Zonotrichia leucophrys* females show a sexual preference for long songs and high song rates [8]. These aspects of song also seem to guide choice of extra-pair mates. For instance, in the barn swallow *Hirundo rustica*, the probability of having extra-pair offspring in a nest is correlated negatively with the song output of the male [9]. Interestingly, we know of no field study that has looked at individual variation in song amplitude, a variable that is probably correlated positively with male quality.

### Repertoire size

Repertoire size is the number of different elements or songs that a male can produce (Box 1). In the laboratory, receptive females of most species show strong

preferences for large song repertoires [10]. However, most field studies have found repertoire size to be a poor predictor of pairing success after correcting statistically for territory quality or male arrival date [11,12]. Exceptions are *Acrocephalus* warblers and the European starling *Sturnus vulgaris*, species in which females actively select males with large repertoires [13,14]. Repertoire size also plays a role in extra-pair paternity in the great reed warbler *Acrocephalus arundinaceus*, where cuckolders have larger song repertoires than do cuckolded males [15]. These interspecific differences suggest that something other than repertoire size is the target of selection in many species.

A problem with research on repertoire size is the lack of direct experimental manipulation of song in males. Although repertoire size can be manipulated by tutoring young birds in the laboratory [16], this has never been done in a study of the relationship of repertoire size with male–male competition or mate choice.

### Specific song content

There is increasing evidence that the content, rather than the size of song repertoires is important in sexual selection. There are at least four distinct phenomena involved:

- Song sharing. In many territorial species, close neighbours share a significant percentage of their

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repertoires. Recently, Beecher and colleagues reported that the ability of a male song sparrow *Melospiza melodia* to keep a territory is related to his degree of song sharing with neighbours, rather than to his repertoire size [17].

- **Dialects.** Many bird species have local dialects [1] and, in some species, females mate preferentially with males that sing their local dialect [18].
- **Special syllables.** In some species, the presence of a single syllable type in the song explains most of the variance in male success. For instance, female canaries *Serinus canaria* are particularly sexually responsive to fast trills of large bandwidth [19]. The attractiveness of large repertoires could be due to the higher probability of them containing attractive syllables. In the water pipit *Anthus spinoletta*, the only variable in the song that predicts pairing success is a particular kind of buzz that is neither particularly complex nor modulated [20].
- **Song frequency.** Between-species differences in song fundamental frequency are related to body size [21]. If this constraint also operates within species, females could use song fundamental frequency as an indicator of male size. It might also be used by males as an honest index of size in male–male competition.

#### Timing of singing

The time of day or season in which a bird chooses to sing could also be an indication of quality. There are at least two situations where this might be involved:

- **Weather.** If singing is limited by energy or by feeding time budget, only high-quality males might be able to sing in bad weather. Females should be most responsive to variables of male quality that show high variance between individuals, and this variance should be higher in adverse meteorological conditions.
- **Dawn chorus.** In many passerines, there is a pronounced peak of singing before dawn (dawn chorus) during the breeding season that is contingent with female fertility [22]. This is best interpreted as males investing more heavily in a sexually selected trait at a time of year when females can indulge in extra-pair copulations, and at a time of day when mate guarding is not possible [23]. Although it has been shown mathematically that dawn singing could have a low cost [24], this does not account for the fact that singing is earliest at the peak of female fertility. On the contrary, this pattern suggests that singing earlier than average might have a higher cost. For example, in the field, black-capped chickadees *Parus atricapillus* start their chorus earlier than do subordinates [25]. It remains to be tested whether males are indeed paying higher costs by singing earlier, and whether females are sensitive to this variation.

#### Countersinging patterns

Territorial birds often engage in directed countersinging, where two or more birds sing in alternation. During these interactions, males grade their own degree of

aggressiveness, for example, by singing the same song as their opponent (matching) [26], by overlapping the opponent's song [27] or by increasing the rate at which song-types are switched [26].

However, we do not know whether there is individual variation in the use of these countersinging patterns in any species, and whether these characteristics relate to territory tenure or to female choice.

#### Costs and constraints: what are the currencies?

The limiting factors maintaining signal reliability can be divided into two main groups depending on whether cheating is controlled by the cost paid by the signaller, or by the behaviour of receivers [28]. Furthermore, a distinction can be made between those signals in which individuals can vary their investment, and those signals whose limit is set by physical constraints [26]. These distinctions have important theoretical implications for the evolution of signals, because theory predicts a close match between signal design and cost type [26].

#### Energy and time budgets

Singing involves complex muscular contractions [29] that need energy, and we expect all the song characteristics grouped under the heading Performance-related traits to be constrained by energetic costs. Ample circumstantial evidence that singing presents a significant energetic cost comes from studies of food supplementation and from positive correlations between ambient temperature and singing [30]: males sing more when it is warm, and also when provided with extra food. Although these data suggest that singing is energetically costly, the same could be predicted solely from the fact that feeding and singing are incompatible activities [5]. On this account, taking time for singing from the feeding time budget would represent an indirect cost that would constrain song rates and singing time irrespectively of singing being costly *per se*.

The metabolic cost of song production has been studied by measuring oxygen consumption rates during singing under laboratory conditions. Oxygen consumption rate rose dramatically during singing in a *Thryothorus* wren: from between 2.7 and 8.66 times that of the basal metabolic rate [31]. However, these results have been questioned because of methodological problems [5]. Indeed, a recent study of several bird species has shown that metabolic costs of singing are much lower, representing a mere 1.05–1.38-fold increase over pre-singing metabolic levels [32]. Most importantly, between-species differences in oxygen consumption were very small, suggesting that song content does not represent specific energetic costs. However, loud song was found to be significantly more costly than was quiet song, and this might be an important problem of this type of study, because birds in captivity do not sing the loud songs typically sung in the field.

A comparative analysis of a mixture of taxa showed that species with higher metabolic rates have lower song outputs [33], which suggests that song output is

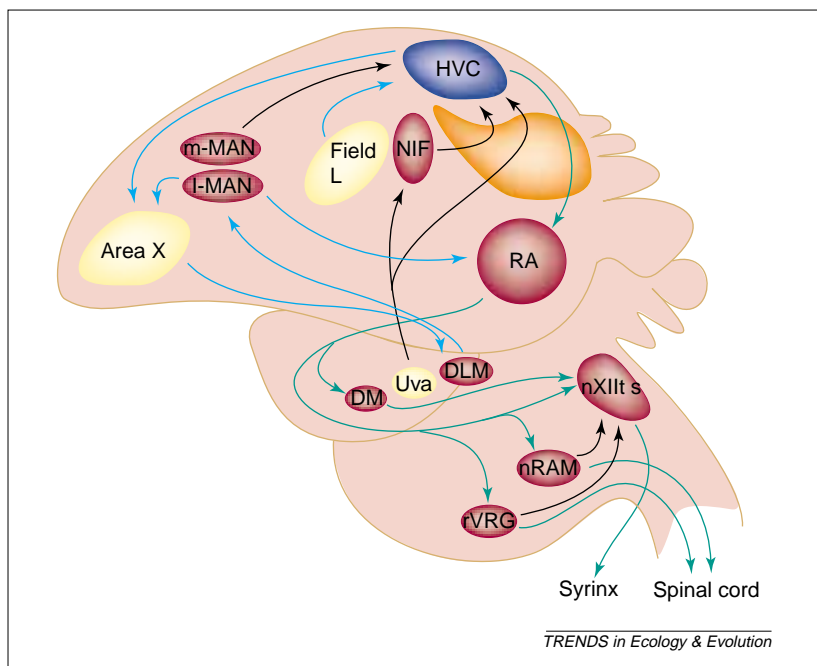


Fig. 1. A schematic parasagittal view of the song system of songbirds indicating the major projections (arrows), areas that express androgen receptors only (red), androgen and estrogen receptors (blue), and aromatase (orange). The descending motor control pathway (green arrows) includes the forebrain vocal areas HVC and RA, which are necessary for the production of learned vocalizations [45]. The auditory forebrain loop (blue arrows) includes the forebrain areas I-MAN and Area X, which are involved in vocal learning. Black arrows are known connections that might have modulatory effect on song activity. Yellow areas either do not express or express infrequently androgen receptors. Electrophysiological work in the zebra finch *Taeniopygia guttata* suggests a hierarchical organization of the song system with HVC activity coding for motor unit sequences, such as syllables, and RA activity coding for subsyllable components [42]. RA probably connects the forebrain song system to further motor systems that are active during singing, such as beak, tongue and larynx control circuits [41]. Abbreviations: DLM, nucleus dorsolateralis thalamus, pars medialis; DM, nucleus dorsomedialis; HVC, nucleus hyperstriatalis ventralis, pars caudalis; I-MAN, lateral part of nucleus magnocellularis anterioris; m-MAN, medial part of nucleus magnocellularis anterioris; NIF, nucleus interfascialis; nRAM, nucleus retroambigualis; nXIIIs, nucleus hypoglossus pars tracheosyringalis; RA, nucleus robustus archistriatalis; rVRG, rostroventral respiratory group; Uva, nucleus uvaeformis. Data taken from [64,65].

limited energetically. However, direct tests of the exact energetic cost of singing in the field are still needed. Even if the energy needed to sing one song is small, adding up this cost across the long bouts of loud song typically produced by many passerines is likely to represent a significant part of the energy budget.

#### Physical and developmental constraints

A constraint that limits the general condition of a bird and its expression of ornaments is probably established early in life. Thus, song quality could reflect the developmental stress experienced by the bird as a nestling [34]. Evidence comes from a recent study of the great reed warbler, where measures of individual nestling body condition correlated positively with the size of adult song repertoires [35]. Physical constraints can be more specific and relate to particular aspects of the song. Some syllables or phrases might be particularly difficult to produce if, for instance they require the fine coordination of special respiratory mechanisms [29] or if they depend on body size [21]. Podos has elegantly shown, by means of comparative [36] and experimental work [37], that there are constraints in syllable production, identifying a major tradeoff between trill rate and frequency bandwidth. Birds faced with learning fast

trills of a large frequency width would break the syntax or reduce the bandwidth of the song. Sexual selection could favour birds that produce song elements that are on the border of what is physically possible [19].

#### Social aggression

In the case of badges of status (apparently cost-free plumage traits that correlate with dominance), it has been proposed that the honesty of the signal is guaranteed through a permanent social process by which individuals who display the dominance badge are challenged by other males [38]. Therefore, as only good quality males can counter this level of aggression, dominance badges reliably reflect male fighting ability.

Some special song syllables might also constitute badges of status [20]. If so, territorial males that produce these syllables should be challenged by conspecifics more often than are those that do not. This reasoning can also be applied to other song traits, such as song rate, repertoire size, song matching or song overlapping, predicting that birds will be subject to higher levels of aggression when they display larger or more aggressive signals.

Indeed, playback studies show that some singing patterns, such as song matching [39] or overlapping [27], elicit strong aggressive responses from territorial birds. It remains to be tested, however, whether these playback experiments are actually mimicking the conditions of territory establishment in the wild.

#### Predation

Predators can locate their prey by using their calls as cues. In many bird species, males sing from high, exposed perches, which can render them especially vulnerable to attack from aerial predators. Songbirds stop singing and deliver inconspicuous alarm calls when predators are detected [1]. A recent playback experiment has shown that brown skuas *Catharacta antarctica* locate their main prey by using their mating calls [40].

#### Age and experience

Song learning has been found in all oscine passerines studied to date [1]. Although the timing of learning varies between species, an important constraint might be the availability of song tutors, which might not be present between hatching and the time when the young male settles on his own territory. Under these conditions, certain characteristics of song, such as song sharing and matching, or the use of the local dialect, will be honest signals of age [17,18].

#### Neural costs

Neural cost is one of the most debated aspects of bird song. In addition to general avian vocal control areas in the brainstem and midbrain, songbirds have specialized forebrain auditory-vocal areas (Fig. 1) [41], which control the temporal pattern of song, the frequency modulations of song units and the sound amplitude [41,42]. The main argument for the existence of neural costs for song is based on intra- and interspecies structural



## Box 2. The size of forebrain vocal control area

The size of brain areas, such as HVC (nucleus hyperstriatalis ventrale, pars caudale), depends on the combined effect of several factors, including the genetic determination of the initial neuron populations and epigenetic mechanisms that alter the size of the nucleus after forebrain growth ends [a]. In zebra finches *Taeniopygia guttata*, variance in HVC size increases about threefold between 30 days of age and adulthood [a]. Individual variation in HVC size is very large (0.39–0.88 mm<sup>3</sup>; CV = 37.8) [b] and the total volume of the forebrain song system occupies ~1.65% of the forebrain, with a variation of CV = 17.15 among individuals [b].

Bird song is one of the few systems in which behaviour has been successfully linked to anatomically defined brain structures, based on four different kinds of evidence:

- Comparisons within species. These studies examine individual male variation in song in relation to the size of several song nuclei. HVC is positively correlated with repertoire size [b,c], although evidence is often contradictory [d].
- Comparisons between sexes. Although singing is usually restricted to males, species do vary in the extent to which females are vocal. Accordingly, HVC and RA are larger in males than in females, and the extent of this difference is correlated with the extent of sexual dimorphism in singing behaviour and repertoire size [e]. This trend does, however, include some important noise, such as large HVC sexual differences in species with similar song repertoires in both sexes, for example, the bush shrike *Laniarius funebris* [f].
- Comparisons among species. Several comparative analyses have revealed positive interspecific correlations between HVC volume and repertoire size across species [g]. However, only one third of the variation in song repertoire is accounted for by differences in HVC size [g].
- Comparisons among seasons. In several species, seasonal changes in singing behaviour parallel changes in HVC size [h]. However, this pattern is not universal, and some species do not show such a correlation [i].

Together, these studies suggest a link between song repertoire size and HVC size. However, mixed evidence suggests that the picture is far more complex. Several possibilities can account for the often poor correspondence between song behavioural and neuronal phenotype:

- The same syllable might be produced with different motor programmes in individuals of different species or of the same species. For instance, zebra finches do not need syringeal muscles to define syllable length, whereas brown thrashers *Toxostoma rufum* do [j,k].
- The unit of vocal motor pattern storage is unknown and might be different in different species, depending on the physical properties of the vocal tract. For instance, the contribution of the two sides of the syrinx to the production of sounds is highly species specific [j].
- Vocal areas might be involved in tasks other than singing, such as auditory recognition [l].

### References

- a Gahr, M. and Metzdorf, R. (1999) The sexually dimorphic expression of androgen receptors in the song nucleus hyperstriatalis ventrale pars caudale of the zebra finch develops independently of gonadal steroids. *J. Neurosci.* 19, 2628–2636
- b Airey, D.C. and DeVogd, T.J. (2000) Greater song complexity is associated with augmented song system anatomy in zebra finches. *NeuroReport* 11, 2339–2344
- c Nottebohm, F. *et al.* (1981) Brain space for a learned task. *Brain Res.* 213, 99–109
- d Leitner, S. *et al.* (2001) Seasonal activation and inactivation of song motor memories in wild canaries is not reflected in neuroanatomical changes of forebrain song areas. *Horm. Behav.* 40, 160–168
- e MacDougall-Shackleton, S.A. and Ball, G.F. (1999) Comparative studies of sex differences in the song-control system of songbirds. *Trends Neurosci.* 22, 432–436
- f Gahr, M. *et al.* (1998) Sex difference in the size of the neural song control regions in a duetting songbird with similar song repertoire size of males and females. *J. Neurosci.* 18, 1124–1131
- g DeVogd, T.J. *et al.* (1993) Relations between song repertoire size and the volume of brain nuclei related to song: comparative evolutionary analyses amongst oscine birds. *Proc. R. Soc. London B. Biol. Sci.* 254, 75–82
- h Tramontin, A.D. and Brenowitz, E.A. (2000) Seasonal plasticity in the adult brain. *Trends Neurosci.* 23, 251–258
- i Gahr, M. (1997) How should brain nuclei be delineated? Consequences for developmental mechanisms and for correlations of area size, neuron numbers and functions of brain nuclei. *Trends Neurosci.* 20, 58–62
- j Suthers, R. *et al.* (1999) The neuromuscular control of birdsong. *Philos. Trans. R. Soc. London Ser. B* 29, 927–939
- k Williams, H. and McKibben, J.R. (1992) Changes in stereotyped central motor patterns controlling vocalization are induced by peripheral nerve injury. *Behav. Neural Biol.* 57, 67–78
- l Del Negro, C. *et al.* (2000) Sexually stimulating signals of canary (*Serinus canaria*) songs: evidence for a female-specific auditory representation in the HVC nucleus during the breeding season. *Behav. Neurosci.* 114, 526–542

differences in song control areas of the male brain (Box 2). Although the evidence for a direct relationship between male brain structure and song behaviour is controversial (Box 2), let us assume that it exists and examine five possible neural costs that arise from it.

- Developmental costs required to organize the vocal circuit, such as neurogenesis and neuronal differentiation. Songbirds use between 1.5% and 2.1% of their forebrain for song production [43]. Assuming that the neurons involved are of the same phenotype as neurons in other brain areas, the main investment in the development of these areas would be in neuron number rather than neuron phenotypes. Variability in the size of the forebrain vocal areas in individuals of species such as the zebra finch suggests that this investment includes between 0.75 and 1.05% of forebrain neurogenesis [excluding

the neurons of vocal nucleus Area X (Fig. 1) of lobus parolfactorius, which develop independently of the song system]. Given this limited figure, it seems unlikely that individual variation in song repertoire size or other brain-based variation in songs would impose differences in developmental costs.

- Maintenance costs of the components of the song system in adulthood. Neurogenesis in adulthood, the process suggested to update and renew vocal memory [44], could also represent an important cost. However, neurogenesis is an ongoing process in adult birds, and is unrelated to whether birds differentiate forebrain vocal areas [44]. This could indicate that any cost of this process that is identified will not be related to individual song variation.
- Energetic cost of the neuronal activity related to the song system. Estimations of the neural bioenergetic

### Box 3. The endocrinology of bird song

In birds, testosterone (T) is the main androgen secreted by the testis, and seasonal changes in singing activity and song structure correlate with periods of dramatically increased testis size and T production [a]. The action of T on target areas is often mediated through its metabolic conversion into estrogen or 5 $\alpha$ -dihydrotestosterone. The conversion of T to estrogen is driven by aromatase [a,b], which is present in several areas of the forebrain (Fig. 1, main text). The presence of androgen receptors (red) and estrogen receptors (blue) indicates the sensitivity of the neural song system to these steroids (Fig. 1, main text). Steroid-sensitive neural circuits undergo high structural and neurochemical plasticity in juvenile and adult life [c]. In particular, estrogens derived from T in the brain appear intimately involved in the development and activity of the neural sexual phenotype of the vocal control system [a,d,e]. Protein synthesis rates in vocal areas increase greatly with increasing levels of circulating sex hormones [f]. Raising levels of T in adult songbirds modifies the morphology and chemistry of neurons of male forebrain vocal areas [a,b,g].

Although the overall relationship between T and singing is well established, there are only a few studies of how variation in steroid levels relate to individual variation in song. Experimental manipulations show that T levels in the dark-eyed junco *Junco hyemalis* [h] positively influence song rates. However, two correlative studies provide negative evidence for such a relationship in other species: T levels are not related to song output in the barn swallow [i], or to repertoire size in the red-winged blackbird [j]. This is to be expected if there are individual differences in the responsiveness of the brain song system to T, which is mediated by, among other processes, seasonal changes in the levels of brain aromatase [b] (Fig. 1, main text). Future studies relating steroid levels to song should consider variations in this type of enzymatic activity. Finally, if song characteristics are dependent on hormone levels during song development, identifying these patterns in adult birds might not be relevant. Future studies should examine whether early steroid levels influence later song production [k].

#### References

- a Ball, G.F. (1999) The neuroendocrine basis of seasonal changes in vocal behavior among songbirds. In *The Design of Animal Communication* (Hauser, M.D. and Konishi, M., eds), pp. 213–253, Bradford
- b Fusani, L. *et al.* (2000) Seasonal expression of androgen receptors, estrogen receptors, and aromatase in the canary brain in relation to circulating androgens and estrogens. *J. Neurobiol.* 43, 254–268
- c McEwen, B.S. (1994) How do sex and stress hormones affect nerve cells? *Ann. New York Acad. Sci.* 743, 1–18
- d Gurney, M.E. and Konishi, M. (1980) Hormone-induced sexual differentiation of brain and behaviour in zebra finches. *Science* 208, 1380–1383
- e Dittrich, F. *et al.* (1999) Estrogen-inducible, sex-specific expression of brain-derived neurotrophic factor mRNA in a forebrain song control nucleus of the juvenile zebra finch. *Proc. Natl. Acad. Sci. U. S. A.* 96, 8241–8246
- f Konishi, M. and Akutagawa, E. (1981) Androgen increases protein-synthesis within the avian brain vocal control-system. *Brain Res.* 222, 442–446
- g Gahr, M. and Metzdorf, R. (1997) Distribution and dynamics in the expression of androgen and estrogen receptors in vocal control systems of songbirds. *Brain Res. Bull.* 44, 509–517
- h Ketterson, E.D. *et al.* (1992) Testosterone and avian life histories: effects of experimentally elevated testosterone on behavior and correlates of fitness in the dark-eyed junco (*Junco hyemalis*). *Am. Nat.* 140, 980–999
- i Saino, N. and Möller, A.P. (1995) Testosterone correlates of mate guarding, singing and aggressive behavior in male barn swallows, *Hirundo rustica*. *Anim. Behav.* 49, 465–472
- j Weatherhead, P.J. *et al.* (1993) Parasite faunas, testosterone and secondary sexual traits in male red-winged blackbirds. *Behav. Ecol. Sociobiol.* 33, 13–23
- k Nowicki, S. *et al.* (1998) Song learning, early nutrition and sexual selection in songbirds. *Am. Zool.* 38, 179–190

costs of singing are difficult. We know that, in humans, the whole brain uses a significant amount of energy, ~10–15% of the daily budget. Assuming that this also applies to birds, and that the cost of song-associated neural activity is related to the total number of song neurons and time spent singing, the brain area involved in singing would consume only a small amount of the daily energy budget – between 0.2 and 0.6% (Box 2). Although this is small, it might be significant in times of energetic stress. However, this cost is unlikely to affect repertoire size, because singing involves the activity of most neurons of vocal areas regardless of the songs produced [42,45].

- Tradeoffs in brain space devoted to song and other functions. This is a very popular hypothesis based on the rationale that, if a given brain area involves more space in some individuals than in others, then this extra space must be taken away from other areas of the brain [46]. However, there is no evidence showing that the development of one part of the brain draws on resources or space that could be used for another. On the contrary, a recent comparative analysis shows that specialized brain areas in mammals have evolved independently of each other [47], implying that tradeoffs between brain areas do not constrain brain evolution.
- Endocrine costs of the brain song system. The song system differs from other avian forebrain sensory-motor circuits in that its development, maintenance and functional properties in adult life depend on gonadal steroids and their receptors (Box 3). We believe that the most probable candidates for a neural cost of song will be those that are related to the endocrine mechanisms that regulate brain song areas (Box 3). Costly neuroendocrine control of singing might act at several stages, from the processes of high plasticity in neuronal protein turnover [48] during song development, to the transfer of peripheral steroids for brain-based steroid metabolism [49]. However, no systematic studies to date have addressed this issue. Costs of this activity might be either direct, such as energetic expenditure in the increase of the gonads and the maintenance of long periods of high steroid production, or indirect. Indirect costs are likely to impinge on the steroid-sensitive constraints of the immune system, or on more general tradeoffs between investment in immune defence and physiology [50].

#### Immunocompetence costs

In 1992, Folstad and Karter [51] proposed that the expression of male ornaments was limited by the negative effect that androgens have on the immune system of male vertebrates. This immunocompetence handicap hypothesis is based on the assumption that the expression of male ornaments is androgen dose-dependent, and that these substances have, in turn, suppressive effects on the immune system. Recent evidence confirms the immunosuppressive effects of testosterone (T), which might represent a cost of the expression of sexual traits [52]. This hypothesis

Table 1. Relevance of different limiting costs to several bird song characteristics

Limiting cost or constraint	Song characteristic				
	Performance aspects	Repertoire size	Specific syllables	Timing	Countersinging patterns
<b>Energy</b>	Probably important for long singing bouts and loud song <sup>a</sup>	Unlikely to depend on song content <sup>a</sup>	Unlikely to depend on song content <sup>a</sup>	Probably higher in bad weather conditions <sup>b</sup>	Unlikely
<b>Social aggression</b>	Higher song rates or song amplitude probably increase aggression by other males, or probability of being detected	Unlikely, because large repertoires are a more effective keep-out signal <sup>c</sup>	Proposed for the water pipit <i>Anthus spinoletta</i> <sup>d</sup>	Unlikely	Song matching and overlapping elicit high levels of aggression <sup>e</sup>
<b>Predation</b>	Probability of being detected by a predator probably increases with increasing song rate, time spent singing and song amplitude	Unlikely	Syllables with frequency modulation are easier to localize than are those with constant frequency <sup>c</sup>	Possible where birds display in the presence of predators <sup>f</sup>	If greater aggressiveness is elicited by some countersinging patterns, vigilance might be impaired
<b>Age/experience</b>	Unlikely	Age might be a limiting factor if opportunities to learn a repertoire are scarce	Age is a limiting factor for learning shared songs or dialects only encountered after the first spring <sup>g</sup>	Unlikely	For matching to happen, songs must be shared, which might require a minimum age
<b>Neural costs</b>	Unlikely, although song-bout length correlates with HVC <sup>h</sup> size in starlings <i>Sturnus vulgaris</i> <sup>i</sup>	Very common assumption, but no convincing evidence of brain space and neuron numbers having a cost <i>per se</i>	Unlikely	Unlikely	Unlikely
<b>Immune/hormonal costs</b>	Most probable during song production <sup>j</sup>	Most probable during song development, hormonal dependency of neural phenotype might be costly <sup>k</sup>	Probable if syllables or songs increase aggressiveness of other males, therefore increasing T levels among males concerned	Immune defence likely to be compromised in bad weather	Probable if countersinging increases aggressiveness of other males, therefore increasing T levels among males concerned
<b>Physical and developmental constraints</b>	Early nutrition is a possible limiting factor <sup>l</sup>	Positively correlated with indexes of early nutrition <sup>m</sup> , but no experimental data available	Body size limits sound frequency produced <sup>n</sup>	Unlikely	Unlikely
<sup>a</sup> [32].	<sup>b</sup> [59].	<sup>c</sup> [1].	<sup>d</sup> [20].	<sup>e</sup> [27,39].	<sup>f</sup> [60].
<sup>g</sup> [61].	<sup>h</sup> Abbreviation: HVC, nucleus hyperstriatalis ventrale, pars caudale	<sup>i</sup> [34].	<sup>j</sup> [62].	<sup>k</sup> [56].	<sup>l</sup> [54,55].
<sup>k</sup> [56].	<sup>l</sup> [34].	<sup>m</sup> [35,63].	<sup>n</sup> [21].		

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provides a functional link with theories of parasite-mediated sexual selection, which propose that the development of ornaments is an indication of the bearer's heritable resistance to parasites [53]. The original immunocompetence hypothesis has now been extended to include general tradeoffs between immune defence and life-history traits [50], in the sense that all these traits compete for the same resources. Although the relationship between bird song and androgens is well established (Box 3), no study has so far addressed experimentally whether any aspect of bird song is directly limited by immunocompetence.

A basic distinction should be made between immune costs during song development and those during song production, because different aspects of song will be limited at each of these stages. On the one hand, song performance (song output, rate, etc.) is most likely to be affected by resources allocated to immune function during song production. Consistent evidence for this

comes from studies of the barn swallow *Hirundo rustica*, in which song output is correlated with lymphocyte concentration [54], and experimental infection with mites results in a reduction of song output [55].

On the other hand, aspects of song related to learning, such as repertoire size, are more likely to be constrained by allocation to immune function during song development. If this is true, there should be a positive relationship between the size of the song repertoire and the length of time during which T and its metabolites are required for the development of song brain nuclei. Although no experimental study has tested this, several lines of evidence suggest that this might be the case.

In the sedge warbler *Acrocephalus schoenobaenus*, males with blood parasites have smaller repertoires than do birds without [56]. This pattern is probably due to immune defence competing with song acquisition or crystallization, rather than with song production *per se*. Comparative analyses also report evidence linking

repertoire size and parasites. Hamilton and Zuk found that species with a high prevalence of parasites had complex repertoires and bright plumage ornaments [53], although some of these results have been confounded by phylogeny and should be interpreted with caution [57]. A recent comparative study has found that species with larger repertoires have relatively larger spleens (organs involved in immune defence) [58], a correlation that is consistent with the idea that repertoire size draws on immunocompetence costs. However, there is a great need for studies examining the dose dependency among vocal, immune and neural phenotypes at the species level.

## Conclusion

Our intention here has been to clarify the constraints that could limit the expression of bird song in the multiple ways in which it varies. It is surprising that hypotheses of the honesty of bird song still lack substantial evidence (Table 1). Bird song research has grown exponentially in the past few decades, through the effort of ethologists, behavioural ecologists and neurobiologists [1]. However, unravelling the factors that limit the expression of individual variation in song needs an integration of knowledge of all these fields.

## References

- Catchpole, C.K. and Slater, P.J.B. (1995) *Bird Song: Biological Themes and Variations*, Cambridge University Press
- Andersson, M. (1994) *Sexual Selection*, Princeton University Press
- Grafen, A. (1990) Biological signals as handicaps. *J. Theor. Biol.* 144, 517–546
- Rowe, L. and Houle, D. (1996) The lek paradox and the capture of genetic variance by condition dependent traits. *Proc. R. Soc. London B. Biol. Sci.* 263, 1415–1421
- Gaunt, A.S. *et al.* (1996) Is singing costly? *Auk* 113, 718–721
- Hoi-Leitner, M. *et al.* (1995) Song rate as a signal for nest site quality in blackcaps (*Sylvia atricapilla*). *Behav. Ecol. Sociobiol.* 37, 399–405
- Alatalo, R.V. *et al.* (1990) Singing rate and female attraction in the pied flycatcher: an experiment. *Anim. Behav.* 39, 601–603
- Wasserman, F.E. and Cigliano, J.A. (1991) Song output and stimulation of the female in white-throated sparrows. *Behav. Ecol. Sociobiol.* 29, 55–59
- Møller, A.P. *et al.* (1998) Paternity and multiple signalling: effects of a secondary sexual character and song on paternity in the barn swallow. *Am. Nat.* 151, 236–242
- Searcy, W.A. and Yasukawa, K. (1996) Song and female choice. In *Ecology and Evolution of Acoustic Communication in Birds* (Kroodsma, D.E. and Miller, E.H., eds), pp. 454–473, Cornell University Press
- Searcy, W.A. (1992) Song repertoire and mate choice in birds. *Am. Zool.* 32, 71–80
- Gil, D. and Slater, P.J.B. (2000) Multiple song repertoire characteristics in the willow warbler (*Phylloscopus trochilus*): correlations with female choice and offspring viability. *Behav. Ecol. Sociobiol.* 47, 319–326
- Buchanan, K.L. and Catchpole, C.K. (1997) Female choice in the sedge warbler, *Acrocephalus schoenobaenus*: multiple cues from song and territory quality. *Proc. R. Soc. London B. Biol. Sci.* 264, 521–526
- Mountjoy, D.J. and Lemon, R.E. (1996) Female choice for complex song in the European starling: a field experiment. *Behav. Ecol. Sociobiol.* 38, 65–71
- Hasselquist, D. *et al.* (1996) Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. *Nature* 381, 229–232
- Brenowitz, E.A. *et al.* (1995) Brain space for learned song in birds develops independently of song learning. *J. Neurosci.* 15, 6281–6286
- Beecher, M.D. *et al.* (2000) Territory tenure in song sparrows is related to song sharing with neighbours, but not to repertoire size. *Anim. Behav.* 59, 29–37
- O’Loghlin, A.L. and Rothstein, S.I. (1995) Culturally correct song dialects are correlated with male age and female song preferences in wild populations of brown-headed cowbirds. *Behav. Ecol. Sociobiol.* 36, 251–259
- Vallet, E. *et al.* (1998) Two-notes syllables in the canary songs elicit high levels of sexual display. *Anim. Behav.* 55, 291–297
- Rehsteiner, U. *et al.* (1998) Singing and mating success in water pipits: one specific song element makes all the difference. *Anim. Behav.* 55, 1471–1481
- Ryan, M.J. and Brenowitz, E.A. (1985) The role of body size, phylogeny, and ambient noise in the evolution of bird song. *Am. Nat.* 126, 87–100
- Mace, R. (1987) The dawn chorus in the great tit is directly related to female fertility. *Nature* 330, 745–746
- Gil, D. *et al.* (1999) Seasonal patterns of singing in the willow warbler: evidence against the fertility announcement hypothesis. *Anim. Behav.* 58, 995–1000
- Hutchinson, J.M.C. *et al.* (1993) Song, sexual selection, starvation and strategic handicaps. *Anim. Behav.* 45, 1153–1177
- Otter, K. *et al.* (1997) Honest advertisement and song output during the dawn chorus of black-capped chickadees. *Behav. Ecol.* 8, 167–173
- Vehrencamp, S.L. (1999) Handicap, index, and conventional signal elements of bird song. In *Animal Signals: Signalling and Signal Design in Animal Communication* (Espmark, Y. *et al.*, eds), pp. 161–184, Tapir Academic Press
- Naguib, M. (1999) Effects of song overlapping and alternating on nocturnally singing nightingales. *Anim. Behav.* 58, 1061–1067
- Guilford, T. and Dawkins, M.S. (1995) What are conventional signals? *Anim. Behav.* 49, 1689–1695
- Suthers, R. *et al.* (1999) The neuromuscular control of birdsong. *Philos. Trans. R. Soc. London Ser. B* 299, 927–939
- Thomas, R.J. (1999) Two tests of a stochastic dynamic programming model of daily singing routines in birds. *Anim. Behav.* 57, 277–284
- Eberhardt, L.S. (1994) Oxygen consumption during singing by male Carolina wrens (*Thryothorus ludovicianus*). *Auk* 111, 124–130
- Oberweger, K. and Goller, F. (2001) The metabolic cost of birdsong production. *J. Exp. Biol.* 204, 3379–3388
- Read, A.F. and Weary, D.M. (1992) The evolution of bird song: comparative analyses. *Philos. Trans. R. Soc. London Ser. B* 338, 165–187
- Nowicki, S. *et al.* (1998) Song learning, early nutrition and sexual selection in songbirds. *Am. Zool.* 38, 179–190
- Nowicki, S. *et al.* (2000) Nestling growth and song repertoire size in great reed warblers: evidence for song learning as an indicator mechanism in mate choice. *Proc. R. Soc. London B. Biol. Sci.* 267, 2419–2424
- Podos, J. (1997) A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution* 51, 537–551
- Podos, J. (1996) Motor constraints on vocal development in a songbird. *Anim. Behav.* 51, 1061–1070
- Rohwer, S. and Ewald, P.W. (1981) The cost of dominance and advantage of subordination in a badge signaling system. *Evolution* 35, 441–454
- Vehrencamp, S.L. (2001) Is song-type matching a conventional signal of aggressive intentions? *Proc. R. Soc. London B. Biol. Sci.* 268, 1637–1642
- Mougeot, F. and Bretagnolle, V. (2000) Predation as a cost of sexual communication in nocturnal seabirds: an experimental approach using acoustic signals. *Anim. Behav.* 60, 647–656
- Wild, J.M. (1997) Neural pathways for the control of birdsong production. *J. Neurobiol.* 33, 653–670
- Yu, A.C. and Margoliash, D. (1996) Temporal hierarchical control of singing in birds. *Science* 273, 1871–1875
- Airey, D.C. and DeVogt, T.J. (2000) Greater song complexity is associated with augmented song system anatomy in zebra finches. *NeuroReport* 11, 2339–2344
- Alvarez-Buylla, A. and Kirn, J.R. (1997) Birth, migration, incorporation, and death of vocal control neurons in adult songbirds. *J. Neurobiol.* 33, 585–601
- Jarvis, E.D. and Nottebohm, F. (1997) Motor-driven gene expression. *Proc. Natl. Acad. Sci. U. S. A.* 94, 4097–4102
- Harvey, P.H. and Krebs, J.R. (1990) Comparing brains. *Science* 249, 140–149
- Barton, R.A. and Harvey, P.H. (2000) Mosaic evolution of brain structure in mammals. *Nature* 405, 1055–1058
- Konishi, M. and Akutagawa, E. (1981) Androgen increases protein-synthesis within the avian brain vocal control-system. *Brain Res.* 222, 442–446
- Ball, G.F. (1999) The neuroendocrine basis of seasonal changes in vocal behavior among songbirds. In *The Design of Animal Communication* (Hauser, M.D. and Konishi, M., eds), pp. 213–253, Bradford
- Sheldon, B.C. and Verhulst, S. (1996) Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. *Trends Ecol. Evol.* 11, 317–321
- Folstad, I. and Karter, A.J. (1992) Parasites, bright males, and the immunocompetence handicap. *Am. Nat.* 139, 603–622
- Peters, A. (2000) Testosterone treatment is immunosuppressive in superb fairy-wrens, yet free-living males with high testosterone are more immunocompetent. *Proc. R. Soc. London B. Biol. Sci.* 267, 883–889



- 53 Hamilton, D.W. and Zuk, M. (1982) Heritable true fitness and bright birds: a role for parasites? *Science* 218, 384–387
- 54 Saino, N. *et al.* (1997) Song and immunological condition in male barn swallows (*Hirundo rustica*). *Behav. Ecol.* 8, 364–371
- 55 Møller, A.P. (1991) Parasite load reduces song output in a passerine bird. *Anim. Behav.* 41, 723–730
- 56 Buchanan, K.L. *et al.* (1999) Song as an indication of parasitism in the sedge warbler. *Anim. Behav.* 57, 307–314
- 57 Read, A.F. and Harvey, P.H. (1989) Reassessment of comparative evidence for Hamilton and Zuk theory on the evolution of secondary sexual characters. *Nature* 339, 618–620
- 58 Møller, A.P. *et al.* (2000) The evolution of song repertoires and immune defence in birds. *Proc. R. Soc. London B. Biol. Sci.* 267, 165–169
- 59 Reid, M.L. (1987) Costliness and reliability in the singing vigour of Ipswich sparrows. *Anim. Behav.* 35, 1735–1743
- 60 Cresswell, W. (1994) Song as a pursuit deterrent signal, and its occurrence relative to other anti-predation behaviors of skylark (*Alauda arvensis*) on attack by merlins (*Falco columbarius*). *Behav. Ecol. Sociobiol.* 34, 217–223
- 61 O’Loghlin, A.L. and Rothstein, S.I. (1993) An extreme example of delayed vocal development: song learning in a population of wild brown-headed cowbirds. *Anim. Behav.* 46, 293–304
- 62 Bernard, D.J. *et al.* (1996) Age- and behavior-related variation in volumes of song control nuclei in male European starlings. *J. Neurobiol.* 30, 329–339
- 63 Doutrelant, C. *et al.* (2000) Blue tit song repertoire size, male quality and interspecific competition. *J. Avian Biol.* 31, 360–366
- 64 Fusani, L. *et al.* (2000) Seasonal expression of androgen receptors, estrogen receptors, and aromatase in the canary brain in relation to circulating androgens and estrogens. *J. Neurobiol.* 43, 254–268
- 65 Gahr, M. and Metzdorf, R. (1997) Distribution and dynamics in the expression of androgen and estrogen receptors in vocal control systems of songbirds. *Brain Res. Bull.* 44, 509–517

# Early development, survival and reproduction in humans

Virpi Lummaa and Tim Clutton-Brock

**Environmental factors commonly influence the growth and early development of individuals in wild populations of mammals. Such influences can exert downstream effects on the phenotypic quality and breeding success of the same individuals in adulthood, as well as on the growth and subsequent reproductive success of their offspring. Recent studies of humans indicate that similar effects occur both in Western human populations and in human populations subject to nutritional stress. Here, we compare evidence for the effects of early development on growth, survival and breeding performance in humans to similar trends in food-restricted populations of other mammals. We highlight the relevance of findings from animal studies to humans and vice versa, and suggest that the integration of wild animal and human studies could increase our knowledge about how early development shapes reproductive performance across generations.**

In food-limited populations of wild mammals, ecological factors affecting growth rates of juveniles before or immediately following birth can have pronounced consequences for their subsequent growth, survival and breeding success [1–3]. In Scottish red deer *Cervus elaphus*, the mean birth weight of calves rises by ~8% for every 1°C increase in mean daily temperature during April and May, the two final months of gestation [4]. Differences in average birth weight among cohorts of calves are associated with intercohort differences in neonatal survival, relative development at specific ages and the age at first reproduction [5]. Other environmental factors that influence early growth can have similar consequences. For example, in Soay sheep *Ovis aries*, high population density in the winter preceding birth is associated with reduced birth weights, as well as with reductions in neonatal survival, adult body size and fecundity [6,7].

In sexually dimorphic species, the effects of adverse environmental conditions during early development are commonly more pronounced in males, leading to

either reductions in the relative numbers of males born [1], or reductions in their growth and breeding success [7,8]. In red deer, the proportion of male calves born declines with increasing population density in the preceding winter [9], whereas in bighorn sheep *Ovis canadensis*, sex differences in adult body size decline as population density increases [10]. Similar effects have been recorded under controlled conditions. Restricting food given to golden hamster *Mesocricetus auratus* females during their first 50 days of life causes them to produce smaller litters and female-biased sex ratios during adult life, even after they have been replaced on *ad libitum* diets [11]. In wild house mice *Mus musculus*, experimental food deprivation during gestation has much greater negative effect on the subsequent reproductive success of sons than on that of daughters, possibly because of a disruption in the organizational effects of testosterone in neonatal male mice [12].

Studies of wild mammals also suggest that early development has effects that span generations. For example, cohorts of female red deer characterized by relatively low birth weights produce light calves and the survival of calves born to different cohorts of mothers varies from <10% to >60% [5,6]. Some evidence suggests that, like effects within generations [8], these intergenerational effects are more pronounced in males. For example, in hamsters, the daughters of food-restricted females, themselves reared on *ad libitum* diets, produce smaller litters and relatively fewer sons than do daughters of control females that were not food restricted [13].

Accumulating evidence suggests that similar growth and survival effects also occur in human

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