

(1) *A common signal is used because there is a benefit in coordinating reproduction with the metabolic decisions that lead to loss of longevity.* The most probable explanation for this is a resource allocation tradeoff: if metabolic resources for reproduction have to be released via a 'tap' from a store (or diverted from other purposes), and once mobilized are lost if not exploited for reproduction, then readiness for the uptake of mobilized resources should be coordinated with resource mobilization: readying the gamete production system and turning on the mobilization tap should be synchronized. *daf-2* (-) mutants that result in a partially closed tap will reduce fecundity and increase longevity, but mutants or experimental manipulations that suppress fecundity without turning off the tap will result in the mobilized resources being lost without a concomitant increase in longevity. Although mutants that increase fitness¹ seem to rule out this explanation, they also beg the question why the mutation has not arisen in the past and replaced the wild type. This suggests instead that fitness has not been measured in the wild-type environment.

(2) *The metabolic cost of having two separate signals outweighs the benefit of controlling the two processes independently.* The idea that physiological mechanisms can be subjected to cost-benefit analyses² and that the costs of control mechanisms should be included in optimality models of life-history traits³ are not new. Under this explanation, the link between fecundity and longevity would not occur if there was no cost to adding a second independent signal. Given the possible fitness costs of linking fecundity and longevity, it seems unlikely that the metabolic costs of a second signal would be sufficient for this explanation to hold.

(3) *A common signal is no longer adaptive, but the close integration of the signalling system prevents evolutionary change because this would require several simultaneous changes; that is, the system is trapped on a low adaptive peak.* The phylogenetic conservatism of signalling systems in disparate taxa is a possible footprint of such evolutionary entrapment, but could also be explained by consistent selection pressures through evolutionary time, as might be applied by a resource allocation tradeoff.

In his title – 'Molecular signals versus the *Loi de Balancement*' – Leroi presents molecular signals and resource allocation tradeoffs as alternatives. We agree that these are alternative proximate mechanisms, and that the evidence for *Caenorhabditis*, at the very least, supports molecular signals. However, proximate mechanisms are not an alternative to functional explanations: both are required to fully understand any trait. In our judgement, the current evidence does not rule out a resource allocation tradeoff as the functional explanation for a common signal (Explanation 1). The implied conclusion that the signalling system is not 'for' the allocation of some common limiting resource¹ seems premature.

We do indeed rejoice in the progress made in understanding the mechanisms underlying life-history traits. However, we believe that the greatest progress will be made by combining mechanistic and evolutionary approaches and we hope that those studying such mechanisms will be as enthusiastic about evolution as we are about the fascinating mechanisms that Leroi reviews¹.

Kate Lessells*

Netherlands Institute of Ecology, PO Box 40, 6666 ZG Heteren, The Netherlands.

*e-mail: lessells@cto.nioo.knaw.nl

Nick Colegrave

ICABP, University of Edinburgh, Ashworth Laboratories, King's Buildings, West Mains Road, Edinburgh, UK EH9 3JT.

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Digit homology of birds and dinosaurs: accommodating the cladogram

The idea that birds are living dinosaurs has gained widespread acceptance, especially in the popular press¹. However, problems exist, the most serious of which is the mismatch of the digits; whereas

theropods have a highly derived hand composed of digits I–II–II, digits II–III–IV occur in birds².

In the *Journal Club* section of *TREE*, Galis³ argued that recent papers reconcile the differences in digit homology. Wagner and Gauthier⁴ suggested that alterations in digit identity result from homeotic changes (i.e. changes in the identity of a structure), so that theropod digits are the same as those in birds. Drossopoulou *et al.*⁵ showed the developmental independence of the determination of digit number and identity by manipulating the Sonic hedgehog (*Shh*) gene to produce phenotypes with the same number of supernumerary digits, but with differences in digit identity. However, the question is not whether a homeotic change could occur, but whether it did occur.

Burke and Feduccia^{6,7} demonstrated that all amniotes (including birds) share a stereotyped, early developmental pattern, which is characterized by a Y-shaped condensation. The strongly staining, postaxial element forms a 'primary axis', a linear array that invariably identifies, in sequence, ulna–ulnare–distal carpal IV, and ultimately, digit IV. An eight-day chick or duck hand with digits II–III–IV and vestigial V, with a gap where digit I should be, is in stark contrast to the late Triassic *Herrerasaurus* hand with digits I–II–II and vestigial IV and V (Ref. 6).

If there was a frame shift, it would have occurred only in the forelimb and not in the hindlimb because, in birds, the same conserved developmental pattern occurs in anterior and posterior appendages. Embryological evidence is based on conservative developmental pattern and connectivity (i.e. classical homology), whereas the argument advanced by Galis³ is based on end-point morphology (i.e. analogy).

Paleontologists continue to assess homology *a posteriori* from cladistic analysis of multiple synapomorphies and to explain discrepancies by mechanisms such as the frame-shift hypothesis. In spite of developmental evidence that overwhelmingly supports a II–III–IV bird hand, in contrast to the I–II–III theropod hand^{8,9}, paleontologists will do whatever is necessary to accommodate the cladogram.

Alan Feduccia

Dept of Biology, University of North Carolina, Chapel Hill, NC 27599-3280, USA.
e-mail: feduccia@bio.unc.edu

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Digit homology of birds and dinosaurs: accommodating the cladogram

Response from Galis

When hypothesizing evolutionary transitions, scientists attempt to construct the most parsimonious scenario. As Feduccia states¹, most scientists agree that the scenario in which birds descend from dinosaurs is the most parsimonious. However, this scenario faces one major hurdle – the mismatch of the digits. When we assume that birds are derived from theropod dinosaurs and that the digits of birds are II–III–IV, there are two possible hypotheses: (1) avian ancestors had digits II–III–IV or (2), as was proposed by Wagner and Gauthier², there has been a homeotic shift from digits with identity I–II–III to digits with identity II–III–IV. On the basis of the present fossil record, the second hypothesis is the most probable.

Feduccia claims that the gap at the position of digit I in the embryonic hand of an eight-day chick argues against a

homeotic shift. I disagree. Let us compare the situation to that in vertebrae. In homeotic changes of vertebrae, two half somites that would normally develop into a given vertebra develop the identity of a neighbouring vertebra instead. Therefore, for a homeotic change of digits, the initial Anlagen of digits should form normally, as occurs in somites. Subsequently, the Anlage of digit II is expected to develop with the identity of digit I, digit III with the identity of digit II, etc. In the embryonic wings of ducks, ostriches, terns, chicks, penguins and gulls prechondrification-Anlagen of four, or possibly five, digits are formed^{3–10}. In the chondrification phase of all these species, digit II has shifted half of the way, or even wholly, towards the position of digit I. In the hand of a gull (Fig. 1a), digit II clearly lies in the position of digit I in the foot (Fig. 1b) (Refs 3,4), digits III and IV have hardly shifted and there is a gap between digits II and III. Subsequently, digit II develops an identity that is similar to that of theropod digit I, III of II and IV of III, in agreement with a homeotic shift.

To analyse the plausibility of a homeotic shift further, it is useful to compare the vertebral situation. The most common homeotic changes occur in vertebrae at the border of a region¹¹. For example, in ~5% of humans, the first lumbar vertebra changes into a thoracic one. Importantly, such a change is often accompanied by a homeotic change of the last lumbar vertebra into a sacral one¹¹. This leaves the normal number of lumbar

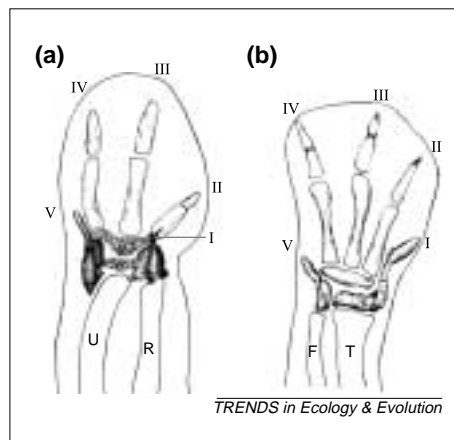


Fig. 1. Embryonic hand (a) and foot (b) of the gull, *Larus canus*. Note that the position of digit II in the hand is approximately in the position of digit I in the foot. Holmgren and others^{3–5,8} claim to recognize digit I in some bird species, but this is disputed, at least for the chicken¹⁰. Abbreviations: F, femur; R, radius; T, tibia; U, ulna. Reproduced, with permission from Ref. 3.

vertebrae, but the lumbar region starts one vertebra lower. Presumably, all lumbar vertebrae have shifted identity. Therefore, in the vertebral column, at least, identity shifts of serial structures do occur.

Thus, in addition to the independence of the determination of digit number and identity demonstrated by Drossopoulou *et al.*^{12,13}, there is indirect support for a homeotic shift from the early development of vertebrae in several bird species. As long as no fossils of theropods are found with four digits and the first one reduced, the hypothesis of Wagner and Gauthier² provides us with the most probable explanation for the digit identity of birds and theropods.

Frietson Galis

Institute of Evolutionary and Ecological Sciences, University of Leiden, PO Box 9516, 2300RA Leiden, The Netherlands.
e-mail: galis@rulsfb.leidenuniv.nl

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