knowledge of the developmental programme outside *Drosophila* is fragmentary, we would obviously not claim that the zootype as we know it is complete. There are likely to be other conserved components and these will doubtless not be confined to the antero-posterior axis.

Finally, Peter Gilliver and Eleanor Lawrence have told us that we are not the first to use the term 'zootype'. In the *Oxford English Dictionary* (2nd edn, 1989) two previous usages are listed: in 1905 the *Daily Chronicle*, 4 September, referred to "Egyptian hieroglyphics and Totemic zootypes", and in 1897 the *Annual Report of the Smithsonian Institute* included the sentence "Out of this worm form type . . . all the higher ranges of zootypic evolution have sprung". We are grateful to know of these antecedents.

Jonathan Slack
Peter Holland
Chris Graham
Department of Zoology,
University of Oxford,
Oxford OX1 3PS, UK

Bateson and peacocks' tails

SIR — Enquist and Arak's paper[1] and the accompanying News and Views article by Howlett[2] about modelling the evolution of characteristics using a neural network are taken as qualified support for Darwin's sexual selection hypothesis. In the process, several problems emerge. First, the results are more consistent with the views of Bateson[3] than of Darwin. Second, and consistent with Bateson's arguments, there is no justification for imagining that exaggerated male traits were selected. By this I do not mean to criticize sexual selection, or the competing hypotheses[2], *per se*. Rather, I wish to draw attention to the assumption that characters judged by us to be spectacular must have arisen by selection.

Bateson's views anticipated the theory of punctuated equilibrium, wherein dramatic and quantum changes can occur suddenly, providing the necessary variation for discontinuity between species. Whereas in Darwin's view variations were shaped over time by selective forces, Bateson believed that the physiology or genetics of organisms had the capacity to drive the observed discontinuity within a single generation. Enquist and Arak's work vindicates Bateson's views more than Darwin's. The provocative conclusions that ". . . the recognition mechanism itself exerts selection pressure on the signal. . ." and "that biases in the sensory apparatus . . . may have existed before the appearance of the same signals among males"[1] are consistent with Bateson's contention that evolution is driven by the physiological variation of organisms themselves[3].

Moreover, to argue that traits, such as a peacock's tail, are the products of selection is an inappropriate use of the evolutionary theory because it allows the generation of exclusive, yet unfalsifiable, hypotheses for the origin of traits[3]. Darwin's theory is appropriately used as evidence of the common descent of organisms. Its predictions are verified by the laboratory demonstration that variants are acted upon by natural selection[4,5]. However, it does not provide a means for reconstructing the origins of any particular trait. The plethora of mechanisms described by Howlett demonstrates that reasonable people can construct equally reasonable alternative hypotheses based on the same data. This is because evolutionary theory is unidirectional: one can impose a selective force on a population to select variants but one cannot demonstrate that any given variation has been acted upon by natural selection.

To use the theory otherwise creates an argument that is circular: an 'important' trait must have been selected because selection acts on important traits. Furthermore, utility is not an explanation of a trait's origin. Taking away a sparrow's feathers to prevent flight might make the sparrow less 'fit', but that does not mean that the advantages provided by flight drove the evolution of feathers[6].

Given the universality that the authors claim for their model of neural networks, bias should occur independently of sex. Therefore, outrageous traits should arise in both sexes, in all species, and in all network-controlled behaviours. Instead of a selection for deleterious characters, perhaps it is just as easy to imagine that ". . . animals live not only by virtue of, but also in spite of what [they] are"[3]. I am also troubled that the hypotheses offered to explain outrageous characteristics[2], and the experiment described in Fig. 3 of ref. 1, invoke successive modifications. Is there reason to believe that such a series of males actually existed? I do not wish to detract from the suggestion that neural networks may be internally biased[1]. But although this may explain peculiar female preferences, it may be a mistake to attribute the origin of traits to sexual preferences.

Jack A. Heinemann
NIAID, NIH,
Rocky Mountain Laboratories,
Hamilton, Montana 59840, USA

SIR — With regard to Rory Howlett's News and Views piece about sexual selection[2], I wish to point out that the ornamental 'tail' feathers, each with its iridescent eye pattern (shown in the accompanying photograph), are actually not part of the tail at all, but are the upper tail coverts. These remarkably elongated and elaborated feathers originate from the feather tract on the back, and create the stupendous 'train' that entirely hides the tail when the bird is at rest. The peacock's 'true' tail feathers are considerably shorter, dull-coloured, and otherwise uninteresting. In typical birds the tail coverts are short and unremarkable and only cover the base of the tail feathers.

For another sexually dimorphic pheasant, the great argus (*Argusianus argus*), it is the tail feathers and extremely modified secondary wing feathers that have evolved to great length and size, whereas the upper tail coverts are neither elongated nor specialized. This is an example of the reticulate nature of evolution, in which even closely related species have evolved, through sexual selection, oversized display ornaments from entirely distinct parts of the plumage.

Bruce M. Beehler
Wildlife Conservation Society and
Conservation International,
c/o Division of Birds MRC 116,
Smithsonian Institution,
Washington, DC 20560, USA

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Delayed dispersal

SIR — J. Komdeur (*Nature* **358**, 493–495; 1992) reported that lifetime reproductive success (LRS) payoffs predicted the observed dispersal behaviour in a group-territorial warbler, and that birds chose when and where to disperse on this basis. I suggest that a null hypothesis that does not involve comparisons of habitat quality or LRS payoffs could also explain his observations. If birds survey only contiguous territories (the neighbourhood) for vacancies and contest for them when breeding opportunities appear, regardless of quality, the data interpreted by Komdeur as consistent with choice on the basis of anticipated LRS can be explained simply on the basis of reported mortality rates, the number of territories in the three qualities of habitat, and their location relative to each other.

As evidence of LRS-based dispersal, Komdeur stated, "Yearlings born on high-quality territories were more likely to remain at home as helpers (92.7%;