The birds and the wasps: a sex-ratio meta-analysis

Those who work on sex ratios of parasitoid wasps have long been lulled by the idea that, because of a haplo–diploid sex determination mechanism, these insects have a high degree of control over the sex of their progeny. Meanwhile, those working on birds and mammals have been subjected to the rather burdensome notion that heterogametic sex determination mechanisms severely constrain the production of biased sex ratios, and thus that these taxa are probably unable to achieve sex-ratio control. The latter view has been challenged recently by remarkable sex ratios in several higher vertebrate species, such as the Seychelles warbler *Acrocephalus sechellensis*; but does the constraint still hold in general? A new meta-analysis by West and Sheldon [1] of sex ratios in parasitoid wasps, birds and mammals concludes that it probably does not, and also that the sex ratios of wasps and birds are similarly influenced by environmental uncertainty.

The data used are on the accuracy of sex-ratio adjustment when the fitness of male and female offspring varies differentially with environmental conditions, rather than on sex ratios at the population level, neatly avoiding the pitfall that population sex ratios are often hard to predict and interpret (because of sexually differential fitness variation). Although such Trivers–Willard-type logic has been employed to understand sex-ratio adjustment in response to a wide range of environmental conditions, predicting the direction of any sex-ratio adjustment often requires detailed information on life histories that is not generally available. This restricted the study of higher vertebrate sex ratios to a maternal response to mate quality (females with an attractive mate should produce sons) and to a response to the need for helpers-at-the-nest (when helpers are needed, the sex that provides the most help should be produced). In both cases, sex ratios showed a significant facultative adjustment in the predicted direction.

Having found that heterogamety need not prevent sex-ratio control, West and Sheldon go on to compare sex-ratio adjustment in birds with that of solitary parasitoid wasps, which are predicted to adjust the sex ratio according to host (i.e. environmental) quality, laying male eggs in smaller hosts and females in larger hosts. Wasps were categorized as those in which the host's development ceases on parasitization (idiobionts) and those in which the host continues to grow (koinobionts). Environmental quality is thought to be less predictable for koinobionts, because the host has not reached its final size when parasitoid sex is decided. Sex-ratio adjustment differed among groups considered in this comparison but, surprisingly, the difference was not between birds and wasps but between 'idiobiont wasps plus birds responding to helpers' and 'koinobiont wasps plus birds responding to mate quality', with the former group exhibiting the greater precision of adjustment. This throws a spotlight on environmental predictability as an important influence on sex ratios, and further suggests that, for birds, mate quality might be harder to assess than is the need for helpers.

1 West, S.A. and Sheldon, B.C. (2002) Constraints in the evolution of sex-ratio adjustment. *Science* 295, 1685–1688

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All people who on Earth do dwell

Explaining the latitudinal gradient in species richness is one of the fundamental challenges in ecology, and one that we have yet to fully meet. Several potential causal factors for this phenomenon have been invoked, including topographical heterogeneity, environmental stability, parasitism, time since major disturbance, and productivity. Elizabeth Cashdan [1] adds a new twist to this debate by elucidating another latitudinal pattern that applies to a single species – namely, the decrease in human ethnic diversity as we move from the equatorial regions to the poles.

In explaining this gradient, Cashdan draws heavily on the ecological literature. She is able to reject differences in productivity – as well as the chief determinants of productivity (mean annual rainfall and temperature) – as correlates of latitudinal patterns in ethnic diversity. Instead, ethnic diversity is best explained by climate variability and pathogen loads; regions with unpredictable climates and low pathogen loads have relatively few ethnic groups. Low climate predictability potentially forces populations (human and otherwise) to exploit wider ecological niches, becoming generalists when a single resource or set of conditions cannot be counted upon. High pathogen loads potentially made invasion or conquest difficult, as invading groups, armies, or colonial administrators could not tolerate the new diseases encountered. Habitat diversity, as measured by heterogeneity in vegetation types, is also associated with ethnic diversity, particularly among nonstratified societies.

Ecologists should be interested in these findings for several reasons. First, the differences that Cashdan uncovers for causal factors in complex versus simple societies might make us think more creatively about the key features of different taxonomic groups – particularly social groups – that might serve as the 'pressure points' upon which climatological, topographical, or biological forces act to drive latitudinal gradients in species richness. At the same time, the pervasiveness of these latitudinal patterns for biological and sociobiological phenomena (others have documented, for instance, latitudinal gradients in linguistic diversity) should lead us to look with more vigor for the general, ultimate explanations that might unite all patterns. Finally, this paper should remind us that human geography cannot be seen solely as a product of environmental determinism, nor can pre-modern ecological patterns be seen as being independent of human influences. Instead, both human and nonhuman populations are responding similarly to common environmental influences, potentially reinforcing emerging patterns across human and ecological systems in a long-term 'coevolutionary' dance.

1 Cashdan, E. (2001) Ethnic diversity and its environmental determinants: effects of climate, pathogens, and habitat diversity. *Am. Anthropol.* 103, 968–991

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