Modeling the Evolution of Sex Ratios and Other Traits Subject to Selection at Multiple Levels

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Overview

The sex ratio is a trait ideally suited to explore multilevel selection processes. One to one sex ratios are expected as a result of frequency-dependent individual selection within panmictic populations (Fisher 1930) while biased sex ratios may evolve as a result of selection acting above or below the individual (Williams 1966; Hamilton 1967; Wilson and Colwell 1981; Frank 1983; Avilés 1993; Werren and Beukeboom 1998). When different levels of selection oppose each other, as may be the case with sex ratio evolution, the forces and factors responsible for the emerging equilibrium can be more easily appreciated. Here, I will consider the evolution of sex ratios in subdivided populations to illustrate how computer simulations can be used to understand multilevel selection processes in general.

I will consider a model (Avilés 1993) in which diploid sexual organisms are individually represented by their genotypes. Genomes consist of multiple loci that code for the proportion of males produced in a clutch. The genetic system allows for processes that mimic mutation, meiosis, recombination, and the formation of zygotes. In the simulations, the sex ratio mean and variance evolve in response to different degrees of population subdivision and turnover of local populations or “colonies.” The more or less isolated colony lineages grow for multiple generations before giving rise to daughter colonies or becoming extinct. This is a population structure characteristic, for instance, of the social spiders, organisms in which highly female-biased sex ratios have evolved (reviewed in Avilés 1997).

I use different techniques to show that selection acting both among and within groups is involved in determining the overall equilibrium sex ratio. Within colonies, mating is panmictic and the sex ratio becomes less biased as the colonies age. An overall bias is generated or maintained, however, because faster-growing, more female-biased colonies are more likely to proliferate. I show that if this group-level selective advantage is removed, female-biased sex ratios do not evolve despite strong population subdivision and large rates of colony turnover. The global equilibrium, therefore, is dynamic and a compromise between the values favored by selection acting at the two levels.

I also explore the factors responsible for the equilibrium sex ratio and show that the outcome of a multilevel selection process depends on two distinct and independent properties of the entities at each of the levels: the amount of genetic variance available among them and their relative rates of turnover. In the simulations, more female-biased sex ratios evolve under smaller size of the founding groups, lower intercolony migration rates, and higher rates of colony turnover. I show that propagule size and migration rate affect the equilibrium sex ratio by changing the amount of genetic variance present within and between groups. Colony turnover rate, on the other hand, affects the equilibrium sex ratio by changing the relative frequency of selective events at the group and individual level.

I argue that multilevel selection processes in general can be cast under this light, regardless of the type of traits or levels involved. The term "more-female biased sex ratios" in the conclusions laid out above can be substituted by "lower levels of virulence", "greater degree of altruism", "lower transposition or replication rates", "lesser extent of meiotic drive", etc. Likewise, the levels involved could be transposons within genomes, organelles within cells, cells within bodies, parasites within hosts, individuals within social groups, trait groups, or populations, or the latter within populations, metapopulations, or species. In all cases, the outcome of a multilevel selection process will depend on how the particular idiosyncrasies of the various systems shape the relative amounts of genetic variance and rates of turnover of the entities at each of the levels. These properties, in turn, will determine the strength of and opportunity for selection at each of the levels.

A complementary question that I explore in an associated poster (see Avilés, L. Nonlinear Dynamics and the Evolution of Sociality, Alife VII) and elsewhere (Avilés 1998, 1999) concerns the evolution of traits such as group-joining and cooperative tendencies that may be responsible for the hierarchical structure of life and, thus, for the origin of multiple levels on which selection may act.

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