Statistical analyses of population genetic data

In addition to the methods recently reviewed in TREE by Rouset and Raymond1, the introduction of coalescence theory by Kingman in 1982 (Refs 2,3) has changed the field of theoretical population genetics considerably by allowing us to recover information about the shared history of individual genes, given a sample from a population. This knowledge of the genealogy can be used to directly estimate population parameters such as effective population size2-3, migration rates4-5, recombination rates6, population growth7, and selection. Most promising are maximum likelihood (ML) forward estimators7-11 (Table 1), which take the uncertainty of the genealogy into account by integrating over all possible genealogies using Markov chain Monte Carlo importance sampling. For DNA and microsatellite data these ML estimators are currently the best estimators for population size7,8.

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References
8 Nielsen, N. (1997) Genetics 146, 711–716

Hymenopteran sex allocation

Hepburn1 provided a useful account of the important work by Ode et al. on sex allocation in the hymenopteran parasitoid wasp Bracon hebetor. Sperm-depleted B. hebetor females can produce only males. Ode et al. found that, as predicted by Godfray’s model of constrained sex allocation1,2, inseminated females produced sex ratios that were female-biased to the degree expected, given an adaptive response to the all male output of the sperm-depleted males. This occurred without local mate competition, which is frequently responsible for female bias in parasitoid sex ratios4. Hepburn1 concluded that the work of Ode et al. represents ‘my knowledge, the first study to provide an explanation for female-biased sex allocation under parasitism by an insect in the field.’ However, this statement overlooks the female-biased sex allocation found in parasitic field populations of some social Hymenoptera (ants, bees and wasps), which has been successfully explained by Trivers and Hare’s5 theory of workercontrolled sex allocation combined with relatedness asymmetries due to haplodiplody6-7. This work surely deserves full inclusion in the canon of sex-ratio studies.

Table 1. New programs using a coalescent approach

| DNA, microsatellite, allelotype | COALESCE, FLUCTUATE, MIGRATE, | Maximum likelihood (ML) methods, estimation of population size, exponential growth rate, data migration rates. Three programs available as C source code or binaries for a wide variety of systems. http://evolution.genetics.washington.edu/rararac.html |
| DNA | PRIMATE, TIMESIM, RECOM, | ML methods: estimation of population size, exponential growth rate, recombination rate, migration rate, time of the last common ancestor. Contact the authors of Refs 9–11 for programs |
| DNA | SITES | Pairwise estimators: population size, last common ancestor, last for gene flow between two populations. C source code, OS or GS1 binaries. http://heylab.rutgers.edu/ |

In addition, it is worth noting a strong analogy between the situation modelled by Godfray and those arising in social Hymenoptera that have been considered in a parallel development of theory by several other authors12-14. All these cases arguably involve an expanded view of sex allocation behaviour that includes non-hamiltonian responses to mating structure1. In particular, extending work by Taylor2 and Nonacs15, Boomsma and Graen16 considered a population in which some colonies lose their queen and can then produce only males derived from reproductive, virgin workers. The colonies retaining their queen correspond to the inseminated females in Godfray’s model, and the queenless colonies to the sperm depleted or otherwise ‘constrained’ females.

In Boomsma and Grafen’s analysis, the stable population sex ratio equals the relatedness asymmetry of the party controlling sex allocation in the colonies with a queen. In contrast to the male-only producing colonies, the controlling party is selected to overproduce females until it derives equal per capita fitness from the sexes. This point is given by its relatedness asymmetry, which is defined as the ratio, (regression relatedness to females × sex-specific reproductive value of females)/regression relatedness to males × sex specific reproductive value of males16. From this, the expected degree of female bias in the colonies with a queen can be calculated16. However, because worker male production decreases the ratio of sex-specific reproductive values16, the bias should never be sufficient to restore the population sex ratio fully to its level in the absence of worker-produced males16.

Essentially the same reasoning was applied by Godfray for the case in which a fraction p of females in a parasitoid species produces males that arise through virgin or sperm depletion1. The stable population sex ratio should now equal the inseminated females’ relatedness asymmetry, which is 1:1. The ratio of sex-specific reproductive values is not affected by male-only producing females, because all parents in the population belong to one generation, there being no worker generation. In other words, the inseminated females should restore the population sex ratio to 1:1 (or 0.5 as the proportion of males). Therefore, if r is the inseminated females’ proportion of sons, (1-p)r + p = 0.5, from which one finds that r = (1-2p)/(2-2p), as Godfray first showed1.

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References