

## Statistical analyses of population genetic data

In addition to the methods recently reviewed in *TREE* by Roussel and Raymond<sup>1</sup>, 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 size<sup>4-9</sup>, migration rates<sup>6,10</sup>, recombination rates<sup>11</sup>, population growth<sup>9</sup>, and selection. Most promising are maximum likelihood- (ML-) based estimators<sup>7-11</sup> (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 size<sup>7,8</sup>.

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## Hymenopteran sex allocation

Heimpel<sup>1</sup> provided a useful account of the important work by Ode *et al.*<sup>2</sup> 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 allocation'<sup>3</sup>, 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 mothers. This occurred without local mate competition, which is frequently responsible for female bias in parasitoid sex ratios<sup>4</sup>. Heimpel<sup>1</sup> concluded that the work of Ode *et al.* represents 'to my knowledge, the first study to provide an explanation for female-biased sex allocation under panmixis by an arthropod in the field.' However, this statement overlooks the female-biased sex allocation found in panmictic field populations of some social Hymenoptera (ants, bees and wasps). This has been successfully explained by Trivers and Hare's<sup>5</sup> theory of worker controlled sex allocation combined with relatedness asymmetries due to haplodiploidy<sup>6,7</sup>. This work surely deserves full inclusion in the canon of sex-ratio studies.

In addition, it is worth noting a strong analogy between the situation modelled by Godfray<sup>3</sup> and those arising in social Hymenoptera that have been considered in a parallel development of theory by several other authors<sup>8-13</sup>. All these cases arguably involve 'an expanded view of sex allocation behaviour that includes non-hamiltonian responses to mating structure'<sup>1</sup>. In particular, extending work by Taylor<sup>8</sup> and Nonacs<sup>9</sup>, Boomsma and Grafen<sup>10,11</sup> 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 response 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  $\times$  sex-specific reproductive value of females)/(regression relatedness to males  $\times$  sex-specific reproductive value of males)<sup>11</sup>. From this, the expected degree of female bias in the colonies with a queen can be calculated<sup>6,11</sup>. However, because worker male production decreases the ratio of sex-specific reproductive values<sup>11</sup>, the bias should never be sufficient to restore the population sex ratio fully to its level in the absence of worker-produced males<sup>8,11</sup>.

Essentially the same reasoning was applied by Godfray for the case in which a fraction  $p$  of females in a parasitoid species produces males alone through virginity or sperm depletion<sup>3</sup>. 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 showed<sup>1,3</sup>.

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Table 1. New programs using a coalescent approach

Datatype	Program names, short description and Website
DNA, microsatellite, allozyme	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. <a href="http://evolution.genetics.washington.edu/lamarc.html">http://evolution.genetics.washington.edu/lamarc.html</a>
DNA	PTREESIM, 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
Microsatellite	MISAT: ML method: estimation of population size using the method of Ref. 4. Power Macintosh binary. <a href="http://mw511.biol.berkeley.edu/software.html">http://mw511.biol.berkeley.edu/software.html</a>
DNA	UPBLUE: Least-Square estimator: estimation of population size. Either www-based or Fortran source code. <a href="http://www.hgc.sph.uth.tmc.edu/fu">http://www.hgc.sph.uth.tmc.edu/fu</a>
DNA	SITES: Pairwise estimators: population size, last common ancestor, test for gene flow between two populations. C source code, DOS or OS2 binaries. <a href="http://heylab.rutgers.edu/">http://heylab.rutgers.edu/</a>