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Kin selection, genomics, and caste-antagonistic pleiotropy

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Model and analysis of intralocus caste conflict

Our model is similar in general construction to that of Hall and Goodisman [1]. We model a population of hymenopteran (i.e., haplodiploid) social insects, such that females (queens and workers) are diploid and males are haploid. We assume a colony consists of a single queen and her daughter workers. All colonies in a population produce reproductives synchronously and generations do not overlap. Mating is random and all queens in a population mate the same number of times, either once under single mating, or many times under multiple mating.

We assume that antagonistic selection arises because variation at a single locus affects a trait that has different optima in queens and workers. Expressing a trait value that is non-optimal results in a reduction in performance. Variation in the trait, and thus performance, is determined by an individual’s genotype at a single locus, which segregates for two alleles, $A$ and $a$. The effects of genetic variation on queen and worker performance is antagonistic. Specifically, the $A$ allele results in higher performance in workers and lower performance in queens, and vice-versa for the $a$ allele. Variation at this locus affects a phenotype that has a different optimum in the two castes, such as flight muscle production, mandible size, or ovary activity. Thus the optimal value of the phenotype that maximizes performance in queens (active ovaries, for example) reduces the performance of workers, and vice versa. Queens that are homozygous $aa$ have the optimal queen trait value, and maximum performance ($= 1$). Likewise, workers that are homozygous $AA$ have the optimal worker trait value, and maximum performance ($= 1$). All other caste genotypes have suboptimal performance.

Caste performance affects colony ‘fitness’, which is equivalent to number of reproductives produced by the colony. If a queen has a genotype that reduces her performance by half, then her colony produces half as many reproductives. Likewise, the production of reproductives by a colony is reduced by half if the average performance of workers is reduced by half. The number of reproductives produced by the colony is the product of queen performance and the mean performance of all the workers in the colony. This framework is essentially identical to that used in models of sexually antagonistic loci in which particular genotypes experience different fitness in males and females (e.g., [2]). For simplicity, we assume additive effects in both castes, such that the performance of the heterozygote falls exactly in between the two homozygotes. The performances of the genotypes are:

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Queen performance</th>
<th>Worker performance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$AA$</td>
<td>$1 - s_Q$</td>
<td>$1$</td>
</tr>
<tr>
<td>$Aa$</td>
<td>$1 - s_Q/2$</td>
<td>$1 - s_W/2$</td>
</tr>
<tr>
<td>$aa$</td>
<td>$1$</td>
<td>$1 - s_W$</td>
</tr>
</tbody>
</table>

where $s_Q$ and $s_W$ are the strengths of selection on performance acting against the $A$ and $a$ alleles in queens and workers, respectively.

The outcome of caste-antagonistic pleiotropy depends on the actual range of selection coefficients in queens and workers. However, little is known about the fitness effects of new mutations on performance of queens and workers in social insects. In addition, we assume that colonies produce equal sex ratios of new queens and males. Thus we do not consider cases of sex ratio bias that may occur in some social species [3].

With these assumptions, we obtain the following recursions in genotype frequencies in queens and males when queens are singly mated:
\[
TF_{AA} = (f_{AA}(1 - s_Q)p_m + f_{Aa}(1 - \frac{s_q}{2})p_m + f_{aa}(1 - \frac{s_q}{2})^2) ;
\]
\[
TF_{Aa} = f_{AA}(1 - s_Q)q_m (1 - \frac{s_w}{2}) + f_{Aa}(1 - \frac{s_q}{2})p_m (1 - \frac{s_w}{2}) + q_m (1 - \frac{3s_w}{4}) + f_{aa}p_m (1 - \frac{s_w}{2}) ;
\]
\[
TF_{aa} = f_{AA}q_m (1 - s_w) + f_{Aa}(1 - \frac{s_q}{2})q_m (1 - \frac{3s_w}{4}) ;
\]
\[
Tp_{m} = f_{AA}(1 - s_Q)
\left( p_m + q_m \left( 1 - \frac{s_w}{2} \right) \right) + f_{Aa}\left( 1 - \frac{s_q}{2} \right)p_m (1 - \frac{s_w}{2}) + q_m (1 - \frac{3s_w}{4}) ;
\]
\[
Tq_{m} = f_{aa}(1 - s_w)
\left( p_m (1 - \frac{s_w}{2}) + q_m (1 - s_w) \right) + f_{Aa}\left( 1 - \frac{s_q}{2} \right)p_m (1 - \frac{s_w}{2}) + q_m (1 - \frac{3s_w}{4}) ;
\]
where
\[
T = f_{AA}(1 - s_Q)
\left( p_m + q_m \left( 1 - \frac{s_w}{2} \right) \right) + f_{Aa}\left( 1 - \frac{s_q}{2} \right)p_m (1 - \frac{s_w}{2}) + q_m (1 - \frac{3s_w}{4}) + f_{aa}(1 - s_w) p_m (1 - \frac{s_w}{2}) + q_m (1 - s_w) .
\]

For multiply mated queens, the recursions are:
\[
TF'_{AA} = f_{AA}(1 - s_Q)p_m (p_m + q_m (1 - \frac{s_w}{2})) + f_{Aa}\left( 1 - \frac{s_q}{2} \right)p_m (1 - \frac{s_w}{2}) + q_m (1 - s_w) ;
\]
\[
TF'_{Aa} = f_{AA}(1 - s_Q)q_m (p_m + q_m (1 - \frac{s_w}{2})) + f_{Aa}\left( 1 - \frac{s_q}{2} \right)p_m (1 - \frac{s_w}{2}) + q_m (1 - s_w) ;
\]
\[
TF'_{aa} = f_{aa}q_m \left( p_m (1 - \frac{s_w}{2}) + q_m (1 - s_w) \right) + f_{Aa}\left( 1 - \frac{s_q}{2} \right)p_m (1 - \frac{s_w}{2}) + q_m (1 - s_w) ;
\]
\[
Tp'_{m} = f_{AA}(1 - s_Q)
\left( p_m + q_m \left( 1 - \frac{s_w}{2} \right) \right) + f_{Aa}\left( 1 - \frac{s_q}{2} \right)p_m (1 - \frac{s_w}{2}) + q_m (1 - s_w) ;
\]
\[
Tq'_{m} = f_{aa}(1 - s_w)
\left( p_m (1 - \frac{s_w}{2}) + q_m (1 - s_w) \right) + f_{Aa}\left( 1 - \frac{s_q}{2} \right)p_m (1 - \frac{s_w}{2}) + q_m (1 - s_w) ;
\]
where
\[
T = f_{AA}(1 - s_Q)
\left( p_m + q_m \left( 1 - \frac{s_w}{2} \right) \right) + f_{Aa}\left( 1 - \frac{s_q}{2} \right)p_m (1 - \frac{s_w}{2}) + q_m (1 - s_w) + f_{aa}(1 - s_w) p_m (1 - \frac{s_w}{2}) + q_m (1 - s_w) .
\]

In all recursions, \( f_{AA}, f_{Aa} \) and \( f_{aa} \) are the frequencies of queens of genotypes AA, Aa and aa respectively, and \( p_m \) and \( q_m \) are the frequencies of A and a males respectively.
To determine the global behavior of the system, we examined the conditions for the initial increase of each allele when rare. Our goal here was to determine the combinations of selection coefficients in queens and workers that resulted in one of four possible outcomes. (1) the \( A \) allele increases when rare and the \( a \) allele is lost when rare. In this case the \( A \) allele is expected to go to fixation. (2) The \( a \) allele increases when rare and the \( A \) allele is lost when rare. In this case the \( a \) allele is expected to go to fixation. (3) Both alleles increase when rare, in which case a protected polymorphism will result [4]. (4) Both alleles are lost when rare, implying that neither allele can invade a population fixed for the other (we never observed this outcome).

The condition for initial increase of an allele is determined by first calculating the Jacobian matrix at each fixation. The leading eigenvalue of the Jacobian matrix determines the stability of the fixation. We used Mathematica (version 9.0.1, Wolfram Research 2013) to calculate the Jacobian and its leading eigenvalue at each fixation. In all cases the leading eigenvalue was real and positive, implying instability when it is greater than 1, and stability when it is less than 1 [5]. The eigenvalues are:

<table>
<thead>
<tr>
<th>Model</th>
<th>Leading eigenvalue</th>
</tr>
</thead>
<tbody>
<tr>
<td>Singly-mated queen</td>
<td></td>
</tr>
</tbody>
</table>
| \( a \) allele fixed   | \[
\frac{(2 - s_q)(4 - 3s_w) + \sqrt{(2 - s_q)^2(4 - 3s_w)^2(72 - 38s_w - s_q(4 - 3s_w))}}{32(1 - s_w)}\] |
| \( A \) allele fixed   | \[
\frac{(2 - s_q)^2(4 - s_w) + (2 - s_q)(4 - s_w)(72 - 34s_w - s_q(68 - 33s_w))}{32(1 - s_w)}\] |
| Multiply-mated queen   |                                                                                  |
| \( a \) allele fixed   | \[
\frac{(2 - s_q)(4 - 3s_w) + \sqrt{(2 - s_q)^2(4 - 3s_w)^2(72 - 70s_w - s_q(4 - 3s_w))}}{32(1 - s_w)}\] |
| \( A \) allele fixed   | \[
\frac{(2 - s_q)(4 - s_w) + \sqrt{(2 - s_q)(4 - s_w)(72 - 2s_w - s_q(68 - s_w))}}{32(1 - s_w)}\] |

The analysis of the magnitude of the eigenvalues relative to 1 elucidated the regions in which the three possible outcomes shown in figure 2b,c: fixation of the worker favored \( A \) allele, fixation of the queen favored \( a \) allele, and protected polymorphism.

The \( A \) allele fixes when it is not too deleterious in queens and is highly beneficial in workers. The \( a \) allele fixes when it is not too deleterious in workers and highly beneficial in queens. Polymorphism results when selection is very strong in both queens and workers, such that the disfavored homozygote in each is very unfit. Finally, when queens are multiply mated, selection through worker performance is less efficacious because worker relatedness to reproductives is lower, and the region of the parameter space leading to fixation of the worker-favored \( A \) allele is smaller.
References


