Equal mating success among male reproductive strategies in a marine isopod

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Three genetically discrete male morphs coexist in *Paracerceis sculpta*, a Gulf of California marine isopod. The large α males defend harems within intertidal sponges, the smaller β males mimic female behaviour and morphology, and the tiny γ males invade and sequester themselves within large harems. If selection is responsible for maintaining this polymorphism, then the mean fitness of each male morph must be equal over time. Here we report that average reproductive success is equivalent among the three male morphs in monthly population samples collected over two years. We have investigated the total opportunity for sexual selection within and among morphs, and find that <0.10% of the total opportunity for sexual selection occurs among morphs. Furthermore, alleles responsible for the expression of this polymorphism conform to the Hardy-Weinberg equilibrium, indicating the absence of differential natural selection among morphs. Conditions necessary for stable coexistence of three alternative male reproductive strategies seem to exist in nature.

When isolated with females, the three male morphs (Fig. 1) do not differ in their ability to sire young successfully. Male fertilization success does depend, however, on the relative density of males and females within spongocoels. Experiments using genetic markers show that α males sire the majority of offspring when defending spongocoels containing a single female and one β, or one γ male (S.M.S. and C. Sassaman, unpublished data). When more than one female is present, β males sire ~60% of all offspring within a spongocoel regardless of female density, although there is considerable variation about this average. The reproductive success of γ males increases linearly with harem size. Paternity rules derived from these data for other combinations of males and females within spongocoels are described in Table 1.

Using these rules, and the observed joint distribution of 825 females and 555 males collected in monthly samples from a natural population over two years (Table 2), we calculated the mean and variance of male mating success and the opportunity

### Table 1: Rules for assigning male mating success

<table>
<thead>
<tr>
<th>Case</th>
<th>Rule</th>
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<tbody>
<tr>
<td>1</td>
<td>α male alone; sires all</td>
</tr>
<tr>
<td>2</td>
<td>β male alone; sires all</td>
</tr>
<tr>
<td>3</td>
<td>γ male alone; sires all</td>
</tr>
<tr>
<td>4</td>
<td>2 α males; each sires half</td>
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<tr>
<td>5</td>
<td>2 γ males; each sires half</td>
</tr>
<tr>
<td>6</td>
<td>3 α males; each sires one third</td>
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<td>7</td>
<td>1 α + 1 β male; β sires 0.50, α sires 0.40†</td>
</tr>
<tr>
<td>8</td>
<td>1α + 1β + 4γ males; β sires 0.60, α sires none, the remaining progeny are divided among γ males</td>
</tr>
<tr>
<td>9</td>
<td>1α + 2β + 3γ males; 0.60 of the progeny are divided between the β males and 0.40 among the γ males</td>
</tr>
<tr>
<td>10</td>
<td>1α + 1γ male; γ sires 0.08, α male sires 0.92††</td>
</tr>
<tr>
<td>11</td>
<td>1α + 2γ males; each γ follows rule 10†</td>
</tr>
<tr>
<td>12</td>
<td>1α + 3γ males; each γ sires 0.08, α male sires the rest</td>
</tr>
<tr>
<td>13</td>
<td>2α + 1γ; γ follows rule 10†, the remaining offspring are divided between the α males</td>
</tr>
<tr>
<td>14</td>
<td>2α + 3γ males; offspring are evenly divided among the γ males</td>
</tr>
</tbody>
</table>

* Laboratory tests.
† Field data.
†† Linear regression based on refs 2 and 3: \( y = -0.047 + 0.113x \).

Fig. 1. The three male morphs in *Paracerceis sculpta*: Left to right, γ male, β male, α male.
direction NNE-SSW and also reactivate earlier structures. The compression probably involves a component of strike-slip displacement, but we have no evidence to constrain this. Overall, the extension and compression combine to produce roughly north-south shortening and east-west extension of central Africa. This kinematic compatibility supports the theory of coeval development, which would allow there to be a common cause for the different tectonic environments.

Figure 4 outlines the distribution and nature of the structures thought to be active during this Permo-Triassic deformation. We cannot define the geometry and continuity of the structural pattern and specific fault linkages completely because the stratigraphic record is sparse and cover sediments are widespread. But it is probable that the structural pattern is mainly controlled by pre-existing basement structures inherited from earlier tectonic episodes and it is therefore unlikely that the pattern is simple or theoretically pleasing.

The active tectonics of central Asia include a similar variety of tectonic environments generated by continental collisions on the southern margin of Asia, notably the collision with India. The effects of this collision are seen more than 3,000 km north of the Indian suture. Northwest Europe has been similarly affected by Alpine deformation, more than 1,000 kilometres from the main orogenic front. By analogy, we argue here that the late Palaeozoic deformation of central Africa is a result of deforming processes acting along the southern margin of the Gondwanaland (Fig. 4). The more obvious effects of this deformation are the Permo-Triassic Cape fold belt and Karoo foreland basin of South Africa, and the Ventana fold belt of South America. Roughly 2,500 km away, the Krio uplift and associated structures of Zaire seem to be an intracontinental response to this deformation. Near the Cape fold belt, but still some 100 km into its foreland, structures similar to those outlined from Zaire have been described in the Karas Mountains of Namibia (Fig. 4). In Namibia, Dwyka tillites and glaciomarine sediments of Permo-Carboniferous age are involved in contractual faulting and folding along a northerly trend. The upper age limit on these structures is poorly constrained, but we suggest that they also developed as an intracontinental response to the deformation that produced the Permo-Triassic Cape fold belt.

This example of collision-related intracontinental tectonics in Gondwanaland involves a plate which had a pre-collisional passive continental margin. Of our two proposed analogues, the situation in northwest Europe is similar to this, whereas central Asia had a pre-collisional active margin. It seems clear that in both cases widespread and variable intracontinental tectonic activity is associated with deformation of the margin. The driving force for the Gondwanan orogenic event is uncertain, although it has been suggested that the Permo-Triassic period was the time of the collision between the Patagonia terrane and Gondwanaland. Widespread, intracontinental deformation is compatible with this model.

This analysis presents the Cuvette Centrale data in its regional setting and outlines a unifying theme for the late Palaeozoic tectonics of southern and central Africa. It also raises two important questions for the tectonics of Gondwanaland and for geodynamics in general. First, to what extent do late Palaeozoic compressional deformatons of Gondwanaland remain unrecognized because of a lack of late Palaeozoic and early Mesozoic stratigraphic data? Second, were the collisional processes described above an instigating factor in the breakup of the continent of Gondwanaland, an event which followed the Permo-Triassic tectonics and early Jurassic volcanism?

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FIG. 4 Gondwana reconstruction showing the major Triassic structures of central Africa and adjacent Madagascar. Note the mixture of normal, strike-slip and thrust structures, and the regional setting of the cross-section in Fig. 2. Stippling shows areas of Permo-Triassic rift sedimentation and cross-hatching the area of the internal zones of the Gondwana orogenic belt. KFB, Karoo foreland basin.
TABLE 2 Distribution of $\alpha$, $\beta$ and $\gamma$ males and females observed in spongocoels

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<th>Harem size</th>
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<th>$1\beta$</th>
<th>$1\gamma$</th>
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<th>$2\beta$</th>
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Sponges containing isopod breeding aggregations were collected monthly between October 1983 and November 1985 from permanent tide pools in the midintertidal zone, 1.5 km SW of Puerto Peñasco, Sonora, Mexico. Within 15 randomly selected 0.25-m² plots along a 100-m transect, all sponges were removed and spongocoels were examined for isopods which were then separated by sex and male type.

for sexual selection$^{10-12}$. The opportunity for sexual selection ($I$) measures the sex difference in the variance of relative reproductive success$^{10-12}$. In many species, the variance in male reproductive success is greater than that in females because of variations among males in the numbers of mates. This sex difference in the variance in fitness permits total selection on males to be stronger than on females, and allows the evolution of sexual dimorphism.

We partitioned the observed variation in relative male mating success into two components, that within and that among males. The within-male component measures the strength of sexual selection acting on males within the same strategy. The among-male component measures the strength of sexual selection acting among the three different male reproductive strategies. When the different male reproductive strategies have equal average mating success, there is no opportunity for sexual selection among the male types.

We found that average mating success is statistically equivalent among the three male morphs, and that <0.10% of the total opportunity for sexual selection is acting among the male strategies (Table 3). Even this small fraction is probably an overestimate because the equal apportionment of paternity within spongocoels, for example by rules 4, 5 and 6 in Table 1, reduces the within-male variance in reproductive success.

Genetic experiments indicate that male morphology in this species is principally influenced by a single, autosomal locus (S.M.S. and C. Sassaman, unpublished data). The 'b allele' at this locus seems to be dominant to both the \( a \) allele and the \( y \) allele, and the \( y \) allele seems to be dominant to the \( a \) allele. Morphological differences among males result from the influence these alleles exert on male growth and maturation rates. Gamma males mature most rapidly (\( \bar{x} \pm s.e. = 57.6 \pm 3.88 \) days; \( N = 21 \)); \( b \) males mature at an intermediate rate (\( \bar{x} \pm s.e. = 62.6 \pm 6.48 \) days; \( N = 9 \)); \( a \) males mature most slowly (\( \bar{x} \pm s.e. = 83.1 \pm 3.47 \) days; \( N = 18 \)). Differences in maturation rate (1/day to maturity) among the morphs could influence their relative contributions to the population. However, reproductive tenure (age at death minus age at maturity) varies inversely with maturation rate (Fig. 2). Life history differences that influence the relative contributions of \( a \), \( b \), and \( y \) males to the population seem, therefore, to cancel.

As a test of this hypothesis we calculated the expected population frequencies for \( a \), \( b \), and \( y \) males, assuming the three alleles at the male locus are in Hardy-Weinberg equilibrium. Morph

![Figure 2](image-url)
frequencies (Table 1) are typical for this population\(^1,2,4,5\) (\(\alpha\) males, 0.814; \(\beta\) males, 0.036; \(\gamma\) males, 0.150; \(N = 555\)). As \(\alpha\) males are recessive homozygotes, the frequency of the \(\alpha\) allele is \((0.814)^{1/2} = 0.902\). The rarity of \(\beta\) males suggests that nearly all \(\beta\) males in the population are heterozygotes. Thus, to a first approximation, the frequency of the \(\beta\) allele is \(1/2(0.036) = 0.018\). Because the sum of the three allele frequencies must equal unity, the frequency of the \(\gamma\) allele is 0.80. Therefore, the expected population frequencies for \(\alpha\) males (\(\alpha^2\)), \(\beta\) males (\(2\alpha\beta+2\beta\gamma\)) and \(\gamma\) males ((\(\gamma^2+2\alpha\gamma\)) are 0.814, 0.035 and 0.151. The observed frequency of the \(\gamma\)-male morph (0.150) conforms to the theoretical expectation ((\(\gamma^2+2\alpha\gamma\)) = 0.151).

Most polymorphisms in male mating behaviour seem to be 'condition dependent', in that males adjust their mating tactics to fit local environmental circumstances\(^6,7,13-27\). The presumed ancestral condition for male alternative strategies\(^8\), however, and the model for the evolution of polymorphism in general, applies to male mating strategies that are genetically distinct\(^3,8,28-30\). Male polymorphism in P. sculptra provides such a model.

We have shown that average mating success is statistically equivalent among the three male morphs and that a tiny fraction of the total opportunity for sexual selection acts among the male strategies. Moreover, alleles responsible for the expression of male phenotype in this species conform to Hardy-Weinberg equilibrium. We conclude therefore that there is no significant selection favouring one male reproductive strategy, and that the necessary conditions for maintaining a polymorphism in male mating behaviour exist in this natural population.

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