Co-option of pre-existing traits as a critical model for the evolution of elaborate male sexual display

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Introduction
How extravagant male displays evolve remains one of the most controversial issues in evolutionary biology.

Currently popular co-evolutionary models (e.g. runaway and some versions of good genes) have weaknesses that have been largely ignored, such as how required genetic correlations are maintained. Preexisting preferences that typically have not been shaped by selection cannot explain the high level of functional adaptation and complexity commonly seen in male display traits.

Co-option of pre-existing male traits has been largely ignored in discussions of the evolution of elaborated sexual displays4, but is very attractive because of 1) its simplicity, 2) abundant supporting evidence and 3) it provides a plausible explanation for how good genes indicators evolve2.

The model
Preexisting male traits may indicate male quality such as heritable good genes. Female preferences for males with high quality variants of these traits increase in frequency due to good genes or possibly good parent benefits for choosing females.

Some types of co-option for sexual display:
1. Traits co-opted from a nonsexual context (e.g. aggressive display, traits that show FA).
2. Courtship traits co-opted for a new function in mate choice (e.g. bowerbird bower).
3. Display elements mimicked from other species (e.g. bird song).

History
A few authors have discussed the co-option of aggressive displays5–7. There has been sporadic suggestion of the co-option of other traits8–12 and of co-option generally12.

Arguments supporting the co-option model:

1. Iconic sexual display traits across many taxa are the result of the co-option of traits initially evolved for other functions (see Fig. above).

2. This simple co-option model does not require the difficult co-evolution of traits and preferences due to genetic correlations yet can allow for mate selection based on good genes. Females need only evolve a preference for males with high quality expression of the preexisting trait.

3. Co-option is a common theme in evolution and explains many complex non-behavioral traits e.g. inclusion of endosymbionts as organelles, diversification of gene families, etc.

4. Costly traits already expressed by a male that are co-opted as indicators of male quality can be honest indicators without great added cost. Novel traits that evolve costliness to provide honesty must have these costs subtracted from the benefits they provide and this may limit their evolution.

5. With the gradual evolution of male traits, it is unclear how cost-dependent honesty is achieved when incipient display traits are small and not costly. Co-option of developed and already expensive traits solves this problem.

Preexisting traits that may be co-opted

Fluctuating asymmetry (FA) - females use preexisting differences in male traits to choose males with more developmental stability6.

Bright male (Hamilton and Zuk) – females use preexisting male differences in plumage brightness to identify disease resistant males2.

Male aggression – females use differences in male aggressive displays, e.g. bird song, to identify physically superior males with good genes2–6.

Chemical cues – females use differences in odor/taste of urine, feces, diffusible molecules to identify healthy or genetically compatible males.

Male constructions – females use differences in nests9, bowers10,11 etc. to identify more healthy and/or neurologically better males.

Conclusions
The importance of co-option in the evolution of sexual display has been vastly underestimated in the literature.

The preexisting traits model suggests that natural and sexual selection both commonly contribute to the evolution of male sexual display.

The co-option model is attractive because of its simplicity, abundant supporting evidence, and its ability to resolve difficult issues in the evolution of male display traits.

A summary of models:

<table>
<thead>
<tr>
<th>Requires Genetic Correlation</th>
<th>Produces Good Genes Effect</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yes</td>
<td>Good genes</td>
</tr>
<tr>
<td>No</td>
<td>Runaway</td>
</tr>
<tr>
<td>No Pre-existing trait</td>
<td>Pre-existing preference</td>
</tr>
</tbody>
</table>

References

For further discussion of these issues please see reference 2 available at: http://www.life.umd.edu/biology/borgialab or search Google: Borgia bowerbird