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Differential allocation and 'good genes'

Comment from Cunningham & Russell

In a recent *TREE* review[1], Sheldon suggests that females might differentially allocate a greater share of resources to offspring sired by a particular male because preferred males provide offspring with 'good genes'. We would like to offer further suggestions to explain this female behaviour.

'Good genes' are paternal genes, inherited and expressed by offspring, that increase viability[2]. When a female mates with more than one male, it would make sense for her to invest more in the offspring fathered by the male of highest genetic quality if these offspring are more likely to survive. However, other advantages of mating with preferred males might also promote differential allocation. These benefits include other types of genetic benefits passed through the paternal line (through Fisherian, compatibility and male-manipulation mechanisms), genetic benefits expressed only in daughters (such as good-mother genes), and/or non-genetic, direct benefits (such as superior resources or protection). It could be argued that male phenotype, and direct benefits provided by a particular phenotype, should correlate with male genotype. In many cases they probably do. However, females could also base allocation decisions on phenotypic characteristics that correlate with benefits provided by males, but that are unrelated to any genes that directly influence offspring viability. In the mallard *Anas platyrhynchos*, for example, attractiveness is determined by hatch date, which is itself governed by whether or not a nest is predated. Although this is unlikely to be related to male genotype, early hatched males might provide more direct benefits than their later hatched counterparts[3].

How might differential allocation occur in situations where females cannot discriminate between their offspring? Females could base their allocation 'decision' on male phenotype before or during mating, or on sperm phenotype after mating. If cryptic female choice can be envisaged as a feasible mechanism by which to choose between males, signals from sperm phenotype could also provide information enabling females to 'choose' how to allocate resources. It should also be noted that artificial insemination *per se* might not exclude the possibility of differential allocation based on non-genetic factors because developmental and environmental effects can also influence sperm phenotype[4–6]. Other more indirect effects could also result in differential allocation. For example, interactions with novel or dominant individuals that influence hormonal levels in females[7] could affect the hormonal levels in subsequent eggs. As a result, the competitive ability of chicks could be affected[8]. In such a scenario, differential allocation could even drive female extra-pair copulation behaviour regardless of whether females could gain any type of genetic benefit from males[9].

We welcome Sheldon's review highlighting the importance of differential allocation. However, this review might suggest conflicts where none should exist – there is evidence for both 'good genes' and differential allocation, although neither supports nor condemns the existence of the other. Evidence for differential allocation adds to many excellent studies that have started to unravel the relative importance of all the factors that affect offspring fitness. Yet another challenge will be to identify how the relative importance of these factors differs between species that raise their young under very different circumstances.

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Differential allocation and 'good genes'

Comment from Gil & Graves

Sheldon provides a good and timely review of differential female allocation in a recent issue of *TREE*[1]. However, we disagree with his statement that pre-laying differential allocation[2,3] does not create problems for the identification of 'good genes'-based sexual selection.

Sheldon states that differential allocation provides 'strong evidence in support of "good genes" '. However, the only unequivocal evidence for 'good genes' is that the offspring of preferred males have higher fitness as a result

