

solely comprised of relentless publishers would be a joyless place for eager students. Leaving that aside, our impression is that h and m contain small kernels of truth. We think it would be foolhardy to use modest differences in m values to rank individuals, but researchers with high m values, say ≥ 1.5 , are those who would, by a conventional peer-review process, also be ranked as highly influential. That said, W.D. Hamilton, E.O. Wilson, R. Trivers, R. Dawkins and S.J. Gould all have $m < 1$, which neatly illustrates the risk of indiscriminate use of the h index.

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Female finery is not for males

Natasha R. LeBas

School of Animal Biology, The University of Western Australia, Crawley, WA 6009, Australia

There has recently been an increase in interest in the notion that female ornamentation is selected through male choice, rather than being an artefact of selection on male ornamentation. There are, however, key differences between the sexes in the type of selection pressures that are likely to generate ornamentation and important differences in investment tradeoffs. Here, I discuss that female ornamentation might be selected more often through female competition over resources than through competition over mates, as exemplified in a recent study by Heinsohn and colleagues.

Shifting paradigms

Lower investment in offspring and higher variance in reproductive success usually leads to sexually selected ornamentation in males rather than in females [1]. In accordance, there are numerous studies documenting male competition and female choice of males [1]. By contrast, female ornamentation has been considered an artefact of a genetic correlation with male ornamentation and is rarely investigated [2,3]. This paradigm has recently been questioned [3] and the broader circumstances under which males might be expected to be prudent over mating partners have been recognized [4–7]. In addition, comparative studies suggest that female ornamentation can evolve independently of male ornamentation [3]. Most recent empirical studies of female ornamentation have concentrated on male choice of

females and, although there are increasing examples of such choice [3,8–12], they remain rare; in some cases, the benefit to the female from investment in ornamentation appears inadequate to offset the cost of the ornamentation. A recent study by Heinsohn *et al.* [13] highlights a much understudied alternative explanation for female ornamentation, that of female resource competition.

Colourful parrots

Heinsohn and colleagues [13] examined crypsis and intrasexual competition in the highly sexually dichromatic *Eclectus roratus* parrot (Figure 1), which has a polygynandrous mating system (both the male and female have multiple mates) and females reside at their nest tree for ~11 months each year. Up to five males attend each nest and provide all the food for the female and offspring over the breeding period. Females are a vivid blue and red, whereas males are bright green, yet Heinsohn *et al.* state that there is no evidence that *E. roratus* are sex-role reversed. Instead, observations suggest that intrasexual competition is strong in both sexes. Females compete over and defend rare breeding hollows and have been observed to kill one another in these aggressive encounters. Before their restriction to their nest hollow for breeding, females display high in the canopy. Heinsohn *et al.* used sophisticated colour analysis techniques to show that the red and blue coloration of the females gave them the greatest contrast against this leafy background. Given that females nest in hollows, the authors propose that the evolution of their bright coloration has been unconstrained by selection for crypsis during egg incubation.

Corresponding author: LeBas, N.R. (nlebas@cyllene.uwa.edu.au).

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Figure 1. Female (left) and male (right) *Eclectus roratus* parrots. Reproduced with permission from HB-294 ©Hans and Judy Beste / Lochman Transparencies.

Heinsohn *et al.* also show that, when signalling environments differ between the sexes, their ornamentation can reach different optima [13]. Male *E. roratus* were most conspicuous against tree trunks and least conspicuous against leaves. These findings fit with observations that males primarily forage in the canopy, where there is the greatest need for crypsis, and that most male competition over females is at the entrance to the nest hollow, where males would need to be the most conspicuous. Heinsohn *et al.*'s study suggests that the type of ornamentation that is selected through female resource competition need not be the same type of ornamentation that is sexually selected in males. The next step in the *Eclectus* parrot system will be to quantify accurately the selection pressures on coloration in both sexes.

The findings of Heinsohn and colleagues highlight the importance of resource competition as a potential selection pressure for female signal evolution. With the recent increase in interest in selection acting directly on female ornamentation, Heinsohn *et al.*'s work brings to the fore the question of whether it is either intersexual selection or resource competition that is the main selective force acting on female ornamentation.

Intersexual selection or resource competition?

Consideration of female ornamentation has largely relied upon relating our knowledge to females of the selection pressures and investment patterns relevant to male ornamentation. There are, however, key differences between the sexes in the type of selection pressures that are likely to generate ornamentation and in investment tradeoffs.

Male quality variation is advertised with signals of good genes, whereas, in females, it comprises variation in

quality, as encompassed by good genes models, as well as fecundity variation, such as egg size, number and maturity (e.g. time to laying). Although this fecundity variation might co-vary positively with female good genes advertisement, differences in fecundity are likely to be the main component of overall female quality variation. Unlike good genes variation in males, fecundity variation in females is often directly assessable as female body or abdomen size, making the need for any ornamentation redundant. Even in species in which fecundity variation is not directly assessable, such as birds, some cost to honest female ornamentation must be assumed and females that invest in ornamentation might be less able to invest in offspring than are females with equivalent resources who invest only in offspring [14]. When female ornamentation is the consequence of a genetic correlation with male ornamentation that reflects good genes, the genetic correlation between quality and ornamentation in males will also be expected in females. The benefits to males of choosing females based on female ornamentation will depend upon whether the fecundity cost to the female of expressing the trait outweighs the underlying relationship between ornament and quality.

A further limitation to sexually selected female ornamentation is that, unlike most males, females can invest directly in offspring for which they have guaranteed parentage. The benefit to females of investing in ornaments must outweigh those of investing the resources directly in their offspring instead. The indirect benefit of mating with a good-quality male seems unlikely to exceed the benefit for the female from directly investing her resources into offspring rather than in mate-attracting ornamentation. Breeding prerequisites that are limited, such as nest hollows in the case of *E. roratus*, or direct benefits from males, such as gifts and parental care, are more likely to have the selective strength necessary to make female investment in ornamentation worthwhile. Indeed, nuptial gifts provided by male empidid flies appear to be a sufficiently valuable resource for females to have invested in ornamentation, even though the females themselves are still choosy [8]. Empidids are one of the few taxa in which there is ornamentation in females that is completely absent in males. The prevalence of bright female coloration in birds might also be an example of where hidden female fecundity and male parental care has been a sufficient selective force to make female investment in mate-attracting ornamentation worthwhile, as increasing examples of mutual mate choice attest [3,15].

These important differences between male and female investment in ornamentation have been largely ignored. In species with male parental care, models of male allocation to ornamentation and care [16] are similar to the models required for female allocation to ornamentation and offspring, but the differences outlined above require models that specifically address female signal evolution.

Female resource competition

As exemplified in the study by Heinsohn and colleagues [13], access to resources is more likely to have the large

Box 1. A role for male choice?

Heinsohn *et al.* [13] do not mention any relationship between the bright coloration of females and male choice and, indeed, such choice might be unexpected given the scarcity of females in their system. Neither do the authors mention whether there is a relationship between female quality and the bright coloration that is used in female contests. However, in systems in which male prudence is expected, males might also make use of a reliable signal of female dominance (that is selected through resource competition) in their choice of mate. Female ornamentation used in signalling dominance is expected to reflect competitive ability honestly and, hence, quality. In addition, any benefits that dominant females receive from the resources that they obtain are likely to further enhance fecundity. This will reinforce any underlying relationship between female ornamentation and quality and, thus, also the value of the ornamentation to prudent males [8]. Choosy males might obtain fitness benefits by making use of the information available in such ornamentation, but female investment in the ornamentation is not due to any benefits that the female obtains from being chosen by the male (although any benefits from being

chosen will increase selection on that trait). Thus, male choice is not what generates or maintains female ornamentation even if males make use of the ornamentation in their mate choice. This scenario in females is in direct contrast to the situation in males, in which female choice is often a key selection pressure behind male investment in ornamentation.

There are an increasing number of empirical studies investigating the relationship between female quality and ornamentation, and male choice for these traits (e.g. [10]). It is generally assumed that some aspect of the male choice, obtaining a better quality male for example, is the selective force acting on the ornamentation. As discussed here, this need not be the case and there might be many examples of male sensitivity to female ornamentation where the selection pressure maintaining female investment in the ornamentation is not the benefit of being chosen. This could explain perplexing cases of male choice of female ornamentation in which the benefits to females of investment in such traits to obtain a high-quality male appear insufficient.

fitness benefit that is required to make female investment in ornamentation a net fitness gain. Access to resources, such as breeding space, territories and feeding sites, is likely to have a large impact on female fitness and, consequently, the benefits to females of honest signals of dominance might readily outweigh the costs of trait investment. This 'social competition', as termed by West-Eberhard [17], appears evident in many taxa, such as birds, primates and lizards, where there are opportunities for dominant females to obtain fitness benefits [3,10,15,17]. Despite calls for more research in this area [3], it remains largely unexplored.

Competition over resources in males is hard to disentangle from competition over mates owing to the frequent covariance of these variables. In *E. roratus*, the resource competition is over nest hollows, which are a prerequisite for breeding and, hence, this type of resource competition also comes under the banner of intrasexual selection (see also [18]). In other types of female resource competition, however, such as competition over food, territories or roosting sites, the competition is distinct from competition over mates, in that the resources themselves benefit the female and do not necessarily provide access to more or higher quality mates. In females, there might be value in defining this non-sexual resource competition separately from that of resource competition over breeding sites, to distinguish it from the sexual selection process. Under conditions of male prudence over mating partners, males might utilize pre-existing, resource competition-selected female ornamentation in mate choice; however, crucially, this male choice is not what generates or maintains the female ornamentation (Box 1). Again, these differences between the sexes emphasize the need to consider the interesting selection pressures acting on females in their own right.

Future directions

Heinsohn *et al.*'s study demonstrates the greater consideration that we should be giving to resource competition among females as a source of selection for female ornamentation. We need to recognize the limitations of

forcing male ornamentation theory to fit females and instead investigate the complex interplay of selection pressures that are likely to act on female signals. Evolution of female ornamentation through resource competition does not rule out male choice, but instead enables male choice without the restrictive requirement that the benefit of being chosen is what generates the ornamentation.

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Letter

Impacts of global atmospheric change on tropical forests

Simon L. Lewis, Oliver L. Phillips and Timothy R. Baker

Earth & Biosphere Institute, School of Geography, University of Leeds, UK, LS2 9JT

In a recent *TREE* review, Wright [1] concluded that the structure and dynamics of tropical forests are changing, caused by large-scale alterations in the abiotic environment. However, his assertions that the evidence for such a response comes ‘almost exclusively from censuses of tree plots and is controversial’ requires further clarification. We suggest that a more complete review of recent forest-plot research and the inclusion of studies from fields outside community ecology considerably reduces the controversy and exclusivity of the plot-based results.

Wright [1] reports that long-term forest-plot data show simultaneous increases in stem density, recruitment rates, mortality rates, basal area (BA) and aboveground biomass (AGB) [2–4]. But a crucial result was overlooked: forest growth (stand-level BA growth: the sum of BA increments of surviving trees plus the BA of newly recruited trees) has also significantly increased at rates similar to stem fluxes within the same plots [3]. Because stand-level BA growth is 10–30% of net primary productivity, forest productivity is also likely to have increased substantially over the past two decades. Wright makes a complex case, suggesting that recent plot-based results might be a combined artefact of methodological limitations, fieldwork errors and historical disturbances. However, none of these can account for the large, sustained increase in wood production [3].

More generally, over the past decade, several potential biases have been proposed to explain individual patterns of forest change, including the effects of past disturbance and changing project personnel causing ‘ghost recruitment’, which Wright suggests have been overlooked (e.g. [3,5]). However, many of these potential biases have now been resolved ([2–5] and references therein). Although a critical approach to assessing the evidence is essential, we suggest that the extensive debate over these issues demonstrates that it is difficult for either simple or complex artefactual explanations to explain the full suite of observed changes.

Wright presents ‘independent evidence’ to test the results from long-term plot networks [1], but each of the four studies that he cites addresses a single locality and

therefore cannot, by definition, test hypotheses about global-change phenomena. In addition, alternative interpretations of the two studies giving apparently inconsistent results are possible. First, the single-cohort growth data [6] are difficult to interpret because temporal changes reflect an unknown mixture of environmental changes, ontogenetic changes of an ageing cohort, and switches in allocation from wood to reproduction as trees mature [7]. Second, on the Barro Colorado Island 50-ha plot, four of the seven habitats surveyed had significant increases in AGB over the 15-year study, with the Amazonian results in the middle of the range (Table 1). We suggest that the spatial variation in AGB change, notably increases in AGB in habitats where soil water availability is generally high, provides valuable data on, rather than contradictions of, the potential impacts of global change, as Wright claims. Moreover, for the 50-ha plot as a whole, Wright cites AGB change results if all trees with point-of-measurement changes, predominantly from buttress growth, are set to zero growth. If average growth rates are used, given that these trees contribute to forest productivity, then the change is $+0.6 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ [8], similar to many Amazonian plots [2].

Independent evidence from other disciplines suggests that a long-term reorganisation of tropical forests is occurring. First, analyses of paired satellite images from intact forest on three tropical continents are consistent

Table 1. AGB change from seven habitats on Barro Colorado Island, Panama, 1985–2000^a, and the Amazon mean over the 1980s and 1990s^b

Habitat type	AGB change (Mg ha yr^{-1})
Swamp	+2.69 ^c
Stream-sides	+2.28 ^c
Young forest	+1.28 ^c
High plateau	+0.51 ^{c*}
Mixed habitats	+0.17*
Low plateau	−0.07*
Slope	−0.38*
Amazon mean	+1.22 ^c

^aFrom text in [8] or linear regression of data in [8], Table 6, denoted by *, trees with problematic measurement set to zero growth.

^bFrom [2].

^cReported significant difference from 0 ($P < 0.05$).

Corresponding author: Lewis, S.L. (slewis@pobox.com).

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