

implicates paternal-genome imprinting as a mechanism of sex determination in the parasitoid wasp *Nasonia vitripennis* [18]. Comparing these distinct mechanisms at the genetic level would provide fascinating insights into their evolution, and might help explain why advanced social Hymenoptera and other taxa depend upon an outbreeding mating system rather than imprinting or multiple complementary loci to avoid diploid males. These comparisons might also be extended to explore mechanisms of sex determination in species for which male haploidy results from loss of the paternal genome during development [2,19].

Finally, molecular characterization of *csd* sets the stage for population-genetic studies at this locus in bees and other arthropods. Characterization of functionally distinct alleles at this locus will help us to test models proposed to explain how social haplodiploids deal with a key genetic load (non-viable males resulting from homozygosity of *csd*) through the mitigating factors of multiple mating and the recognition and removal of diploid males [4]. Assuming orthologues are identified in other taxa, it should be possible to measure the sex-determination costs of small population sizes or bottlenecks throughout the Hymenoptera, and the effects of these costs on the balancing selection at *csd*. This will be especially relevant for understanding the population dynamics, and possible control strategies, for invasive species, such as fire ants (USA, [20]), bumblebees (Tasmania) or European wasps (New Zealand), which undergo population bottlenecks during colonization. As a second applied benefit, honeybee breeders and researchers endeavouring to develop genetically homogeneous lines should be able to avoid a very direct cost of inbreeding by choosing matings (even full-sibling matings) between individuals with distinct *csd* alleles. Screenings such as this could be used in the planning of germplasm banks (i.e. based on stored sperm, [21]) used to maintain unique honeybee lineages.

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Are men and women really so different?

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Distinct differences in the behaviour and preferences of men and women have conventionally been attributed to Trivers' powerful insights regarding the impact of parental investment on sexual selection and mating

systems. This has spawned a huge literature about the evolutionary significance of human sex differences. But are men and women really so different? An elegant new study shows that men and women are strikingly similar in their mate preferences. Have conventional models blinded us to the obvious, and precluded the posing of far more interesting questions?

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Over the years, there have been many papers about human mating preferences founded on parental investment theory. The argument goes something like this. Because the sex with the smaller pre-mating investment (male) has a higher reproductive rate than does the more heavily investing sex (female) [1], males tend to be limited by their access to fertile females, whereas females tend to be limited by access to the resources that they need to nourish their offspring. In humans, a species where males often control the resources necessary for reproduction, the classic application of this idea has been that men look for markers of fertility and sexual fidelity in their long-term partners, and that women favour partners with wealth, status and a sense of family commitment [2]. Perhaps because of the voluminous support for this idea (derived most commonly from undergraduate questionnaire responses), a profound sense of ennui emanates from any new paper starting in this ilk: ‘in line with the predictions of Trivers [3] and Bateman [4] this paper shows...’. Aside from some uncomfortable innuendos that some of us, perhaps unfairly, take from this kind of research, there is the more substantive question of what these new studies teach us about human nature. Anthropologists are particularly uncomfortable with these predictions, recognizing that, across the world, human mating systems are highly variable, and the costs and benefits of different mating preferences are likely to be locally contingent [5]; for example, in some systems, husbands might not be the primary providers for their wives [6,7].

It is against this background that a recent paper by Buston and Emlen [8] caught my eye. In a study of human mate preference, they show that support for the classic Trivers–Bateman predictions regarding sex differences is eclipsed statistically by a much stronger tendency for men and women to show a preference for partners who are similar to themselves across several characteristics. Although based on a questionnaire format that raises obvious methodological problems (Box 1), this is the first study to test the classic parental investment hypothesis against competing hypotheses; it also takes us far beyond conventional studies of assortative mating, incidentally thereby honouring the scholarship of the late Linda Mealey, to whom the paper is dedicated.

We already know that men and women’s preferences are relative: individuals not only assess their own quality as a mate relative to that of their companions, but also form a mate preference based on this self perception [9]. For instance, analyses of the wording of ‘lonely hearts’ columns show that women claiming to be physically attractive, as well as men claiming to be wealthy or high status, make higher overall demands of prospective partners than do advertisers with no such apparent credentials [10]. Buston and Emlen look more closely at these relative demands, asking whether individuals prefer partners with reproductive potential that is similar to their own (the ‘potentials attract’ hypothesis) or whether individuals prefer partners who are highly ranked on similar traits (the ‘likes attract’ hypothesis). For example, do men who view themselves as well endowed with sex-specific traits that are indicative of reproductive potential (wealth, high status and family commitment) prefer, as long-term partners, women who

Box 1. Methodological issues

Studies examining the hypothesis that males and females differ in their mate preferences have, for the most part, been conducted using questionnaire data. Typically, students enrolled in introductory psychology classes are asked either to complete a questionnaire themselves, or to hand out such a questionnaire to one or more of their acquaintances. Although large samples are cheaply accrued by this method, inevitable questions arise concerning the reliability of self-reports. For example, investigators concerned with sex differences have found that reported sex differences in behaviour (although not in attitudes) are affected by whether the subject is assured anonymity [18]. More generally, we do not know how much subjects, even with anonymity ensured, play down (or alternatively exaggerate) their true preferences in this kind of study as a result of discomfort with the methodology. Furthermore, we can only guess at the effects of other biases, such as sample skew, which arise from people refusing to fill out the questionnaire.

Methodological issues also challenge the study of assortative mating [19]. Assortative marriage (unions involving phenotypically similar individuals, or homogamy) was first studied systematically by Galton, and is seen by some as a human ‘norm’. Based on shared traits among extant pairs, it is difficult to determine whether similarities emerge as a result of marriage rather than predate the union. Furthermore, even for traits that generally predate the marriage (such as educational level), it is hard to tease out to what extent highly educated people actually prefer highly educated spouses as opposed to merely encounter such people more commonly in their daily lives. There are also suggestions that assortative unions last longer (even produce more offspring) than do unions among less similar individuals [20], but without prospective studies that measure traits before marriage, that include assays of partner preference, that sample both successful and unsuccessful marriages, and make direct comparisons between similar and dissimilar marriages using survival analyses, these results are open to various explanations.

are also endowed with sex-specific indicators of reproductive potential (attractiveness and sexually fidelity), or are they keener on finding a woman who is similarly wealthy, high status and family committed? This is by no means a trivial question. A psychological mechanism based on the ‘potentials attract’ hypothesis emphasizes the difference between the sexes, whereas one based on the ‘likes attract’ hypothesis underscores qualitative similarity. Such emphasis on the traits shared by the sexes makes for refreshing reading.

Buston and Emlen’s study shows that the ‘likes attract’ hypothesis does much better than does the ‘potentials attract’ hypothesis. Results from a questionnaire completed by 1000 young men and women living in Ithaca (USA), in which subjects ranked traits in a prospective mate and then in themselves, reveal that women who rated themselves as attractive were much more concerned with the attractiveness rather than wealth of their mate. Similarly, wealthy men (again self rated) were fussier about a mate’s wealth than about her sexual fidelity, and so on. In other words, we look in our long-term partners for the traits that we believe we rank highly on ourselves. The inference here, largely untested in the literature (Box 1), is that partnerships between similar individuals might be more stable than partnerships based on matched reproductive potential, and that more stable partnerships leave more offspring.

Trivers’ influential paper [3] exploring the implications of Bateman’s experiments [4], specifically the significance

of differential pre-mating reproductive investment for sex differences in parental investment and sexual selection, has been a major source of inspiration for behavioral ecologists, not least those working with humans. Gradually, however, we are weaning ourselves off this powerful but somewhat blinding formula. In a strangely neglected paper, Johnstone *et al.* [11] use a mutual mate choice model to explore the impact of sex differences in both processing time and intrasexual variation in quality on the optimal choosiness that males and females should exhibit in selecting a mate; sex differences in parental investment can, under some circumstances, be eclipsed by intrasexual variation in quality (although the authors here are still thinking of sex-specific reproductive potential). More recently, Wade and Shuster [12], in a radical reanalysis of Maynard Smith's classic desertion model (which was also based on inferences from Bateman), show convincingly that differential investment does not always drive sexual selection. Rather, they find that, if the costs of desertion vary among males (depending on chances of subsequent successful matings), then competition among males (sexual selection) can drive differential parental care and not *vice versa* [13]. We have known about this kind of intrapopulation variation in the successful pursuit of new mates in humans for a long time; for instance, Central African Aka hunters with brothers in their camp (who act as allies) marry multiple wives and invest little time in their offspring, whereas those without brothers have a single wife and put much more effort into each child [14]. All the same, in spite of similar observations from contemporary western society [15], we have tended to gloss over such findings, perhaps because of our old fixation with the parental investment model.

Buston and Emlen's intriguing finding opens yet another new door towards extending analyses of human mate choice beyond the Trivers–Bateman formulation, and exploring inter- and intrapopulation differences in mate choice preferences. One could readily speculate that, in this domain of human behaviour, natural selection has favoured facultative cognitive mechanisms: these might promote selectivity on sex-specific partner qualities in some circumstances and trait-specific similarities in others, perhaps through their effects on the durability of marriage. For instance, it might be that partner stability would be particularly adaptive in situations where the costs of mate switching are high, perhaps where there is a high prevalence of sexually transmitted disease or where divorce is economically disruptive, whereas choosing for sex-specific partner qualities would be better suited to situations where there is high variation (both across individuals and over time) in the quality of males and females as mates. Economists have a raft of game theoretic models for exploring what they call 'two-sided matching' that might prove useful [16]. Furthermore, there are still some crucial assumptions to examine: (i) do individuals assess themselves accurately?; (ii) are preferences converted into choice?; (iii) are partnerships between similar individuals more stable than other partnerships?; and (iv) does partnership stability enhance reproductive success?

An intriguing question remains for comparative anthropological analysis: in what social and/or ecological

conditions does the 'likes attract' mechanism hold (or not hold)? Closely matched partners might lose out where marriage is viewed as a division of labour, with the competitive edge going to partners bringing complementary skills to a marriage; among the foraging Hadza, for example, there is some evidence that the best hunters marry the best gatherers [17]. However, in societies where there is less division of labour in marriage, positive assortment might pay off. Specifically, the matching produced by the 'likes attract' mechanism increases the provision of public goods in a marriage, and might therefore minimize the space for bargaining; if I want to go to the pub and my spouse does too, there will be no argument and we will both be happy. Perhaps this anticipation of shared leisure lies behind the 'likes attract' finding among Ithaca students. Alternatively, by marrying someone similar to you, it might be easier to coordinate over childcare, shopping and cleaning the house, or simply be the best way of ensuring your partner doesn't walk out on you. These are all questions to be addressed with improved methods across different social and ecological contexts.

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Letters

Nature is changing in more ways than one

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As wild habitats continue to dwindle and native species continue to decline in abundance, conservation biologists have begun to document the patterns of these declines. In a recent issue of *TREE*, Balmford *et al.* [1] review the current state of our ability to track trends in the status of populations and habitats. They emphasize the need to track both population and habitat losses across taxonomic groups and broad spatial scales. Their synthesis reveals roughly similar losses (0.5–1.5% per year) across biomes and vertebrate groups. In contrast to habitat-based estimates of expected future extinctions, estimates of biome and population loss translate directly into lost ecosystem functions and probable economic losses [2,3].

We applaud efforts to develop synthetic indicators of habitat and population losses and Balmford *et al.*'s challenge to expand the scale, scope and consistency of these monitoring schemes. We particularly urge researchers involved with WWF's and UNEP's 'Living Planet Index' efforts to expand their tallies beyond vertebrates and to consider metrics beyond population trends. Although many vertebrates are sensitive to anthropogenic disturbance, statistics on their population declines provide less than a complete picture of ecological change.

In contrast to tracking populations of vertebrates, tracking changes in plant populations demands far less effort. Studies of herbaceous plant populations in temperate prairies and forest woodlands reveal losses similar to those documented for vertebrates (Table 1). These studies further reveal increases in exotic species [4–6] and declines in habitat specialists [6]. The replacement of specialists by habitat generalists caused average species similarity among sites to increase by 31% in northern

Wisconsin, USA over 50 years, in comparison to average population losses of 18.5%. Such biotic homogenization might be as widespread as habitat and species losses, but it is clearly a distinct phenomenon that demands separate monitoring [6,7]. Both population losses and homogenization in northern Wisconsin appear to be unrelated to the direct effects of habitat loss.

These examples make clear that different mechanisms might be driving habitat loss versus the loss (or homogenization) of populations within extant habitats. If we are to understand these mechanisms, we must track the various patterns of change separately and in more detail. Unfortunately, the broad metrics reported by Balmford *et al.* [1] can conflate habitat loss with population declines, making it difficult to diagnose the mechanisms threatening species persistence. We therefore urge biologists to develop metrics that distinguish these processes and go beyond simple tallies of habitat and population loss to reflect significant shifts in community composition or structure. Metrics based on species identities such as the 'Floristic Quality Index' [8] appear particularly sensitive for tracking changes in community composition. We also urge biologists to think carefully about how best to merge data when reporting broad trends. Averaging values across taxonomic groups and regions can obscure important processes occurring at smaller scales.

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Table 1. Losses of herbaceous plant species in historical studies^a

Location (period)	No. of species lost per site	% loss per year	Refs
Bialowieza forest, Poland (1969–1992)	45% of 133 species	2.2	[11]
Middlesex Fells, MA, USA (1894–1993)	37% of 422 species	0.37	[4]
Staten Island, NY, USA (1879–1991)	41% of 1082 species	0.36	[5]
Heart's Content, PA, USA (1929–1995)	59% and 80% (2 stands)	1.12–1.21	[9]
N Wisconsin, USA (1950–2000)	18.5% (average over 62 sites)	0.37	[6]
S Wisconsin prairies, USA (32–52 years)	8–60% (54 sites)	0.5–1	[10]

^aAll but the last study focused on temperate forests.