The evolution of mating preferences and the paradox of the lek

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Why do females prefer elaborate male mating displays in species where they receive little more from males than their sperm? Here we review three hypotheses for the evolution of mating preferences: direct selection, the runaway process and the parasite mechanism. There is growing support for direct selection, in which preferences evolve because of their direct effects on female fitness rather than the genetic effects on offspring resulting from mate choice.

THE evolution of the exaggerated mating displays made by animals that meet in groups, or leks, during the breeding season is one of the most enduring problems in evolutionary biology. In animals as diverse as the birds of paradise, guppies, frogs and insects, males congregate in leks to display to females (Fig. 1). Each female chooses from among the assembled males, and seems to receive little more from her mate than his sperm. Females often show strong unanimity in their choice, and so a few males acquire most of the matings. The successful males are typically those with the most extreme plumage, vocalizations and displays. Consequently these secondary sexual characters have evolved to such extremes that they decrease male survival (Fig. 2). Why should females have evolved such strong preferences when they seem to receive no tangible benefit from their choice? This puzzle has been called the 'paradox of the lek'.

The status of this problem has recently been transformed by two developments. First, detailed mathematical models have allowed the identification of a variety of evolutionary forces that could cause the evolution of preferences for exaggerated male displays (Table 1). This situation contrasts strikingly with that of just a decade ago, when only two mechanisms were discussed and even those were not fully understood. Second, there is now a growing body of empirical research attempting to determine which of these mechanisms are actually operating in natural populations. Current efforts involve quantitative field studies, experiments under controlled laboratory conditions, and phylogenetic (cross-species) comparisons.

Despite substantial efforts, the primary factors responsible for the evolution of preferences remain controversial. Most recent attention has focused on three of the possibilities listed in Table 1: direct selection on preferences, indirect selection of preferences through their interaction with parasites (the Hamilton-Zuk[1] hypothesis), and indirect selection of preferences by a 'runaway process'. In this review we synthesize our current understanding of these three hypotheses; a broader perspective is given in other recent reviews[2,3]. We begin by describing a 'null model' as a reference for understanding the effects of different mechanisms proposed for preference evolution. We then consider the three specific hypotheses, first describing their theoretical bases and then reviewing the empirical evidence. Although we limit our discussion to these mechanisms, we emphasize that they are only three of many possibilities, and that more than one of them could operate simultaneously (see Box).

Three hypotheses for preference evolution

Before discussing specific hypotheses, it is helpful to understand what happens in a null model that has been intentionally stripped of all complications. The simplest possible situation involves the evolution of a male trait that affects both male survival and attractiveness to females, and a preference that influences how females mate but that has no other effects on female survival or fecundity[4-6]. (In the evolutionary sense, a 'preference' is any trait that biases the probabilities that females mate with different kinds of males, and does not necessarily involve any cognitive process.)

Under the null assumptions, several genetic models reveal an evolutionary equilibrium that balances male survival against male mating success. The degree of elaboration in the male trait that produces this balance depends on the average preference in females. Consequently, there is a line or curve of evolutionary equilibria relating the average female mating preference to the average male trait in the population (Fig. 3). Once a population reaches a point on this curve, there will be no further evolutionary tendency in the female preferences. Specifically, if a preference for one type of male is established by some mechanism, then alternative preferences for males that survive better (or worse) will not be favoured[5,6]. Although females mating with males that survive better will have sons of high viability, those offspring will have lower mating success than other males with traits that are more preferred by females. While this simple picture becomes more complicated when certain assumptions about the behaviour and underlying genetics are made[7-9], it serves as a useful benchmark for discussing more complex situations.

The null model further shows that a genetic correlation (resulting from linkage disequilibrium) between the preference and male trait can develop because females with the most extreme preferences mate with the most extravagant males and so produce offspring that carry genes for extreme values of both the

TABLE 1 Proposed mechanisms for the evolution of mating preferences in polygynous animals

Mechanism	References
1. Direct selection of preferences	16
A. Males provide resources to females or offspring	12, 15, 17
B. Costs of searching for mates	11, 13, 14, 51
C. Selection against hybridization	52, 57
D. Males differ in sperm fertility	18
E. Pleiotropic effects of preference genes	
F. Disease or parasite transmission	
2. Indirect selection of preferences	
A. Runaway process	5, 10
B. Good genes	
(i) Host-parasite coevolutionary cycles	21, 53, 58
(ii) Unconditionally advantageous mutations	13, 17
(iii) Unconditionally deleterious mutations	21, 54, 55
C. Genetic epistasis and dominance	8, 9
D. Social system	7
E. Mutation pressure on trait	16
3. Other mechanisms	
A. Random genetic drift	5
B. Group selection	56
C. Mutation pressure on preference	16

References are to detailed theoretical studies.

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Interaction of direct selection and the parasite mechanism

Female mating preferences may experience several forms of selection simultaneously. One way to assess the evolutionary potential of these mechanisms is to consider how they interact[11,13,14]. Here we consider the interaction of direct selection (resulting, for example, from search-costs or pleiotropic effects of preference genes) and the parasite mechanism using a highly simplified quantitative genetic model.

A form of direct selection that may act on many preferences is stabilizing selection. When variation in preference genes affects female survival or fecundity, there may be an optimum value for the preference that maximizes female fitness (see Fig. 4, top). The per-generation evolutionary change in the average preference of females caused by direct stabilizing selection is approximately

$$\Delta\bar{p} = \frac{G_p^2}{\omega^2}(\theta - \bar{p}) \qquad (1)$$

where $\bar{p}$ is the mean of the preference among females, θ is the preference optimum, G_p^2 is the additive genetic variance for the preference, and ω^2 is the width of the fitness function favouring the optimum preference θ (smaller values of ω^2 correspond to stronger stabilizing selection towards the optimum). An implication of equation (1) is that the force of selection tending to restore the mean preference to its optimum is proportional to the deviation of the mean from the optimum.

Now consider the effects of indirect selection generated by the parasite mechanism. Female preferences become exaggerated as a side-effect of the evolutionary increase in parasite resistance. The per-generation change in the mean preference caused by the parasite mechanism is approximately

$$\Delta\bar{p} = G_{rp}\beta_r \qquad (2)$$

where G_{rp} is the additive genetic covariance between the mating preference and the parasite resistance, and β_r is the selection gradient (a measure of the strength of directional selection) acting on parasite resistance. (A more detailed model would account for the oscillating selection pressure that from the parasite hypothesis is postulated to be acting on parasite resistance.)

These equations illustrate an important qualitative difference between direct and indirect selection. With direct selection, the strength of selection depends on the mean preference in the population (equation (1)). By contrast, the strength of indirect selection produced by the parasite mechanism is independent of the mean preference (equation (2)). When both forms of selection operate, the equilibrium for the mean preference is at a point that balances these two forces:

$$\hat{p} = \theta + \frac{\omega^2 G_{rp}\beta_r}{G_p^2}. \qquad (3)$$

At equilibrium, the preference will lie in a vicinity of its optimum, θ, but will deviate from it by an amount proportional to the strength of the indirect selection caused by the parasite mechanism.

Two conclusions follow. First, the parasite mechanism will pull the mean preference away from its fitness optimum. By decreasing the average fitness of females, the parasite mechanism lowers the population's total reproductive output (mean fitness). Thus 'good genes' mechanisms can actually have deleterious evolutionary effects. Second, the parasite mechanism will not cause indefinite elaboration of the preference and male trait when direct selection is also present. The preference is evolutionarily constrained by direct selection to the vicinity of its optimum. The parasite mechanism will only have a substantial effect on the evolution of the preference when direct selection is relatively weak compared with the strength of indirect selection resulting from the parasite mechanism.

trait and preference[4,10]. The genetic correlation does not itself cause evolution of the preference, but is a necessary component of indirect selection, as we will discuss below.

An important message from the null model is that neither preferences for extravagant traits that decrease male survival nor preferences for traits that enhance male survival will necessarily spread among females without the action of some additional evolutionary force. What might that be? Most attention has focused on three hypotheses: direct selection of preferences, indirect selection in a runaway process, and indirect selection by the parasite mechanism.

■ **Direct selection of preferences.** Direct selection on mating preferences arises whenever the preferences affect the survival or fecundity of females. Direct selection results from many processes (Table 1). If the females that prefer more conspicuous males, for example, spend less time searching for mates than females preferring drab males, they will be favoured by direct selection. A second and possibly important form of direct selection occurs when preferences have pleiotropic effects that affect female survival and fecundity through effects unrelated to mate choice. In fact, some form of direct selection will act on preference genes unless they have absolutely no effect on immediate fitness. The simple generalization emerging from theoretical studies is that direct selection favours preferences that increase the average fitness of females. This result occurs with models of a variety of mechanisms that produce direct selection[3,5,11-17], and was recently rederived by Grafen[18]. Once a mating preference is established by this process, it dictates the equilibrium for the male trait (Fig. 4). Although adaptive from the females' point of view, these preferences can cause the evolution of elaborate male displays that decrease male survival.

■ **Indirect selection of preferences: the runaway process.** The second and third hypotheses we discuss both involve indirect selection. This mode of evolution depends on the evolutionary exaggeration of a character that is genetically correlated to the mating preference. Evolution of that character causes the preference to be exaggerated as a side-effect. Although a genetic correlation is not required for the exaggeration of the preference or the male display trait under direct selection, it is necessary for indirect selection to operate.

Evolution of a male display trait itself can cause a preference to evolve this way, because a preference and its trait can become genetically correlated (see above). If the evolutionary exaggeration of the preference is sufficient, theory shows that an unstable runaway process can result[5,10]. In a runaway, the male trait cannot reach an equilibrium because the force of sexual selection generated by the ever-more extreme preference accelerates more rapidly than the trait can evolve (Fig. 4). Ultimately, changes in either the genetic variation in the population or the force of viability selection acting on the male trait would bring the process to a halt. A runaway could cause substantial evolution of the trait and preference in a small number of generations. Like direct selection, a runaway will generally establish preferences that are arbitrary with respect to male survival. For a runaway to be initiated, the genetic correlation between the preference and trait must be larger than a threshold determined by the strength of viability selection acting on the male trait and the form of the mating preference[5]. Several factors, including direct selection on preferences and random genetic drift, can decrease the possibility of a runaway occurring. Whether the conditions for a runaway have ever been realized in a natural population is unknown.

The runaway process was first discussed by the theoretical population geneticist R. A. Fisher[10] in 1958 and earlier. The attention that it now receives comes more from its historical importance as the first modern hypothesis for preference evolution than from any empirical support for it.

■ **Indirect selection of preferences: the parasite hypothesis.** The third hypothesis has its roots in the experience of many field naturalists. They have often observed that females in species that form leks seem to mate with the most vigorous and healthy males. This impression naturally led to the so-called 'good genes' hypotheses for preference evolution. The intuitive argument behind all good genes hypotheses is that preferences for males with genes that enhance viability are favoured by evolution. By mating with a vigorous male, a female gains an evolutionary advantage by passing those genes on to her offspring[19,20]. A serious challenge to this logic appeared when the first null models showed that preferences for high viability males will not

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FIG. 1 Clockwise from top left: Male bird of paradise, *Paradisaea raggiana*, performing a courtship display to a female (courtesy of B. Beehler). Male moth, *Creatonotos gangis*, attracting females with pheromones (courtesy of M. Boppré). Calling male glass frog, *Centrolenella fleischmanni*. Male platyfish, *Xiphophorus variatus*, and male swordtail, *X. helleri*.

FIG. 2 Calling male túngara frog, *Physalaemus pustulosus*, being eaten by a bat, *Trachops cirrhosus* (courtesy of Merlin Tuttle, Bat Conservation International).

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necessarily spread even in the ideal situation where females can correctly identify those males (see above). More complex variations of the good genes argument have been developed, however, and recent theoretical work has confirmed that these mechanisms could work under some circumstances[17,21].

The good genes hypothesis that has attracted the most attention is Hamilton and Zuk's parasite hypothesis[1]. They noted that parasites are ubiquitous, and suggested that continuous coevolution between parasites and their hosts might drive the evolution of preferences for extreme male displays. Hamilton and Zuk postulated a correlation between the genes for resistance to parasites and the expression of the male trait. A variety of mechanisms could produce this correlation, the simplest being that more resistant males will be healthier and in better condition to grow elaborate plumage and perform strenuous displays[21,22]. Then females with preferences for the most extreme males will also tend to mate with those males that are the most resistant to disease. This establishes a genetic correlation between the preference and resistance genes so that the evolution of greater parasite resistance also causes the evolution of more extreme preferences. The male trait will become exaggerated as a result (Fig. 4). The critical assumption that keeps the trait and preference from reaching an equilibrium as it does in the null model is that the genes responsible for resistance are assumed to be constantly changing.

Predictions, tests and inferences

Although these three hypotheses differ in several fundamental ways, no definitive support for any of them has so far been obtained for two reasons: variation in mating preferences is more difficult to quantify than it is for many other types of traits (such as male displays), and many observed preferences are consistent with several evolutionary hypotheses. Two approaches have been used to test the hypotheses: studies of single species and cross-species comparisons. Here we outline the data that would be ideal to test each hypothesis and assess the evidence that is presently available.

■ **Direct selection.** Direct selection on preferences could be demonstrated by observing a correlation between a female's mating preference and her survival or reproductive success. So far, there are no studies showing directly that variation in female preferences affects female survivorship or fecundity. But there are data that implicate direct selection.

In species that do not form leks, female preferences seem to have evolved to maximize resource quality or quantity. Abundant data show that when males provide a nest site, food or care for the young, females prefer mates who provide resources that enhance female fecundity[23-25]. But the paradox of the lek derives from female choosiness in the absence of such material resources. Direct selection on preferences in species that form leks must result from other factors.

A subtle form of direct selection may be very important. It occurs when genes that affect the female's mating preference also affect other aspects of her life, the well known phenomenon of pleiotropy[3,26,27]. Because females use their sensory systems for other tasks besides mate choice, these systems will often be subject to natural selection for other reasons, such as foraging ability or predator detection, with the side-effect that preferences for traits that decrease male survival are likely to be established. One example comes from studies of insectivorous anolid lizards[28]. Their visual system is exquisitely adapted to detect the motion of prey. The male 'pushup' courtship display seems to have evolved to match these sensory biases in order to attract the attention of females. Other possible examples of pleiotropy come from how selection for predator detection might result in ommatidial organization that also favours construction of courtship pillars in crabs[29], and how selection on body size to avoid desiccation might influence call-frequency preference in frogs[30].

Several mechanisms other than pleiotropy can also cause direct selection in species that form leks. All females receive sperm from their mates, and in some of these species the males' size and physical condition might betray variation in their ability to fertilize. Direct measures of female fecundity have shown that in frogs[31] and fruitflies[32], females prefer to mate with males whose phenotypes maximize fertilization success. Contagion of diseases and ectoparasites will select for female preferences to avoid transmission. This effect has been implicated in the evolution of mating preferences in several animal groups[33,34,59]. The time, energy and risk of searching for a mate can also expose preferences to direct selection. Although female search costs have been identified in some species[35], there is still no evidence that variation in search costs results in selection favouring particular preferences in any species that form leks.

Phylogenetic comparisons have recently been used with two groups of animals to reject the possibility that their mating preferences originated through indirect selection caused by either the runaway or parasite mechanisms. The results suggest some form of direct selection was involved. The frog *Physalaemus pustulosus* (Fig. 2) adds chucks to its introductory whine call and females prefer calls with chucks[36]. Only *P. pustulosus* and its sister species *P. petersi* produce chucks, and the chuck seems to have evolved in their most recent common ancestor. In the close relative *P. coloradorum*, however, females also prefer calls with chucks, despite the lack of this call component in their male's repertoire. This suggests that the preference was present in the common ancestor of all these species, and thus the preference evolved before the chuck (M. J. Ryan and A. S. Rand, personal communication) (Fig. 5). The fish genus *Xiphophorus* consists of two groups, the swordtails and the platyfish. Swordtails have a sword-like elongation of the caudal fin for which females show preferences. The sword must have evolved after the swordtail and platyfish lineages diverged

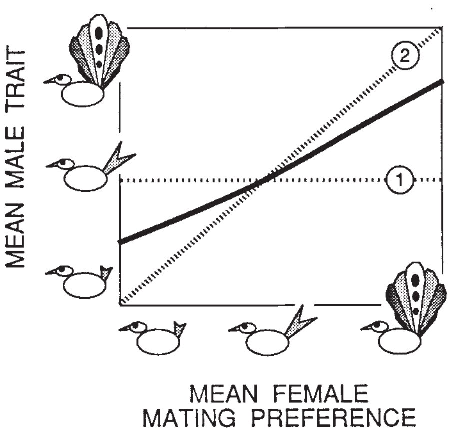

FIG. 3 Equilibria for preference and trait in the null model (heavy line). Females are imagined to have an absolute search-image for the type of male with which they would prefer to mate. The evolutionary equilibrium for a male display trait (such as tail length) represents a compromise between what maximizes survival (dashed line ①) and what maximizes mating success, which depends on prevailing female preferences (dashed line ②). (A qualitatively similar equilibria curve results when mating preferences are open-ended rather than absolute.)

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because platyfish lack swords (Fig. 1). But female platyfish show preferences for conspecific males with artificial swords[37]. As in *Physalaemus*, the male trait in swordtails apparently evolved to match pre-existing female mating preferences (a process called sensory exploitation[26,38]). The female preference and its corresponding male trait did not coevolve together as predicted by the indirect selection hypotheses. The data are consistent with the idea that direct selection established sensory biases with pleiotropic side-effects that influence mate choice.

■ **Indirect selection: the runaway process.** Two kinds of observations would be needed to document a runaway process: an imbalance between natural and sexual selection that was causing directional evolution of the male trait, and a genetic correlation between the preference and trait sufficient to cause the preference to evolve fast enough to maintain the imbalance. It is technically difficult to collect these data in most natural populations. Further, it is unlikely that a runaway would be observed in action because it is not expected to last for evolutionarily substantial periods of time. There also seems to be little hope in making predictions that could easily be tested by comparative methods because the direction of evolution during a runaway is unpredictable. The prospects for confirming the runaway hypothesis therefore seem to be dim.

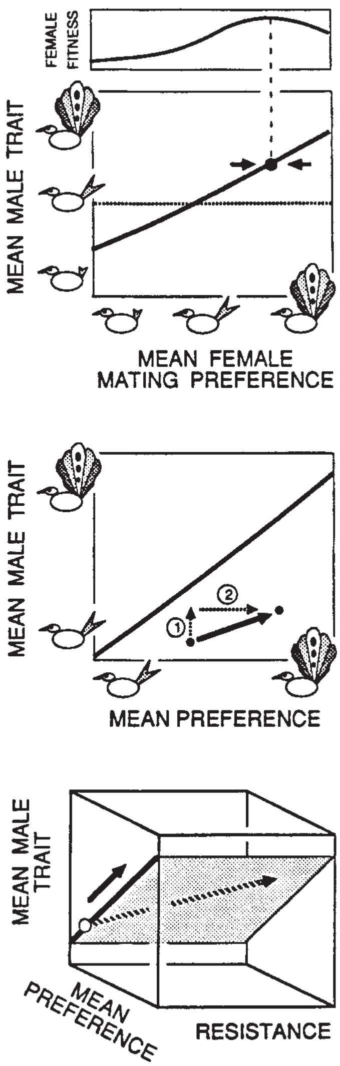

FIG. 4 Three hypotheses for the evolution of preferences. Under direct selection (top), mating preference genes also affect survival or fecundity. This determines the equilibrium for the preference and, through it, the male trait. In a runaway process (middle), the equilibria curve becomes unstable. Selection on the male trait (①) also causes evolution of the female preference through a genetic correlation (②), with the result that trait and preference are exaggerated indefinitely as they evolve away from the equilibria curve. In the parasite hypothesis (bottom), a genetic correlation is established between resistance to parasites and female preferences for a male display trait. Directional evolution of resistance (dashed arrow) results in evolution of the preference, and this causes the preference and trait to coevolve towards greater exaggeration along the equilibria curve (solid arrow).

There have been attempts to observe one of the results of a runaway process by comparing populations to see if those that have the most extreme preferences also have the most extreme male traits. This correlation has been found in guppies, where the elaboration of male colour is correlated with the degree of female colour preference among populations[39,40]. But this correlation offers only weak support for a runaway because it can also result from other mechanisms for preference evolution[39,40].

■ **Indirect selection: the parasite hypothesis.** To observe directly the parasite mechanism in a given species, one would need to find a genetic correlation between the resistance genes and the female mating preference, and document the evolutionary increase in parasite resistance. Because these kinds of observations are impractical in most species that form leks, studies of single species have turned to more limited predictions. Møller[34] recently reviewed almost a dozen such studies. Most show that the expression of male traits is correlated with parasite load and that females prefer males with fewer parasites. In five studies that looked for heritable variation in parasite resistance, it was found. At a recent symposium[41] devoted to this topic, six studies were reported in which traits and preferences were found to be related to parasite load, but in three other studies this relationship was reported to be absent.

Several workers have pointed out that many results consistent with the parasite hypothesis are not necessarily strong evidence in its favour. Consider first the data showing that females prefer mating with less parasitized males. There are many reasons why this might be so. No matter what established a preference, it is likely that healthy males will be more successful than sick males in attracting females. For example, consider a population of plants in which healthy individuals make more flowers and attract more pollinators than diseased individuals: surely this is not because the pollinators have evolved preferences for disease-resistance genes in the plants. A further complication is that preferences to avoid diseased males could be established by direct selection as well as by the parasite mechanism[33,42]. In species with male parental care, including most birds, females who mate with healthy males are at a selective advantage because these males will be better able to help rear young than will sick males. Females that avoid contact with contagious males are also favoured by direct selection (see above). In short, data showing that females mate with less parasitized males are consistent with several interpretations as well as the parasite hypothesis. (This problem is general to all good genes models: there are many reasons why females may prefer to mate with males that are larger, more vigorous, and that survive well.) A second kind of observation used to support the parasite hypothesis is the demonstration of heritable variation in parasite resistance. Again, this is necessary but not sufficient: most fitness components show genetic variation but are not increasing evolutionarily because of tradeoffs with other traits. For the parasite mechanism to cause the exaggeration of mating preferences, resistance must not only be heritable but also increasing.

Cross-species comparisons provide an alternative approach to testing the parasite hypothesis. Hamilton and Zuk[1] predicted that more heavily parasitized species would show more extreme male display traits. If such an unexpected correlation appears in spite of the 'noise' produced by unrelated evolutionary processes, it would represent strong evidence for an evolutionary link between parasitism and male displays. Results of the first comparative studies supported the parasite hypothesis. Researchers reported a significant relationship between male coloration and parasite load in species of North American[1] and European[43]

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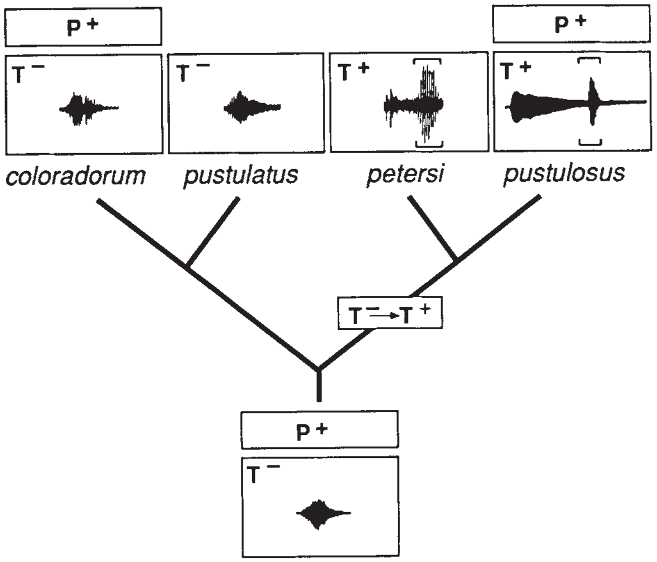

FIG. 5 Male display traits and female mating preferences in *Physalaemus* frogs. Only the closely related *P. pustulosus* and *P. petersi* add 'chucks' to their calls (in square brackets), and so this evolved in their immediate ancestor. Females of both *P. pustulosus* and *P. coloradurum* prefer calls with chucks, from which it is inferred that the common ancestor of all four species (bottom) had the preference. The preference for the chuck therefore evolved before the chuck itself did. (T^-, no male chuck; T^+, male chuck; P^+, female preference for chuck. Oscillogram at bottom is typical of other calls in the genus.)

passerine birds and in British fishes[44], and also between bird song complexity and parasite load[1]. Later studies, however, have suggested that those correlations may be artefacts resulting from the phylogenetic relationships between species and from the methods used to score the male traits. Reanalyses of the North American and European passerine plumages[45], and bird song complexity[46], and a new data set on North American fishes[47] do not find support for the parasite hypothesis.

Conclusions and prospects

Considerable circumstantial evidence has accumulated showing that direct selection is important in the evolution of mating preferences, even in species that form leks and where females receive no material resources from their mates. The data supporting indirect selection of preferences is more equivocal. The runaway hypothesis has the least empirical support, but is also the most difficult to test. Results of most (but not all) within-species studies are consistent with the parasite hypothesis, but are also consistent with alternative interpretations. In the most recent cross-species comparisons, no statistically significant correlations have been found that support the parasite hypothesis. We conclude that the present evidence for direct selection is stronger than that for either the runaway or parasite hypothesis. It is impossible to know whether the lack of strong support for the indirect selection hypotheses stems from the difficulties of testing them or because indirect selection is a weak force in the evolution of mating preferences.

Two major opportunities for empirical studies exist. First, within-species studies need to change focus from the variation in male traits and how it affects male mating success to the variation in female mating preferences. A start has been made by pioneering studies that have identified heritable variation for female mating preferences in several species[48-50]. Using such systems, one could quantify direct selection and the other evolutionary forces acting on preferences. Second, cross-species studies will continue to give the advantages of a greater taxonomic perspective and longer time scales. The comparative method may be the most fruitful way to study some hypotheses such as the parasite mechanism and to reconstruct the sequence of evolution of traits and preferences.

We close by returning to our opening theme. Recent research has been devoted largely to a few hypotheses for preference evolution. Little attention has been given to the other mechanisms that have been proposed (Table 1), or to how several mechanisms may work simultaneously. Worthy goals for the next generation of field and theoretical studies will be to broaden the search for the forces causing preference evolution, and to study how these mechanisms interact. ☐

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