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# Sexual selection and speciation

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The power of sexual selection to drive changes in mate recognition traits gives it the potential to be a potent force in speciation. Much of the evidence to support this possibility comes from comparative studies that examine differences in the number of species between clades that apparently differ in the intensity of sexual selection. We argue that more detailed studies are needed, examining extinction rates and other sources of variation in species richness. Typically, investigations of extant natural populations have been too indirect to convincingly conclude speciation by sexual selection. Recent empirical work, however, is beginning to take a more direct approach and rule out confounding variables.

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SEXUAL SELECTION (see Glossary) results from differential mating success among individuals within a population. Competition for fertilization occurs through direct competition between members of the same sex (e.g. male–male competition and sperm competition) or through the attraction of one sex to the other (e.g. female choice). Although long recognized as important in intrapopulation evolution, sexual selection has more recently been invoked as a driving force behind SPECIATION. Speciation, the splitting of one SPECIES into two or more, occurs by sexual selection when a parallel change in mate

preference and SECONDARY SEXUAL TRAITS within a population leads to PREZYGOTIC ISOLATION between populations, and when this is the primary cause of REPRODUCTIVE ISOLATION.

Classic models of speciation<sup>1,2</sup> recognized that reproductive isolation, and subsequent speciation, could be generated by differences in sexual traits (including behaviours). Divergence in sexual traits between allopatric populations was considered to result either from drift, PLEIOTROPY or adaptation to environmental conditions, or following SECONDARY CONTACT, because individuals benefited by avoiding heterospecific matings (i.e. by REINFORCEMENT). It became clear, however, that changes between populations in sexual traits could also result from sexual selection and that this might represent a distinct process of speciation<sup>3,4</sup>. Sexual selection has the potential to lead to rapid divergence between populations, it can be independent of environmental differences, and it is predisposed to generate reproductive isolation because of its direct effect on traits involved in mate recognition. It is important to point out that the rapid change between populations

### Box 1. Sexual conflict and speciation

In species where females have more than one mate, each male is selected to maximize the proportion of the reproductive effort of a female going into his offspring. This is in his interest even if it decreases the lifetime reproductive output of the female. A conflict between the sexes is created as males attempt to both manipulate females and to out-compete other males (even if this is costly to the female) and females evolve to avoid these costs and controls. Such antagonistic coevolution has the potential to drive rapid evolutionary change, particularly in aspects of the reproductive system, giving it the potential to create divergence between allopatric populations<sup>a</sup>.

A mathematical model for the evolution of reproductive barriers via sexual conflict has recently been proposed<sup>b</sup> in which

conflicts of interest between the sexes over mating rate are predicted to cause divergence, because it pays females to reduce the proportion of the male population with whom they are reproductively compatible. The model demonstrates that, under some scenarios, conflict can lead to runaway coevolution driving divergence. Also, in contrast to models where change occurs because of GENETIC DRIFT (see Glossary), sexual conflict generates direct selection on reproductive traits: divergence is expected to be more rapid when populations are larger.

The generality of this model has been questioned on the basis that females will only benefit from incompatibility with a proportion of males if such incompatibilities actually prevent matings. If this is the case, males might be able to

redirect their mating effort, changing the dynamics of the system<sup>c</sup>. An alternative approach to conflicts of interest has been suggested<sup>d</sup> wherein species in which males invest very little in matings might be less prone to speciation, as there will be less selection on males to avoid outbreeding.

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as a result of sexual selection can also play an indirect role in speciation by increasing the overall rate of change within isolated populations<sup>5</sup>. Some have argued that this indirect role might be more important than a direct role for sexual selection in speciation<sup>6</sup>.

Theoretical studies have convincingly demonstrated the potential for speciation to result from sexual selection (see Turelli *et al.*<sup>7</sup>, this issue). Here, we focus on recent empirical evidence for SPECIATION BY SEXUAL SELECTION. Much of this support comes from comparative studies that examine differences in the number of species between CLADES. Patterns of variation in secondary sexual traits and mating preferences between populations or species also suggest that sexual selection plays a role in speciation, but these 'signatures' have the drawback that evolutionary processes cannot be tracked through time and thus exclude alternative explanations.

We discuss the strengths and weaknesses in using the comparative method for understanding the role of sexual selection in speciation. We then consider why the common 'signatures' that lend support for speciation by sexual selection are not conclusive, and discuss criteria for demonstrating the role of sexual selection in speciation.

#### Comparative evidence

Important evidence showing how sexual selection affects speciation comes from comparisons across taxa. Darwin<sup>8</sup> noted that elaborate secondary sexual characters tended to occur in groups that also had high species richness, suggesting that sexually selected ornamentation might cause taxa to diversify, but rigorous tests of this association have appeared only recently. The first such test used 20 sister pairs of

passerine bird tribes that differ in their proportions of sexually dichromatic and monochromatic species<sup>9</sup>. Sister taxa have, by definition, accumulated diversity over the same period of time. Therefore, the tribe with the greater number of extant species necessarily has the higher net speciation rate (rate of speciation minus the rate of extinction). If sexual selection promotes speciation, diversity is expected to be higher in clades with more dichromatic species, assuming that sexual differences in plumage result from sexual selection. Of 15 comparisons with marked differences in the frequency of dichromatism, 12 showed differences in species richness in the expected direction<sup>9</sup>.

Similar comparative studies have since supported speciation by sexual selection: in birds, by comparing the number of species in taxa with different mating systems<sup>10</sup>, and different degrees of feather ornamentation<sup>11</sup>; and in plants, by comparing lengths of nectar spurs<sup>12</sup>. More ornamented species have more subspecies<sup>11</sup>, suggesting ongoing differentiation.

These studies concentrate on the contribution of sexual selection to speciation through divergence in mating signals and preferences. Comparative evidence also suggests, however, that postmating effects promote speciation and that sexual selection influences the evolution of POSTZYGOTIC ISOLATION. If a female mates more than once, the opportunity for sexually antagonistic selection arises (Box 1). If such selection has a role in speciation, MONANDROUS clades should show lower speciation rates than would related POLYANDROUS clades. A strong pattern of this type was recently documented using data from 25 pairwise comparisons in five orders of insects<sup>13</sup>. Another comparative analysis<sup>14</sup> demonstrated that genital morphology evolves more rapidly in polyandrous

### Box 2. Haldane's rule and speciation

In pairs of animal species where premating barriers can be overcome and some hybrid offspring generated, it is common to find that one sex is inviable or infertile. In 1922, J.B.S. Haldane noted a striking pattern in these crosses: the sex that is inviable or sterile is almost invariably the heterogametic (XY) sex. This is one of the strongest 'rules' in evolutionary biology. It is obeyed in 151 out of 157 crosses in *Drosophila* and mammals (male heterogametic) and 91 out of 98 crosses in Lepidoptera and birds (female heterogametic)<sup>a</sup>. Examining the time course of speciation in *Drosophila* suggests that Haldane's rule is a nearly obligatory 'first step in the evolution of postzygotic isolation'<sup>a</sup>.

How does Haldane's rule implicate sexual selection in speciation? There are several competing explanations for the pattern<sup>a</sup>, one of which, the 'faster-male' theory<sup>b</sup>, invokes sexual selection. The argument is that male sterility might be more common than female sterility in hybrids either because spermatogenesis is inherently more sensitive than oogenesis,

or because sexual selection and sexual conflict cause more rapid divergence of genes expressed in males. Divergent loci interact poorly in hybrids, leading to sterility. If spermatogenesis is a sensitive process, this is presumably because sexual selection or sexual conflict favours a high rate of sperm production.

Clearly, this cannot be the only mechanism underlying Haldane's rule because it is unlikely to explain asymmetrical inviability and because it works against the rule in taxa with heterogametic females. However, evidence that it contributes to sterility in taxa with XY males would demonstrate a role for sexual selection in the origin of postzygotic isolation. The faster-male theory is now supported by two lines of evidence. First, chromosome regions introgressed from one species of *Drosophila* into another are more likely to contain male-sterile than female-sterile genes<sup>c,d</sup>. This fits the expectation of more rapid divergence at loci expressed only in males. Second, the faster-male theory is not dependent on the Y chromosome being inert and thus

recessive loci on the X chromosome being expressed in hybrids, which is the basis of the other major explanation for the rule. Taxa with non-degenerate Y chromosomes are, therefore, expected to follow Haldane's rule for sterility but not for inviability. This is exactly the pattern observed in a comparison between two mosquito genera: *Aedes*, where the Y chromosome is homologous to the X, and *Anopheles*, where the Y is inert<sup>e</sup>.

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insect clades, implicating postmating sexual selection in the rapid evolutionary divergence of genitalia. If polyandry generates greater opportunity for sexual selection as well as for sexual conflict, the causal link to speciation remains unclear. Sex-related genes (i.e. those involved in sex determination or any aspect of mating and fertilization) show higher nonsynonymous:synonymous nucleotide substitution ratios between closely related species than do other classes of genes<sup>15</sup>. This suggests divergence resulting from sexual selection around the time of speciation. Finally, the evidence explaining HALDANE'S RULE by faster male evolution (Box 2) strongly suggests that sexual selection can promote genetic divergence underlying hybrid male sterility.

#### Counting species is not enough

Comparisons based on the numbers of species in different groups are not without problems. If taxonomists use secondary sexual traits in species definitions, the numbers of named species could be upwardly biased in dimorphic taxa. Comparative studies also tend to assume that dimorphic traits have diverged by sexual selection, often with limited direct evidence. At best, such studies demonstrate a correlation between speciation and sexual selection (across taxa or in time) rather than a causative link. Comparative analyses must deal with the problem of confounding variables: sexual dichromatism, for

example, could be correlated with some other variable that actually causes elevated speciation rates. The only safeguard against this possibility is to control for as many such variables as possible. A particularly thorough analysis<sup>16</sup> attempted to minimize the problem by simultaneous analysis of six different explanations for variation in species richness among bird families: chance (i.e. by fitting models of random CLADOGENESIS), body size, life history, sexual selection, intrinsic ecological factors and extrinsic abiotic factors. Using comparisons of species numbers in 28 unequivocal sister taxa, strong support was found for an association with sexual dichromatism but not with mating system. Generalist feeding habits, high dispersal and large, fragmented geographical ranges are also associated with high diversity.

Despite the limitations of comparisons based on species counts, comparative studies do suggest that sexual selection can accelerate the net rate of speciation. Divergence in secondary sexual characters might, however, generate reproductively isolated, but ecologically equivalent species unable to coexist in SYMPATRY. Some evidence suggests that the processes of extinction and speciation in birds are determined by different attributes<sup>16</sup> and might, therefore, be uncorrelated. If this is true, it becomes difficult to interpret what net speciation rates tell us about the speciation process. In the insect study mentioned previously<sup>13</sup>, elevation in net speciation rate is much

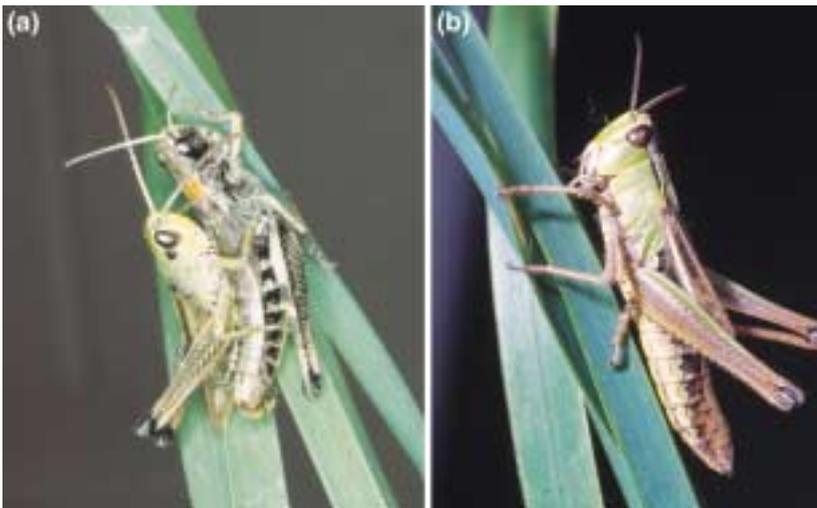


Fig. 1. Examples of sexual selection. (b) A female from the centre of a hybrid zone between subspecies of the meadow grasshopper *Chorthippus parallelus*. A steep cline in female preference across the zone indicates that preference is under selection<sup>24</sup>. (a) A mating pair from a laboratory mate choice test in the meadow grasshopper. There is sufficient divergence between allopatric populations of this species in Europe to generate significant assortative mating. In some cases, this divergence must have been accumulated since the end of the last glaciation<sup>23</sup>. Sexual selection might explain such rapid evolution.

greater in comparisons within than between families (relative rate 3.3 and 1.1, respectively), suggesting only a short-term change in the balance between speciation and extinction. This implies that comparative analyses should focus on recently diverged sister taxa where the signal of elevated speciation rate will be strongest. Although sexual selection might promote speciation, ecological processes are more important in determining the numbers of species that can coexist and, over longer time scales, might obscure the effect of increased speciation rate.

Even if the comparative evidence does point to a role for sexual selection in speciation, it does not directly distinguish between acceleration of divergence in ALLOPATRY, initiation of divergence in sympatry, or involvement in reinforcement. Some attempts have been made to address this problem. Further analysis<sup>17</sup> of earlier data<sup>9</sup>, focusing on the number of species of each taxon living together rather than the total species richness, could not show that more diverse, sexually dichromatic taxa have greater numbers of species in sympatry than do the less diverse, monochromatic taxa. This suggests that sexual selection promotes allopatric divergence rather than promoting SYMPATRIC SPECIATION and that the allopatric species are ecological equivalents, prevented from expanding their ranges into sympatry by competition. In flocks of cichlid fish species, however, frequent sympatric occurrence of different colour morphs suggests that sexual selection can promote sympatric speciation despite a lack of ecological separation<sup>18</sup>.

#### Are there conclusive signatures of speciation by sexual selection?

Via<sup>19</sup> (this issue) refers to patterns that provide indirect evidence of sympatric speciation as 'signatures'. Two signatures might be recognized for speciation by sexual selection: (1) within species, populations will vary in sexually selected traits and associated preferences and this might generate partial premating isolation between populations; and (2) closely related species will differ markedly in

mating signals and preferences; these differences will be the major barrier to gene exchange and the species will differ little in other traits. If sexual selection is a common cause of speciation, these patterns should be encountered frequently.

#### Signatures from population differences

There are many examples of variation among populations in potentially sexually selected traits<sup>20,21</sup>. In some cases, the variable traits can be shown to be under sexual selection within populations (e.g. guppies; Table 1), but, even in these cases, the cause of divergence among populations is usually unclear. In other examples<sup>22,23</sup>, partial premating isolation has been demonstrated among populations; however, the signal traits involved are unknown. Variation in female preference has only been studied rarely, using either mating tests (e.g. grasshoppers<sup>24</sup>; Fig. 1) or playback experiments (e.g. lacewings<sup>25</sup>). Table 1 illustrates the extent to which some recent studies of geographical variation in sexually selected traits have covered these aspects. Clearly, the signature is strongest if all components are included, but this has yet to be achieved.

It is possible that divergence between populations in sexually selected traits and/or preferences could result in speciation. Speciation, however, is just one of several evolutionary outcomes of the sexually selected differences. Upon secondary contact, the partial barrier to gene flow between populations might diminish if postmating isolation is absent and if the differences in behaviour are insufficient to prevent hybridization. For example, isolation could be asymmetrical (i.e. only one population exhibits female preference for males of their own population) as in the case of *Drosophila melanogaster* populations from Zimbabwe (Table 1). These populations exhibit behavioural premating isolation from other non-African populations, but this is the result of asymmetrical female preference, and postmating isolation has not been detected<sup>26</sup>. This suggests that populations would interbreed in sympatry and differentiation would be lost. This type of breakdown of signal differences and ASSORTATIVE MATING is seen in some hybrid zones (e.g. fire-bellied toads, *Bombina*<sup>27</sup>), although natural and sexual selection may restrict hybridization to a narrow region.

The evolutionary outcome of population differences in sexually selected traits and preferences could also depend on whether there is a mismatch between the male trait and the female preference. A mismatch could result if a population changes its male display trait (possibly as a result of environmental pressures), but not in female preference. A study<sup>28</sup> on female preferences in the house finch *Carpodacus mexicanus* illustrates this phenomenon. Geographical variation in male plumage colouration and the amount of ventral pigmentation (patch size) is driven by environmental differences in regional and local access to carotenoid plumage pigments. Females, independently of their

Table 1. Examples of detecting signatures of speciation by sexual selection<sup>a-c</sup>

Taxa	Example <sup>d</sup>	Type of trait	Trait under sexual selection <sup>e</sup>	Preference variation	Prezygotic reproductive isolation <sup>e,f</sup>	Character displacement	Refs
Insects	<i>Drosophila melanogaster</i>	Zimbabwe females prefer Zimbabwe males over non-Zimbabwe males	Unknown	Yes	Asymmetrical	Unlikely	26,52,53
		Asymmetrical female preference among different Israel populations	Unknown	Yes	Asymmetrical	Unlikely	
	<i>D. silvestris</i>	Sex comb row number	Yes	Yes	Asymmetrical	Unlikely	54
	<i>Chrysoperla</i> spp.	Substrate-transmitted acoustic signals	Unknown	Yes, between species and 'song morphs'	Yes	Unlikely	25
	<i>Chorthippus parallelus</i>	Male song, pheromones and assortative mating	Unknown	Yes	Yes, in some population pairs	No	23
	<i>Ephippiger ephippiger</i>	Female preference functions and male calling song (number of syllables/chirp)	Unknown	Yes	Probably	Unlikely	55
	<i>Gryllus texensis</i> and <i>G. rubens</i>	Pulse rate of male song and associated female preference	Yes	Yes, between species	Yes, between species	No	39
		<i>Agrotis segetum</i>	Pheromone blend and male response	Unknown	Yes	Probably weak	Unlikely
	Frogs	<i>Acris crepitans</i>	Male advertisement calls (independent of body size) and female preference for male calls	Unknown	Yes	Probably	No
Fish	<i>Poecilia reticulata</i>	Male colour pattern and female preference for males from their own locality	Yes	Yes	Little	Unlikely	60
	Haplochromine cichlids of Lake Victoria	Sexually dimorphic colouration and associated preferences	Yes	Yes, between species/morphs	Yes, between species/morphs	Possible	18
Birds	<i>Centrocercus urophasianus</i>	Male strut displays, body size and feather morphology differing in the Gunnison Basin, CO (USA) population (recently given species status) compared with Jackson County, CO and Mono County, CA, (USA) populations	Yes	Unknown	Unknown	Unlikely	61,62
	<i>Amblyornis inornatus</i>	Male display traits, such as bower structures, and female preferences in at least one population	Yes	Probably	Probably, but might be asymmetric	Unlikely	45
	<i>Phylloscopus trochiloides</i>	Male song between two sympatric subspecies that do not interbreed, yet are connected by a ring of populations that do interbreed	Yes	Unknown	Only demonstrated between subspecies	No	49, 50

<sup>a</sup>This is not a complete list of examples, but is intended only as an illustration of the phenomenon. Also see Refs 5,6,35.

<sup>b</sup>Most examples included have low genetic divergence as judged by allozyme, DNA or mitochondrial DNA (mtDNA) sequence divergence, or taxonomic status.

*Phylloscopus*<sup>50</sup> ssp. and *Centrocercus* populations<sup>63</sup> show mtDNA divergence between subspecies/species. A Zimbabwean *D. melanogaster* population shows greater population structure compared with North American populations on the basis of DNA sequence divergence<sup>64</sup>.

<sup>c</sup>Some degree of postzygotic isolation has been found between *Chrysoperla*<sup>25</sup> spp. and *Chorthippus*<sup>23</sup> populations. Studies have not demonstrated postzygotic isolation between Zimbabwe and 'cosmopolitan' populations of *D. melanogaster*<sup>26</sup> or between *Gryllus texensis* and *G. rubens*<sup>39</sup>. Postzygotic isolation in the cichlids is inferred to be low. To the best of our knowledge, postzygotic isolation data are not available for the other examples in the table.

<sup>d</sup>Common names: *Acris crepitans*, Cricket frogs; *Agrotis segetum*, Turnip moths; *Amblyornis inornatus*, Vogelkop Bowerbirds; *Centrocercus urophasianus*, Sage grouse; *Chorthippus parallelus*, Grasshoppers; *Chrysoperla* spp., Lacewings; *Drosophila melanogaster* and *D. silvestris*, Fruit flies; *Ephippiger ephippiger*, Bush crickets; *Gryllus texensis* and *G. rubens*, Crickets; *Poecilia reticulata*, Guppies; *Phylloscopus trochiloides*, Greenish Warblers.

<sup>e</sup>Unknown – to the best of our knowledge, data are not available.

<sup>f</sup>Not necessarily complete reproductive isolation.

population, prefer the ancestral male type with the brightest and largest patches. Upon subsequent contact, this mismatch between the male trait and the female preference would probably lead to interbreeding between populations, rather than prezygotic isolation.

Mismatches are also associated with the sensory bias and sensory exploitation model of sexual selection<sup>29–31</sup>. This model proposes that females respond

to certain signals because of pre-existing properties of their sensory system<sup>30,32</sup> and hence male traits evolve after female preferences<sup>33</sup>. This phenomenon has been demonstrated in several taxa (e.g. fish<sup>31</sup>, frogs<sup>33</sup> and spiders<sup>34</sup>)<sup>35</sup> by revealing that females of closely related species prefer males with the heterospecific derived male trait rather than conspecific males without the trait. Population divergence in male traits might or might not occur, depending on the environmental or

developmental constraints on the rapidity with which the male trait could evolve to exploit the female preference. There is also evidence that female sensory biases are rather generalized and can be satisfied by a variety of specific male traits<sup>32,36</sup>. Therefore, different male traits might evolve in response to the same sensory bias leading to divergence in signal traits without increasing isolation. This model of sexual selection seems unlikely to lead directly to speciation given the fact that females, all else being equal, will tend to interbreed with males that exploit their sensory bias, independent of their population. However, it could exaggerate already established species differences<sup>32,35</sup>. Alternatively, it could be that local environmental conditions alter the female sensory bias or make some male traits better at exploiting biases, just as specific traits might be better indicators of male condition in some environments than others<sup>37</sup>. In this case, different coevolutionary paths of signal and preference might generate speciation.

A different perspective on mismatches between traits and preferences suggests that they might provide good evidence for the role of sexual selection in speciation. If female preferences evolve for 'good genes' or Fisherian reasons, they are expected to be open-ended, or at least to have mean preferences for trait values above the male population mean. This is because the sexual advantage of the trait is balanced by its cost to the male. Therefore, if two populations differ in the mean value of the male trait, they are likely to have even greater differences in female preference. This can be contrasted with the expectation for signals and preferences that have evolved for species recognition, where a match between male trait mean and female preference mean would be expected<sup>38</sup>. The mismatch between signal and preference can generate asymmetric isolation between populations with intermediate levels of divergence: this pattern has been observed in tests of mate choice between populations of *Desmognathus* salamanders<sup>22</sup>. However, this model does not explain the pattern of assortative mating observed among *Chorthippus* grasshopper populations<sup>23</sup>.

#### Signatures from species differences

Because we cannot see into the future, observations on divergent populations can only ever show that steps towards speciation might be promoted by sexual selection: how often the process is completed, and by what route, remains uncertain. Studying species differences suffers from the opposite problem: the difficulty of inferring the past. Many morphologically and genetically similar species differ markedly in mating signals and preferences. It might be inferred from this that sexual selection has driven speciation, but to do so requires that other modes of divergence be excluded.

The possibility that species recognition has been an important force in shaping the changes seen between male traits used to attract mates or female

preferences can be difficult to exclude. Species recognition is important when interpopulation or heterospecific mating is costly, producing relatively inviable or infertile offspring. Traits facilitating species recognition might then diverge under natural selection when populations or closely related species have overlapping geographical ranges<sup>2</sup>. Thus, reinforcement or REPRODUCTIVE CHARACTER DISPLACEMENT (RCD) could drive the change in male traits and female preferences, eliminating a direct role of sexual selection<sup>39</sup>. However, it has been proposed<sup>33,40</sup> that sexual selection and species recognition are part of a continuum and that sexual selection might facilitate reinforcement<sup>41</sup>. Several studies have shown (e.g. butterflies<sup>42</sup>; fish<sup>35</sup> and frogs<sup>30</sup>) that male display traits can be both sexually selected and used in species recognition. Contrary results have been found in two sibling species of Hawaiian *Drosophila*, where the sexually selected trait is not used for species recognition<sup>40</sup>.

Evidence favouring speciation by sexual selection rather than reinforcement or RCD could demonstrate that: (1) the trait in question does not differ significantly in areas of sympatry versus allopatry (the opposite trend is a distinguishing feature of character displacement<sup>39</sup>); (2) there is trivial or no postzygotic isolation (i.e. the fitness reduction required to drive reinforcement or RCD is absent); and (3) the trait used in mate acquisition is used both in sexual selection and species recognition. However, it is possible that the initial divergence in traits or preferences could have been the result of natural selection to decrease hybridization and then been subject to sexual selection, or vice versa<sup>33</sup>, making a clean separation difficult.

An analysis of data on 41 species of haplochromine cichlids from Lake Victoria showed that species pairs with a substantial range overlap were more likely to differ in sexually selected colouration than were pairs with little range overlap<sup>18</sup>. This is the pattern expected from reinforcement or RCD, but, in this case, there is little evidence for hybrid fitness reduction and the extremely short time scale for speciation in the lake makes the two stage process of allopatric divergence followed by range expansion and divergence in secondary sympatry improbable. The authors favoured a model of speciation as a result of disruptive sexual selection in sympatry (see Turelli *et al.*<sup>7</sup>, this issue).

#### What should new studies aim to demonstrate?

It is improbable that any single test will separate speciation by sexual selection from other modes of speciation. This is a problem common to all speciation research and stems from our inability to observe the whole process, forcing us either to infer the most probable future course of events or to separate different possible histories. Therefore, recent studies have aimed to overcome these difficulties by accumulating observations consistent with speciation by sexual selection and by trying to

rule out alternative scenarios. These studies have suggested the following major components:

- Substantial differences occur among populations or species in male sexually selected traits with correlated female preferences<sup>43–45</sup>.
- Changes are sufficient to result in prezygotic isolation should populations come into contact<sup>39</sup>.
- There is little genetic differentiation between populations or species, suggesting rapid divergence<sup>43–45</sup>.
- There is little or no reduction in hybrid viability or fertility, although hybrid fitness might be reduced by inappropriate signals or preferences.
- If applicable, there is no character displacement<sup>39</sup>.

Without the first element, there is no case for speciation by sexual selection. As noted earlier, sexual selection should be demonstrated directly from the effect of variation in the trait on mating success rather than simply being inferred from elaboration or sexual dimorphism. The second point is required because divergence under sexual selection does not necessarily result in a substantial barrier to gene exchange. The catch here is to demonstrate that prezygotic isolation is the direct result of the changes in sexually selected traits and not a result of other evolutionary forces (e.g. drift or natural selection) or evolutionary history. This might be difficult, but could be achieved through comparative studies using a phylogenetic approach to help separate independent evolutionary origins from historical effects resulting from common ancestry<sup>35</sup> (see Barraclough and Nee<sup>46</sup>, this issue). Genetic 'dissection' of the mating traits important in prezygotic isolation has also been proposed<sup>47</sup>. This consists of hybridization studies between closely related species to analyse the genetic and phenotypic difference in male traits and female preferences. The third component might be necessary to help rule out pleiotropic effects of genetic divergence<sup>45</sup>. INCIPIENT SPECIES or sibling species could be useful systems to study speciation by sexual selection because they will, by definition, have experienced relatively little genetic divergence. Lack of postzygotic isolation is important for the same reason, as well as helping to exclude the possibility that prezygotic isolation has arisen secondarily rather than being the initial cause of speciation. The final component is important for studies of closely related species that overlap in their geographical range. By ruling out character displacement, a stronger case is made for the role of sexual selection in the speciation event<sup>39</sup>.

These criteria are not applicable to all systems, but the objective should be to cover as many as possible. Some of the best examples from nature that suggest that sexual selection could be involved in the speciation process are listed in Table 1, but it is clear that each one of them falls short of being conclusive. The studies on cichlids suggest that sexual selection could be important in generating sympatric speciation<sup>18,48</sup>. Recent studies<sup>49,50</sup> on greenish warblers (*Phylloscopus trochiloides*) imply that changes in the intensity of sexual selection on song are important in generating prezygotic isolation

between two sympatric subspecies forming the ends of a ring species. Character displacement is improbable because the degree of song variation between allopatric and sympatric populations is small within both subspecies. Work on two cryptic species of field crickets (*Gryllus texensis* and *G. rubens*) demonstrates that: (1) a change between species in male calling pulse rate is genetically correlated with a change in female preference; (2) the difference in male traits and female preferences leads to prezygotic isolation; (3) males are morphologically almost identical (only ovipositor length differs between females); (4) signs of postzygotic isolation are lacking; and (5) there is no evidence for character displacement<sup>39</sup>. However, even this last study was only able to conclude that the data are 'substantially more consistent with speciation by sexual selection than they are with the alternatives' of speciation by reinforcement or by ecological differentiation.

Even when incipient species are described, speciation might not be completed by sexual selection. For example, in the Vogelkop bowerbirds (*Amblyornis inornatus*; Table 1) males from allopatric populations are morphologically and genetically very similar and only differ in their display traits; however, it is not known whether the female preference is symmetrical and whether it will result in prezygotic isolation<sup>45</sup>. Some have also argued that rapid radiation in the Hawaiian *Drosophila* can be explained by other evolutionary forces, such as drift followed by natural selection<sup>51</sup>, or that the sexually selected traits are not involved in species recognition<sup>40</sup>. Thus, sexual selection might not be as important in the origin of some of the Hawaiian *Drosophila* species pairs as it first seemed.

### Prospects

There is no doubt that sexual selection has the potential to play a major role in speciation. Models of both allopatric and sympatric populations indicate that sexual selection has the power to drive rapid divergence and generate reproductive isolation (see Turelli *et al.*<sup>7</sup>, this issue). The evidence suggesting that theory translates to reality comes from comparative studies that repeatedly indicate higher species diversity in more sexually selected clades and from observations of patterns of divergence between populations and species that are consistent with the expectations of speciation by sexual selection. Further comparative studies are needed, examining extinction rates as well as numbers of extant species, confirming the role of sexual selection in the evolution of the traits used as indicators (such as plumage dimorphism in birds) and quantifying ecological and other sources of variation in species richness. Empirical work has taken a more direct approach to demonstrating speciation via sexual selection, but more examples are needed in which all elements of the sexual selection model have been demonstrated and that eliminate, so far as is possible, alternative factors such as character displacement and pleiotropic effects of divergence.

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