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Social behaviour and speciation

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Overview

Speciation results from the evolution of traits that inhibit reproduction between populations. This chapter discusses theoretical and empirical studies that relate to how social behaviour influences those reproductive barriers. Behaviour can influence prezygotic isolation by causing non-random mating or non-random fertilisation. Learning can affect mate recognition through cultural transmission of mate advertisement signals and sexual imprinting. Behaviour can also contribute to reproductive isolation if hybrids are discriminated against as mates or if female re-mating influences fertilisation success.

A general theory of speciation does not exist, but a variety of models have been developed to describe how selection can favour speciation in particular situations. Theory suggests that sexual selection, in particular, should be a diversifying force. However, among vertebrates sexual selection by female choice has favoured expression of condition-dependent traits, which are typically not reliable for species recognition. Better examples of sexually selected traits functioning in both mate-choice and species-recognition contexts can be found among some insects, such as crickets. The best examples of sexual selection influencing speciation in vertebrates come from cases of sexual imprinting in birds where offspring learn species-recognition cues in the nest.

Sexual selection can also operate after mating by sperm competition or cryptic female choice. Either or both of these mechanisms likely contribute to conspecific sperm precedence, which may result in reproductive isolation after mating. Sexually antagonistic coevolution has the potential to drive speciation in systems with sexual conflict. However, evidence demonstrating that sexual conflict causes reproductive isolation is currently equivocal in cases involving traits that influence mating or fertilisation success.

Few studies have attempted to determine the genetic basis of prezygotic isolation in comparison to postzygotic isolation. However, among the exceptions

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are studies in which one or two physically linked genetic factors influence both mate preference and a recognition cue. New methods for genomic mapping in non-model organisms promise to add considerable insight into how genes influence prezygotic reproductive isolation.

A variety of claims have been made that social behaviour accelerates speciation rates in, for example, mammals, birds and social insects. In general, these claims have not been supported by comparative studies. With regard to sexual selection, this may be because extinction rates are also accelerated. Focused research on groups of closely related species that exhibit different mating systems should help to clarify which processes are involved in the initial stages of speciation.

19.1 Introduction

A hallmark of sexual organisms is that populations of reproductive individuals typically exhibit categorical, rather than continuous, differences in morphological and behavioural traits, particularly those related to mating (Maynard Smith & Szathmáry 1995). Whereas the existence of these differences has been used to identify and organise species since Linnaeus first published *Systema Naturae* in 1735, the process and temporal sequence by which a single population diverges over time into two distinct forms, i.e. speciation, remains hotly debated and is arguably the most active area of investigation in evolutionary biology today. An important part of this process involves mate (and gamete) selection. In this sense, behavioural processes that influence mating and fertilisation are key pieces to the puzzle of speciation, and they are the focus of this chapter.

The biological species concept (Dobzhansky 1937, Mayr 1942) defines a species as a group of interbreeding populations that is reproductively isolated from other such groups. Although conceptually simple, this definition can be difficult to apply because breeding opportunities between species pairs may not exist, and in some cases traditional species with morphological differences do not show complete isolation. These issues have led to alternative definitions and considerable debate (e.g. Mallet 1995, Harrison 1998, Shaw 1998). Nevertheless, the biological species concept provides the best framework for considering how social behaviour may influence the speciation process.

A key element of the biological species concept is that speciation requires reproductive isolation. Reproductive isolation describes the outcome of interactions between individuals from two populations and results whenever the temporal sequence associated with the formation and development of a zygote is interrupted. An *isolating mechanism* (Dobzhansky 1937), or *barrier to reproduction*, refers to reproductive failure that occurs at one or more of the following four life-cycle stages: (1) mating, (2) gamete union, (3) hybrid development or (4) hybrid reproduction. Failure at the first two of these steps is prezygotic isolation (either pre-mating or post-mating), whereas failure at the last two is postzygotic isolation (either hybrid inviability or infertility).

In this chapter our goal is to summarise and evaluate the ways in which social behaviour may be involved in the speciation process. In most situations, speciation occurs on timescales that cannot be observed in a lifetime. Thus, inferences about process must rely on phenotypic or genetic differences that can be detected between extant taxa and used to evaluate alternative models. For this reason, we briefly summarise relevant theory, when available, and then consider how selection on behaviour could influence reproductive isolation before or after mating. For example, social behaviour can impact the speciation process if non-random mating occurs, either indirectly through changes in host preference or directly through changes in mate preference. Learning can impact mate recognition through cultural transmission of mate advertisement signals (ten Cate 2000) and sexual imprinting (Bateson 1978). Social behaviour can also contribute to post-mating, prezygotic isolation to the extent that female re-mating influences fertilisation success (Jennions & Petrie 2000, Birkhead & Billard 2007). After reviewing each of these possibilities in turn, we then discuss examples and methods that could be used to determine the number of genetic changes required to cause sexual isolation. We end by considering several ideas for how social behaviour might influence speciation rate.

19.2 Speciation theory

A general theory of speciation does not yet exist (Gavrilets 2004, Turelli *et al*. 2001), and may be difficult to construct given the diversity of ways populations can become isolated. However, a large number of speciation models have been developed for particular geographic situations, which are referred to as *modes* of speciation (Box 19.1), and different selection scenarios. Rather than attempt to summarise those models, we refer the interested reader to Gavrilets (2004) for a comprehensive discussion. Here we use the scheme proposed by Kirkpatrick and Ravigne (2002) to highlight where social behaviour is important in five essential features that can be found in all models of prezygotic isolation. This deconstruction applies only when selection, rather than drift or mutation, is invoked to cause speciation.

Box 19.1 Modes of speciation

The structure of diverging populations in space is typically referred to as the *mode* of speciation.

Allopatric speciation is considered to be the most common mode of speciation (Mayr 1942, 1963). It occurs after a *vicariant* event, e.g. a river, glacier or island, divides the distribution of a species and creates geographically isolated populations. Subsequent adaptation to local environmental conditions or drift then results in genetic divergence over time. Speciation is verified when two previously isolated populations restore contact but remain distinct.

Box 19.1 Continued

Peripatric speciation is a type of allopatric speciation that occurs when small peripheral populations are isolated from a parent population. This process is frequently invoked to explain the origin of island endemics after a colonisation event. The radiation of *Drosophila* in Hawaii (Hollocher & Williamson 1996) and in the Caribbean (Paulay & Meyer 2002) provides compelling examples.

Sympatric speciation, in contrast, occurs when disruptive selection within a single parent population results in daughter populations that are reproductively isolated from each other in the same geographic area (Via 2001). Host switching is one mechanism by which sympatric speciation can occur. For example, the apple-feeding race of the apple maggot fly *Rhagoletis pomonella* is believed to have evolved from the hawthorn-feeding race after apples were introduced into North America. Each race now shows restricted host preferences, and consequently they are reproductively isolated from each other (Bush 1969, Feder *et al*. 1994, 2003). Pea aphids *Acyrthosiphon pisum* that feed on clover or alfalfa provide a second example of host switching at an earlier stage of differentiation (Via 1999, Hawthorne & Via 2001).

Parapatric speciation refers to intermediate situations in which gene flow occurs between neighbouring populations but not between distant populations. This is most dramatically illustrated by what has been referred to as a *ring species*. Greenish warblers *Phylloscopus trochiloides* are forest-dwelling birds that inhabit mountains surrounding deserts in Asia. In central Siberia, two distinct variants coexist with narrowly overlapping distributions. These forms differ in plumage colour and song. Males of each type do not recognise the song of the other form as a competitor, resulting in reproductive isolation. However, the two forms are connected by a series of populations that exhibit geographic variation in morphological and behavioural traits (Irwin 2000, Irwin *et al*. 2001). Genetic evidence indicates that gene flow occurs between all but the most distant populations in the ring (Irwin *et al*. 2005).

The first element of any speciation model is a source of disruptive selection that favours reproduction among different genetic combinations. Disruptive selection prevents gene flow from homogenising the genomes of two incipient species. For example, local adaptation to spatially varying habitats is a common form of disruptive selection, and frequency-dependent natural selection is another. Behaviour might be involved in mediating these processes, e.g. through habitat choice, although such decisions do not require social interactions and so we will not consider them further. However, disruptive selection can also result from sexual selection if populations diverge in female preferences and male traits. We discuss these possibilities in the following two sections.

The second element is the presence of an isolating mechanism. Alternative possibilities for prezygotic isolation include assortative mating, where mating pairs exhibit similar values of a single trait such as body or bill size, and mating preferences, where members of one sex (usually females) prefer members of the opposite sex that exhibit particular display traits. Kirkpatrick and Ravigne (2002) argue that the mode of speciation can be viewed as a mechanism that either enforces (allopatry), or does not enforce (sympatry) assortative mating. While we agree that this is a useful way to think about model assumptions, it is important to recognise that males and females can differ in mate preferences, which might generate mating asymmetries and patterns of gene flow that differ from that expected under simple allopatry or sympatry.

The third element is a way to connect disruptive selection to the isolating mechanism. This can occur by direct selection, e.g. when assortatively mating parents produce more progeny, or by indirect selection, e.g. when genes that affect the isolating mechanism are associated (by linkage disequilibrium or pleiotropy) with genes that are the target of sexual selection. For example, hybrids that suffer reduced mating success would be a case of indirect selection mediated by sexual selection (Liou & Price 1994, Servedio 2000, 2004). Selection for assortative mating to reduce gamete loss after secondary contact of isolated populations is known as *reinforcement* (Howard 1993, Servedio & Noor 2003, Coyne & Orr 2004).

Direct selection is often more efficient than indirect selection, because the strength of indirect selection depends on the genetic correlation between selection and the prezygotic isolating mechanism (Kirkpatrick & Barton 1997). Genetic correlations would not be expected to be high unless there is very strong selection against hybrids, a situation that would only occur in regions of species overlap, such as in hybrid zones. When genetic linkage in this context is caused by pleiotropy, this is referred to as *genetic coupling* (Hoy *et al*. 1977).

The fourth element involves the type of assumption made about the genetic basis of the isolating mechanism. Felsenstein (1981) first recognised that isolation can occur either when two different alleles spread to fixation in two different populations, or when a single allele goes to fixation in both populations. For example, an allele that causes individuals to mate with others of the same size is a single-allele model, whereas mating preferences for two different male forms represents a two-allele model. Single-allele models require an initial difference between populations, and then function to maintain that difference, whereas two-allele models produce tension between selection and gene flow. For this reason, isolation by a one-allele mechanism may evolve more quickly.

The final element is whether or not populations differ at the outset. Most models of speciation have been developed to describe how either sympatric speciation or reinforcement could occur. In many cases, the outcome depends not only on the genetic and ecological assumptions but also on the initial conditions. The situations that do or do not favour fusion of two genetically distinct populations have, therefore, not yet led to general conclusions, particularly with respect to behaviour.

In the next two sections of the chapter we focus on alternative ways in which reproductive isolation, either before or after mating, could be influenced by social behaviour. The five steps outlined above should be kept in mind, because we will discuss both theory and data that pertain to each of these elements.

19.3 Pre-mating isolation

How species acquire distinctive recognition cues has a history of debate. Patterson (1985) argued that pre-mating reproductive isolation arises as a consequence of the evolution of a specific mate-recognition system that involves cooperative coadaptation between males and females in a population, but rejected the possibility that there might be species-recognition cues. In contrast, Mayr (1942) argued that mating barriers arise between populations after secondary contact as a consequence of reinforcement and are subsequently maintained by stabilising selection for distinctive courtship behaviours (e.g. Kyriacou & Hall 1982, Butlin *et al.* 1985, Gerhardt 1991). If species recognition causes reproductive isolation, then cases of reproductive character displacement should be common, i.e. male mating signals should be similar in allopatry but different in sympatry. In contrast, reproductive character displacement is generally thought to be uncommon (Howard 1993, West-Eberhard 1983), although some notable cases have been found (Noor 1995, Higgie *et al.* 2000, Higgie & Blows 2007). The rarity of reproductive character displacement led West Eberhard (1983) to conclude that most cases of prezygotic reproductive isolation are likely the result of sexual selection, a conclusion that has been endorsed by others (e.g. Ryan & Rand 1993, Panhuis *et al.* 2001). However, the extent to which divergence in mating signals causes, rather than evolves after, reproductive isolation is unclear. Understanding the mechanisms of sexual selection helps to appreciate the reasons for this uncertainty.

19.3.1 Sexual selection

Sexual selection is a potentially powerful diversifying force because non-random mating increases the chance that genes influencing traits and preferences will become associated (Chapter 10). As Lande (1981) and Kirkpatrick (1982) have shown, linkage disequilibrium between genes that influence expression of a male ornament and a female preference for it can give rise to a runaway process, as Fisher (1930) envisioned. In the absence of selection on females, a runaway process ends either in extinction or in a neutral line of equilibrium where sexual selection is balanced by natural selection on males, and therefore any combination of trait or preference can be stable. Theoretically, populations that are displaced off an equilibrium line by a chance event will evolve back to the line, but to a different location dictated by the genetic regression of trait on preference. Thus, episodic fluctuations in population size could cause populations to end up at different locations along the equilibrium line. These populations would then possess distinctive male traits and female preferences and might, therefore, be reproductively isolated (Lande 1981).

While a Fisherian runaway process can generate rapid change in male traits and female preferences, the evolutionary outcome of a neutral line of equilibrium depends on the assumption that selection does not act on females either positively or negatively. If females benefit directly from mating, then preferences should converge to maximise female fecundity (Kirkpatrick & Ryan 1991). The strength of selection on preferences for direct benefits is expected to be stronger than for indirect benefits, i.e. benefits attributable to genes inherited by offspring (Kirkpatrick & Barton 1997). Whether preferences for male genetic quality should give rise to disruptive selection in isolated populations then depends on how genetic variation for quality is maintained. If females choose males based on a random process, such as recurrent deleterious mutations (Pomiankowski *et al.* 1991), then isolated populations would only be expected to diverge by drift. However, if females prefer males that are resistant to pathogens, and pathogen resistance is coevolving with pathogen virulence independently in isolated populations, then trait and preference could be under disruptive selection in isolated populations. Female preference for genetic compatibility could also lead to disruptive selection in isolated populations, particularly if the nature of the compatibility depends on some form of genomic conflict (Haig & Bergstrom 1995, Zeh & Zeh 1996, Tregenza & Wedell 2000), such as meiotic drive (Lande & Wilkinson 1999).

If speciation is driven by sexual selection operating through either a runaway or good-genes process, then the male traits that females prefer within a population should also be the traits that are used for mate recognition between populations. Evidence for this prediction is not easy to find (Arnegard & Kondrashov 2004). A common observation is that female vertebrates exhibit directional preferences, such as best-of-*n* (Janetos 1980), for increased levels of display by males (Ryan & Keddy-Hector 1992, Andersson 1994, Alexander *et al.* 1997). Louder calls, faster displays (Gibson & Bradbury 1985), increased levels of pigmentation (Griffith *et al.* 1999, Hill *et al.* 2002) and greater diversity of syllables in a song repertoire (Searcy 1992, Hasselquist *et al.* 1996) provide a few examples in which females prefer extreme male traits. In all cases, the preferred male trait is condition-dependent, i.e. trait expression varies among males depending on their condition. Condition-dependent trait expression provides a reliable mechanism for advertising genetic quality (Grafen 1990, Rowe & Houle 1996) but not for indicating species identity, because individuals are often phenotypically variable within a population. Not surprisingly, extreme male display traits are rarely used for mate recognition in vertebrates (Ptacek 2000).

There are, however, examples in which sexual selection for mating signals in insects appear to be involved in recent speciation events, perhaps because insects are more likely to rely on threshold mating preferences (Alexander *et al.* 1997). For example, male field crickets of the species *Gryllus texensis* and *G. rubens* exhibit different pulse rates, but are otherwise indistinguishable (Gray & Cade 2000). Females exhibit preferences for conspecific song, and female preference exhibits a significant, although weak, genetic correlation with male song. Character displacement does not occur in sympatric populations, and hybrids are readily produced in the laboratory. Thus, reproductive isolation is plausibly attributed to differences in male advertisement signals, although, as the authors note, conspecific sperm precedence provides an untested competing hypothesis. Similar evidence for speciation as a consequence of sexual selection on male courtship song has also been obtained for *Laupala* crickets (Shaw 1996, Shaw *et al.* 2007), and *Chrysoperla* lacewings (Wells & Henry 1992).

Sexual selection on traits that influence mating success need not always lead to behavioural isolation in insects, particularly in species with multimodal displays. For example, *Drosophila heteroneura* and *D. sylvestris* are two closely related species of picture-winged flies that co-occur on the island of Hawaii, but differ in appearance in that male *D. heteroneura* have broad heads whereas male *D. sylvestris* do not. Female *D. heteroneura* exhibit preferences for broad-headed conspecific males yet do not use head width when discriminating conspecific from reciprocal F_1 males (Boake *et al.* 1997). These results suggest that behavioural isolation between these two species depends on other cues, perhaps olfactory or tactile, that are used earlier in the courtship sequence and may or may not be subject to within-species sexual selection (Price & Boake 1995, Boake 2002). We have reached similar conclusions for diopsid stalk-eyed flies, where females from sexually dimorphic species prefer males with longer eye stalks (Wilkinson *et al.* 1998), but populations that exhibit behavioural isolation (Christianson *et al.* 2005) do not differ in relative head shape (Swallow *et al.* 2005), although they do differ in sperm length and female sperm storage-organ size (E. Rose and G. Wilkinson, unpublished data).

Sexual selection could also cause pre-mating reproductive isolation if male–male interactions generate disruptive selection for alternative mating strategies (Gray & McKinnon 2007), as has been described for side-blotched lizards *Uta stansburiana* (Calsbeek *et al.* 2002) and lazuli buntings *Passerina amoena* (Greene *et al.* 2000). Disruptive selection can also occur when two isolated populations come together to form hybrids that then successfully reproduce to form a new species. This process is best known in plants, such as sunflowers in the genus *Helianthus* (Rieseberg 2006, Rieseberg & Willis 2007), but has also recently been reported in some animals. For example, based on patterns of inheritance of wing colour markings, *Heliconius heurippa* appears to be a hybrid butterfly species that was created by the union of *H. cydno* and *H. melpomene* (Mavarez *et al.* 2006). In this case, sexual selection is not driving speciation, but instead is acting to reinforce speciation, because hybrid butterflies prefer to mate with each other rather than with the parental species. Speciation by hybridisation has also been proposed for the swordtail fish *Xiphophorus clemenciae* and for some African cichlid fishes in the *Haplochromis nyererei* complex (Seehausen 2004, Salzburger *et al.* 2002, Meyer *et al.* 2006).

19.3.2 Sexual conflict

Sexual conflict occurs whenever male and female reproductive opportunities differ (Chapter 10; Parker 1979, 2006). One example occurs when there is a cost to females of mating. If the source of the cost is under female control, then females would be expected to minimise their cost (Kirkpatrick 1996). In contrast, if male displays exploit or manipulate female perceptual responses, then males will be under selection to be more persistent and females will be under selection to resist to the extent that females benefit. This process has long been thought to lead to a sexual arms race within species (Trivers 1972, Dawkins & Krebs 1979, Parker 1979), and more recently has been viewed as a form of antagonistic coevolution that may drive speciation (Rice 1998).

Several lines of evidence have been used to argue that antagonistic coevolution between male and female reproductive traits should facilitate reproductive isolation (Arnqvist &

Rowe 2005). First, models of sexual conflict in which there is a greater cost to females than males of producing hybrids (Parker & Partridge 1998), or in which females exhibit less mate compatibility than do males (Gavrilets 2000, Gavrilets & Waxman 2002), have shown that sexual conflict can lead to an arms race between males and females that results in reproductive isolation both in allopatry and in sympatry. Second, females seem likely to be able to evade male courtship efforts in more ways than they can track male traits, as expected by both runaway and good-genes models of sexual selection. Furthermore, if females exhibit perceptual biases in multiple signal modalities, multiple male display traits should evolve (Johnstone 1995, Andersson *et al*. 2002). In general, sexual conflict is expected to produce a variety of trait-combination outcomes because males and females have divergent interests. In contrast, fewer trait-combination outcomes are likely when males and females have convergent interests.

Despite these reasons to expect sexually antagonistic coevolution to drive speciation, evidence that sexual conflict causes reproductive isolation is equivocal. The strongest support comes from an experimental evolution study of the dung fly *Sepsis cynipsea*, where sexual conflict was created by varying fly density (either 500 or 50 flies/line), and contrasted with lines maintained by pair-mating. After 35 generations in these mating regimes females from both sexual-conflict treatments were less willing to mate males from different than from same lines (Martin & Hosken 2003), indicative of incipient reproductive isolation. However, the analysis of these data has been questioned (Bacigalupe *et al*. 2007). Furthermore, two similar experiments on *Drosophila* failed to detect such an effect. After 41 generations of elevated sexual conflict, no decrease in female mating frequency was observed between replicate lines of *D. melanogaster* (Wigby & Chapman 2006). Similarly, after 50 generations female *D. pseudoobscura* actually mated more frequently with males from different sexual-conflict lines than they did with males from their own selection lines – the opposite of the predicted outcome (Bacigalupe *et al*. 2007). In both *Drosophila* studies female resistance to mating increased within the sexual-conflict lines (Wigby & Chapman 2004, Crudgington *et al*. 2005), indicating that the experimental treatment was effective. While it is possible that sexual conflict in *Drosophila* is mediated more by post-mating than pre-mating effects, given that males pass accessory gland proteins to females during mating and these proteins can influence sperm precedence (Clark *et al*. 1995), female re-mating and oviposition rate (Wolfner 2002), these studies cast significant doubt on the role of sexual conflict in causing rapid evolution of pre-mating sexual isolation in *Drosophila*.

In the wild the best example of sexual conflict potentially influencing speciation occurs in water striders, where male claspers and female structures to resist mating exhibit correlated evolution (Arnqvist & Rowe 2002a, 2002b). Unfortunately, by themselves these results do not reveal if the clasping structures evolved before or after reproductive isolation appeared.

Additional studies of sexual conflict and sexually antagonistic coevolution are clearly warranted, especially with regard to post-mating effects (see below), although it must be recognised that sexual conflict can also act to oppose speciation depending on which sex controls reproduction (Parker 2006). If females control mating and fertilisation, population divergence should persist or increase, and speciation is favoured. However, if males control mating, gene flow should be common and operate against speciation. A detailed understanding of how mating is influenced by male and female behaviour is, therefore, essential to inferring the underlying evolutionary process driving speciation (Rowe & Day 2006).

19.3.3 Cultural transmission and sexual imprinting

The ability to acquire mate-recognition traits, such as song (see Chapter 3), by learning has long been viewed as an important mechanism that can contribute to reproductive isolation in birds (Martens 1996, Price 1998, Edwards *et al.* 2005). Models of speciation involving song learning reveal that the ability of males to copy songs of others in allopatry can accelerate the speciation process (Lachlan & Servedio 2004). The reason for this effect is that males with a disadvantageous genotype for singing a particular type of song are nevertheless able to produce the preferred song type if they can learn. Similarly, females with rare preference alleles will mate with the common song type if they learn which males to mate with. In both cases, the difficulty associated with increasing the frequency of a novel allele in an isolated population by drift or directional sexual selection is lessened. Thus, in the short term learning will decrease phenotypic diversity within populations, but over the long term phenotypic diversity between populations will be increased. Song learning is predicted to hinder speciation when male song traits and female song preferences are inherited independently and females only mate once. The Lachlan–Servedio model assumes that songs are learned from unrelated adults in the population (i.e. transmission is oblique). This assumption is clearly false in some cases: e.g. males learn their songs from their fathers in Darwin's finches *Geospiza* spp. (Grant & Grant 1996). Vertical transmission creates an opportunity for mate recognition signals to be acquired by offspring early in life from their parents, a process referred to as sexual imprinting (ten Cate & Bateson 1988, Weary *et al.* 1993, Owens *et al.* 1999a).

Theoretically, sexual imprinting could involve offspring learning species-recognition signals produced by mothers, fathers or unrelated individuals (Irwin & Price 1999). Models of these alternatives reveal that maternal imprinting, where females copy their mother's mate preferences, is most similar to phenotype matching (Hauber & Sherman 2001). This can lead to traits and preferences becoming associated, which favours speciation. Maternal imprinting occurs in many bird species (Kruijt *et al.* 1982, ten Cate & Vos 1999, Witte *et al.* 2000) as well as some mammal species (Kendrick *et al.* 1998). In contrast, when females imprint on their fathers or obliquely on unrelated individuals, genetic associations between trait and preference are weak and unlikely to cause sufficient assortative mating for reproductive isolation (Laland 1994, Aoki *et al.* 2001, Verzijden *et al.* 2005). Paternal imprinting is expected to differ from maternal imprinting if mating success varies among males, thereby reducing the degree to which assortative mating can occur. Mate-choice copying, such as that reported for guppies *Poecilia reticulata* (Dugatkin & Godin 1992), provides an example of oblique transmission of mating preferences. Guppies exhibit a high degree of variation in male colour patterns, but despite evidence for genetic variation in female preferences (Brooks 2002), that variation has not led to reproductive isolation between populations.

The African indigobirds *Vidua* spp. are brood parasites that exhibit heterospecific sexual imprinting (Payne *et al.* 1998, 2000), and they provide a compelling example of sympatric speciation in birds (Fig. 19.1; Edwards *et al.* 2005). Male indigobirds mimic the songs of their hosts, which include several estrildid finch species in the genus *Lagonosticta*, which they learn as nestlings. Females use those songs to choose their mates and to locate nests to parasitise. These behavioural traits insure that a population of brood parasites remains closely associated with a host species. Furthermore, if a female parasitises the nest of

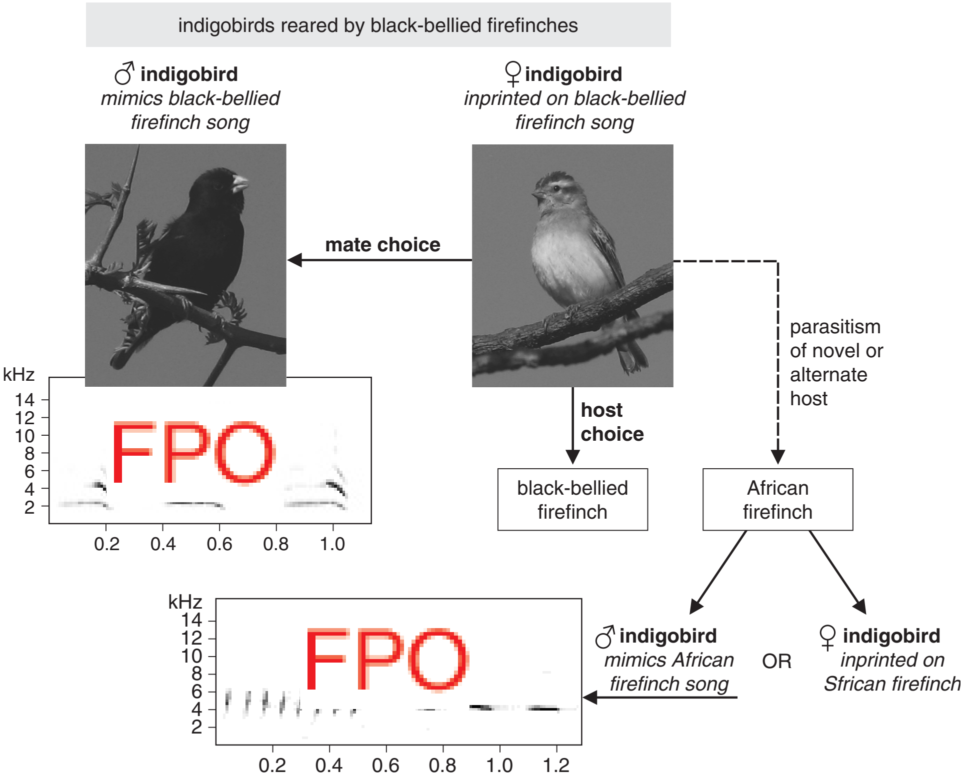

Figure 19.1. Sexual imprinting provides a mechanism for rapid speciation when new hosts are colonised. Male indigobirds mimic the songs of their hosts, whereas females use song cues to choose both their mates and the nests they parasitise (Payne *et al.* 1998, 2000). Rarely, females lay in the nest of a novel or alternate host (i.e. one already associated with another indigobird species). The resulting offspring imprint on the novel host and are therefore reproductively isolated from their parent population (Balakrishnan & Sorenson 2006). Minimal differentiation in neutral genetic markers among the indigobird species within each geographic region support a model of rapid sympatric speciation by host shift (Sorenson *et al.* 2003, Sefc *et al.* 2005)

a different species, her offspring will imprint on the songs produced by males of that species. Thus, host switching potentially results in reproductive isolation. Phylogenetic evidence confirms that indigobirds have speciated much more rapidly than their finch hosts (Sorenson *et al*. 2003). A remarkable aspect of this system is that the brood-parasite chicks mimic the gape patterns of their host species (Payne 2005). Thus, in addition to imprinting, rapid morphological evolution appears to occur among nestling gape patterns of *Vidua* species.

19.4 Prezygotic isolation after mating

The possibility that sexual selection operates after mating on traits that can influence reproductive isolation has been gaining recognition (e.g. Birkhead & Billard 2007). Part of the reason for this recognition is the growing realisation that multiple mating by females is common (Jennions & Petrie 2000), which creates opportunities for postcopulatory sexual selection. In addition, in a growing number of cases the outcome of competition among sperm from heterospecific and conspecific males often favours the conspecific male. The degree to which females mate with more than one male provides, therefore, another way in which behaviour can influence speciation.

Recently, Coyne and Orr (2004) distinguished two types of post-mating, prezygotic barriers: competitive and non-competitive fertilisation barriers. Non-competitive barriers involve factors that cause heterospecific gametes to fail to fertilise ova (see Coyne & Orr 2004 for review). Competitive barriers refer to mechanisms by which conspecific gametes outcompete heterospecific gametes in fertilisation contests. This process is referred to as conspecific sperm precedence, and it has been reported in a variety of animals (Katakura 1986, Hewitt *et al*. 1989, Bella *et al*. 1992, Wade *et al*. 1994, Price 1997, Howard 1999, Dixon *et al*. 2003, Geyer & Palumbi 2005, Ludlow & Magurran 2006, Mendelson *et al*. 2007, Rugman-Jones & Eady 2007). The appearance of conspecific sperm precedence among isolated populations (Fig. 19.2) or incipient species (e.g. Chang 2004) suggests that it can evolve rapidly and could create one of the first barriers to fertilisation (Howard 1999, Coyne & Orr 2004).

The mechanisms responsible for conspecific sperm precedence are not yet well understood in any species, but almost certainly result from postcopulatory sexual selection operating by sperm competition or gamete choice. Gamete choice by females, often referred to as cryptic female choice (Eberhard 1996), involves situations in which there is differential selection by the female reproductive tract or egg for specific types of sperm. Because postcopulatory contests between males occur among ejaculates within females, female behaviour, morphology, and physiology, as well as the number and type of sperm produced by each male, can influence male success in these contests (reviewed in Eberhard 1996).

When females re-mate, sperm are under selection to avoid competition and outcompete other sperm (Parker 1970). If there is variation among populations in female reproductive traits or in the types of sperm strategies used by males, the evolutionary trajectories of

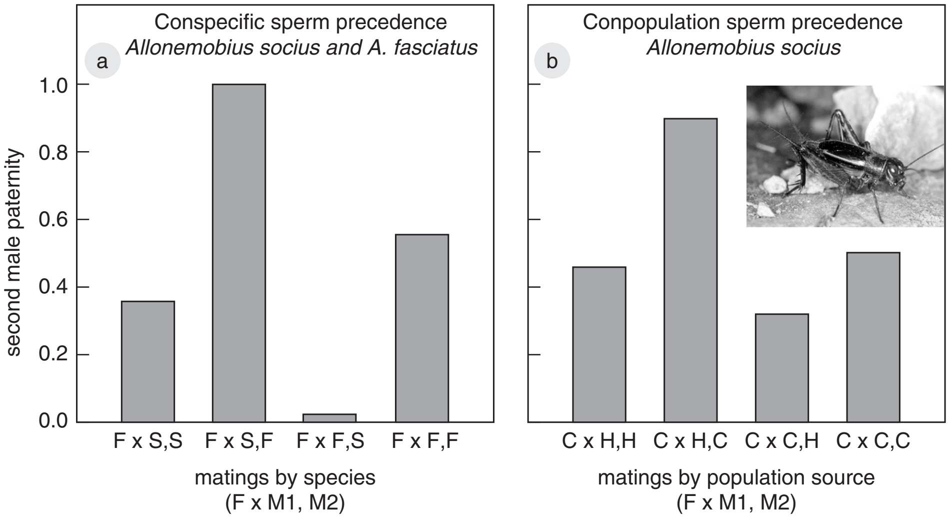

Figure 19.2. Sperm precedence between incipient species provides a mechanism for post-mating, prezygotic reproductive isolation. (a) Reciprocal crosses between allopatric populations of striped ground crickets *Allonemobius socius* (S) and *A. fasciatus* (F) reveals that conspecific males have a fertilisation advantage over heterospecific males (Gregory & Howard 1994). This graph shows the proportion of offspring sired by the second male. Treatments are labelled according to the species of the female followed by the species of the first and second male. (b) In similar reciprocal crosses between allopatric populations, *A. socius* exhibits conpopulation sperm precedence (L. Birge, unpublished data). Treatment labels indicate female population of origin (conpopulation (C) or heteropopulation (H)) followed by source of each male. Thus, fertilisation barriers at the population and species level maintain reproductive isolation. Mating does not appear to be costly in this system, as female fecundity increases with mating opportunities in *A. socius* as a consequence of female consumption of male haemolymph (Fedorka & Mousseau 2002).

male traits may follow different directions in different populations (e.g. Pitnick *et al*. 2003). Moreover, because of the variety of strategies that may evolve, males that are successful in one population may not be successful in another (Attia & Tregenza 2004, Chang 2004, Dixon *et al*. 2003). Thus, sperm competition can result in reproductive barriers between populations that act after copulation but before fertilisation.

If, as seems likely, the female reproductive system influences which sperm succeed at fertilisation, postcopulatory sexual selection can operate in different ways depending on whether copulation has positive, negative or neutral effects on females. Positive effects often occur in systems where there is nuptial feeding, i.e. the male passes nutrients to females during mating (although see Sakaluk *et al*. 2006). In contrast, negative fitness effects lead to sexual conflict, which, as noted above, have been argued to provide an explanation for why populations may diverge in postcopulatory traits. In situations where the act of mating has little or no fitness consequences for females, selection could act directly on the type of sperm chosen. We consider these options below as possible explanations for the patterns of conspecific sperm precedence that have been observed.

19.4.1 Sexual conflict after mating

Finding evidence that antagonistic coevolution operates on postcopulatory traits has proven difficult, because early in the process of divergence it is unclear which males will have a fertilisation advantage (Chapman *et al*. 2003, Rowe *et al*. 2003). One possibility is that males from a different population (heteropopulation) have an advantage because females are not adapted to resist them. This outcome should retard speciation, because gene flow is enhanced. For example, in the house fly *Musca domestica* (Andres & Arnqvist 2001) female oviposition rates are highest when they are mated to heteropopulation males, and in the yellow dung fly *Scathophaga stercoraria* (Hosken *et al*. 2002) females preferentially mate with heteropopulation males.

Alternatively, males from the same population as females (conpopulation males) may have an advantage because they are better adapted to female defences. Such conpopulation sperm precedence reduces gene flow and should drive speciation. For example, reciprocal crosses between populations of the bean weevil *Callosobruchus maculatus* reveal that conpopulation males induce longer refractory periods in females than heteropopulation males (Brown & Eady 2001). Futhermore, conspecific males have a fertilisation advantage when *C. subinnotatus* females are mated to both conspecific and *C. maculatus* males (Rugman-Jones & Eady 2007). Similarly, conpopulation male guppies have a fertilisation advantage over heteropopulation males when females are inseminated with a mixture of sperm obtained from males captured in allopatric river systems (Ludlow & Magurran 2006).

The degree to which the preceding examples provide evidence for sexually antagonistic coevolution can be debated, because in most cases the fitness costs to females of mating are not known. Comparative studies have also yielded conflicting evidence regarding sexual conflict and speciation. For example, the rate of speciation was higher in insects where females mate multiple times as compared to related taxa where single mating occurs, as expected if sexual conflict has driven speciation (Arnqvist *et al*. 2000). However, subsequent studies using different methods and larger samples of other insects and spiders (Gage *et al*. 2002, Eberhard 2004) have failed to find evidence indicating that sexual conflict influences speciation.

19.4.2 Sexually selected sperm

Sexual selection has been hypothesised to operate on sperm in ways analogous to how it operates on males. In the sexy-sperm hypothesis multiple mating by females creates a situation in which eggs are fertilised by the most competitive sperm and sperm competitive ability is inherited by sons (Sivinski 1984, Curtsinger 1991, Keller & Reeve 1995, Simmons & Kotiaho 2007). This process could also operate on accessory gland proteins if better fertilisers produce more competitive accessory gland proteins (Cordero 1995, Eberhard & Cordero 1995). The sexy-sperm hypothesis predicts that fertilisation success varies among males and is paternally heritable (Pizzari & Birkhead 2002, Simmons 2003). Furthermore, female genotype is not expected to influence which male genotypes will be superior fertilisers (Birkhead & Billard 2007). For this process to influence speciation, conpopulation males would be expected to have an advantage over heterospecific males because their sperm are better adapted to female reproductive tracts.

In the good-sperm hypothesis multiple mating by females ensures that ova are fertilised by males of superior genetic quality. This hypothesis predicts that fertilisation success should correlate with offspring genetic quality (Harvey & May 1989, Simmons & Kotiaho 2007, Birkhead & Billard 2007). For example, yellow dung fly males that were superior at sperm competition produced offspring with faster development time independent of female genotype (Hosken *et al*. 2003). For this process to influence speciation, sperm from conpopulation males would also be expected to have an advantage over sperm from heterospecific males, but it should in addition produce better offspring.

The overall importance of the sexy-sperm and good-sperm hypotheses for explaining cases of postcopulatory, prezygotic reproductive isolation is currently unknown (see Birkhead & Billard 2007). Nevertheless, the possibility that competitive barriers to fertilisation evolve rapidly and influence speciation (Civetta & Singh 1998, Panhuis *et al*. 2006) continues to motivate research in this area. From the perspective of social behaviour, if postcopulatory reproductive isolation is important, then females should re-mate more often in areas of sympatry, where the possibility of producing hybrid offspring exists, than in areas of allopatry. To our knowledge, this prediction has yet to be tested.

19.5 Genetic basis of prezygotic barriers

In an influential series of papers, Coyne and Orr (1989, 1997, 1998) summarised a large number of studies in which the degree of prezygotic or postzygotic isolation varies as a function of genetic distance (as measured by allozymes) among species pairs of *Drosophila*. They found several notable patterns. In particular, prezygotic isolation typically evolves faster than postzygotic isolation. Furthermore, prezygotic isolation evolves faster among sympatric taxa than among allopatric taxa (Fig. 19.3), as expected if there has been reinforcement. Despite this evidence for the importance of behavioural traits in rapid speciation, the vast majority of genetic studies of speciation have focused on postzygotic effects, e.g. hybrid sterility and inviability, predominantly in *Drosophila* (Coyne & Orr 2004, Orr *et al*. 2007), and a few in other animals, such as house mice *Mus musculus* (Payseur & Place 2007) and marine copepods (Burton *et al*. 2006). In comparison, relatively little is known about the genetic basis of traits involved in pre-mating isolation. Below, we discuss some of the reasons for this discrepancy, describe a few exceptions to this claim, and then summarise new methods that should make it possible to greatly expand this list in the near future.

Identifying genes that are important for sexual isolation is challenging for several reasons. First, once populations become isolated, they will begin diverging at many loci across the genome. The rate of divergence at each locus depends on selection, recombination and population size (which might vary within the genome, e.g. autosomes vs. sex chromosomes vs. cytoplasmic factors), so determining which changes have behavioural consequences is critical and determining the order in which changes have occurred is

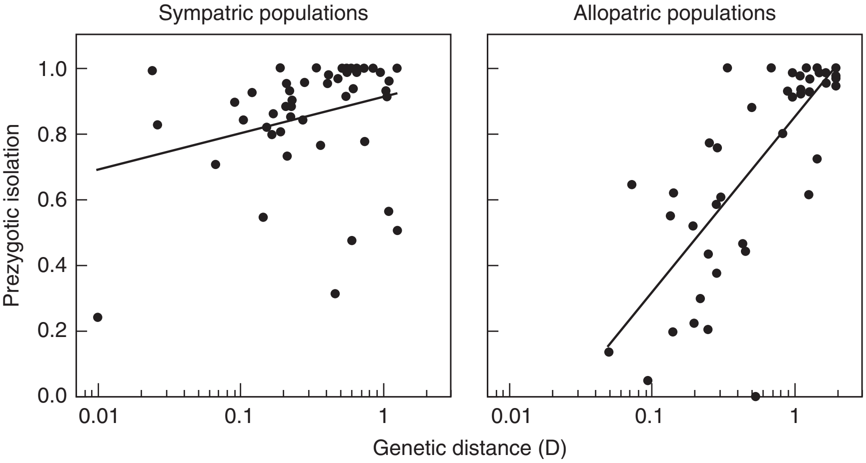

Figure 19.3. Prezygotic isolation, as measured by the ability of males to transfer sperm, evolves more rapidly among closely related, as measured by Nei's genetic distance, species of *Drosophila* that have sympatric rather than allopatric distributions. Each point represents a pair of species. See Coyne & Orr (1989, 1997, 1998) for details.

difficult. Furthermore, estimates of the number of genetic factors involved in isolating any particular pair of species (e.g. Coyne & Orr 1998) could be due either to differences in divergence times or to differences in selection and recombination, or both.

A second issue relates to how species recognition occurs. For example, two species may differ in aspects of courtship song, e.g. *Drosophila heteroneura* and *D. sylvestris* (Boake & Poulsen 1997), but if song only occurs after mate attraction by a pheromone, then genes that influence song variation may be unimportant for sexual isolation. Thus, it is critical that the signal that is involved in mate recognition is identified for study.

Finally, understanding the genetic basis of pre-mating isolation potentially involves studying the genetic basis of mate-recognition signals that are produced by either or both sexes as well as the preference exhibited by each sex for conspecific versus heterospecific signals. Simple experiments that do not attempt to separate signal production from reception can be used to determine the presence of sexual isolation, but typically cannot be used to identify the genetic basis of the traits that are evolving. One exception to this assertion would be when there is a one-allele mechanism of sexual isolation (e.g. Ortiz-Barrientos & Noor 2005).

When there are divergent recognition signals and corresponding preferences, a critical question is how genes for divergent traits and divergent preferences become and remain associated. Two genetic alternatives are possible. One scenario is that the gene influencing the species-recognition signal has pleiotropic effects on the preference for that signal, i.e. there is *genetic coupling* of trait and preference (Hoy *et al.* 1977). The alternative is that genes for the recognition signal and preference are independent, and allelic associations at these loci are maintained by selection.

Whereas the genetic-coupling hypothesis has long been viewed with scepticism (Butlin & Ritchie 1989, Boake 1991, Simmons *et al.* 2001, Simmons 2004), several recent studies provide intriguing evidence consistent with either coupling or close physical linkage of genes that influence a recognition cue and mate preference. The neotropical butterflies *Heliconius cydno* and *H. pachinius* differ in forewing band colour. Recent fine-scale genetic mapping experiments reveal that the genes for forewing colour and for male preference for that colour both map to a small region on an autosome that contains the gene *wingless* (Fig. 19.4; Kronforst *et al.* 2006a). The authors propose that this gene simultaneously influences wing colour and mate preference by influencing the production of pigments that are found in both wing scales and ommatidia. This scenario provides, therefore, a mechanism by which selection on either wing coloration or on preference for wing coloration would drive the other character. Correlated evolution of this type would facilitate the evolution of the remarkable mimicry complexes that are exhibited by *Heliconius* butterflies (Kronforst *et al.* 2006b, 2007). In *D. melanogaster* a mutation in the *desaturase 1* gene influences both signal production and discrimination, apparently as a consequence of pleiotropic effects of this gene (Marcillac *et al.* 2008). Finally, genetic linkage between mate-recognition signals and preferences has recently been reported for pied flycatchers *Ficedula hypoleuca* (Saether *et al.* 2007).

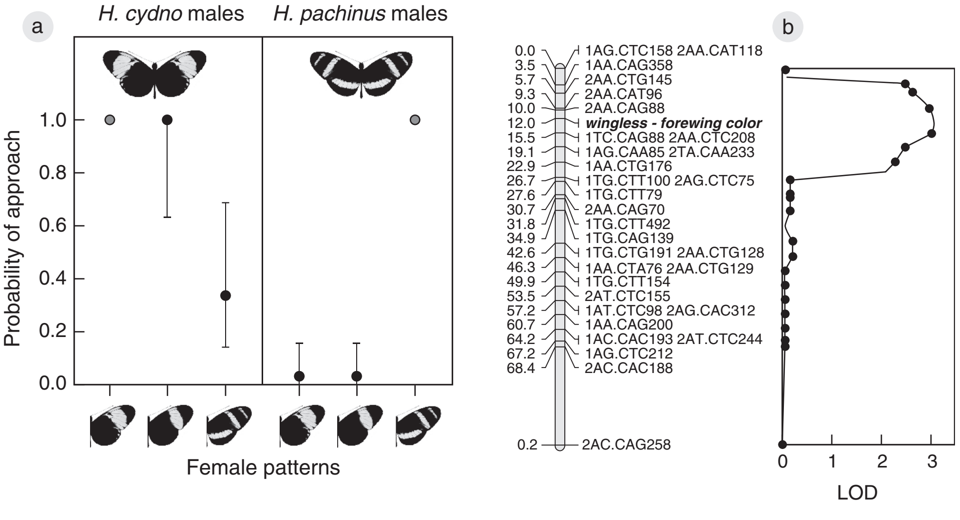

Figure 19.4. Mate preference and mate-recognition cue map to the same genetic region in *Heliconius* butterflies (Kronforst *et al.* 2006b), which provides evidence in support of the genetic-coupling hypothesis. (a) *Heliconius cydno* and *H. pachinus* males recognise conspecific females based on wing colour. This graph shows the probability that a male of each species will approach female wings with either parental or F_1 hybrid colour patterns. (b) Composite interval mapping indicates that male mate preference maps to a small autosomal region that includes *wingless*, a gene that is involved in controlling forewing colour in these butterflies.

The alternative to genetic coupling is that independent loci influence mate recognition signals and preferences. Most evidence from *Drosophila* (Coyne & Orr 1998), particularly that from recently diverged species, is consistent with this view. For example, by testing flies that resulted from backcrosses to either of two parental species, *D. santomea* or *D. yakuba*, Moehring *et al*. (2006) found that the QTL associated with male copulation occurrence or latency were different than those for females, which suggests that the two sexes use different cues for mating and that at least a few genes are important for species discrimination. Similar results have been reported for *D. simulans* and *D. sechellia*, which differ in cuticular hydrocarbons that are used by females for mate recognition (Gleason *et al*. 2005).

With the availability of relatively inexpensive genetic markers, such as amplified fragment length polymorphisms (Mueller & Wolfenbarger 1999), it is now possible to scan the genome of any organism to locate regions potentially important for speciation. Several methods have been proposed (Noor & Feder 2006) and more will likely follow. One approach uses variation in F_{st} at multiple loci to indicate regions of the genome that are adapted to different locations (Beaumont 2005), and is based on the premise that genomic regions near a polymorphic site under positive or negative selection will show deviations from random segregation due to hitchhiking (Maynard Smith & Haigh 1974). Genome scans are attractive because variation in population history can be controlled, and they can be applied without phenotype information because they rely on identifying parts of the genome that exhibit non-random segregation (Vasemagi & Primmer 2005).

An alternative approach for locating genomic regions involved in reproductive isolation is to perform admixture mapping. In effect, this is a form of QTL mapping in which a variety of backcross and other intercrosses are taken from a hybrid zone and used for the mapping population. Genomic heterogeneity among hybrid individuals then reveals regions undergoing strong selection, particularly when compared to populations in allopatry. In the larch bud moth *Zeiraphera improbana*, such analyses have revealed evidence of selection in hybrid populations (Emelianov *et al*. 2004). In those species where microarray technology is available (e.g. Gresham *et al*. 2006), precise localisation of genomic regions involved in reproductive isolation is now possible, as has been demonstrated for races of the mosquito *Anopheles gambiae* (Turner *et al*. 2005).

Association studies (also referred to as linkage disequilibrium mapping) test if a certain genotype (or multilocus haplotype) is associated more frequently with a phenotypic trait than expected by chance using the non-random occurrence of alleles at linked loci, i.e. linkage disequilibrium (LD). The extent of LD depends on many biological and demographic factors, including recombination rate, population history, selection and mating system. As a result, the extent of linkage disequilibrium varies across species, populations and genomic regions (Jorde 2000). Thus, high LD in an organism allows for genome scans with relatively few evenly spaced markers, but fine-scale mapping will be very difficult. In contrast, low LD means that the hitchhiking regions will be small and genomic scans will require many markers to be informative. A hybrid approach is to survey markers near candidate genes for association. One method partitions a haplotype tree into two or more clades, and then estimates the phenotypic association related to the specific substitution(s) in the tree (Templeton *et al.* 2005). Analyses that incorporate an evolutionary framework should be especially useful for candidate gene association studies of behaviour in non-model organisms.

19.6 Social behaviour and speciation rate

Several hypotheses have been proposed to link variation in social behaviour to the likelihood that new species will evolve (see also Chapter 5). In an influential paper, Bush *et al.* (1977) proposed that speciation rate in vertebrates varies with social organisation. The basis of their argument was that species with harem mating systems, particularly mammals such as horses and primates, are likely to have smaller effective population sizes, which allows chromosomal rearrangements to go to fixation more quickly. In support of this idea the authors reported a correlation between the rate of karyotypic change (due to change in chromosome or arm number) and the rate of speciation as measured by estimates of the number of extant and extinct species per lineage among orders of mammals and other vertebrate groups. Bush *et al.* (1977) suggested that this correlation could result either from *stasipatric* speciation (White 1968), where a chromosomal rearrangement goes to fixation in an isolated population and then forms a post-mating reproductive isolating mechanism, or from creation of a coadapted gene complex that resists recombination.

The social organisation/speciation hypothesis motivated a considerable amount of research on the amount of standing genetic variation in populations of different species. An extensive review of that literature indicates that while considerable variation in genetic structure exists among species of social mammals, the amount of gene flow that is typically present in most taxa is more than enough to cast doubt on the drift-induced speciation idea (Storz 1999). Higher rates of karyotypic change and speciation in mammals, as compared to ectothermic vertebrates, has more recently been attributed to differences in genome organisation (Bernardi 1993, Bernardi *et al.* 1997). Correlations between chromosomal change and species diversity have also been reported for some lizards and snakes (Olmo 2005), casting further doubt on any role for social organisation in speciation. The role of chromosomal rearrangements in speciation has, however, experienced a resurgence of interest.

Recent theory (Kirkpatrick & Barton 2006) reveals that new inversions, which capture locally adapted alleles, can increase in frequency under a variety of conditions. Such inversions can then contribute to reproductive isolation via postzygotic isolation (Navarro & Barton 2003, Noor *et al.* 2001), or by prezygotic isolation when the inversions contain loci that affect pre-mating behaviours. High rates of chromosomal rearrangement have recently been associated with rapid speciation in lycaenid butterflies, murid rodents and gerbils (Pialek *et al.* 2001, Dobigny *et al.* 2002, Veyrunes *et al.* 2006, Kandul *et al.* 2007). The extent to which social behaviour contributes to any of these cases remains to be determined.

A very different hypothesis for how social behaviour affects speciation rate has recently been proposed for birds. In a large phylogenetic analysis of parental care in birds, Cockburn (2003) found that cooperative breeding is often the ancestral trait (see also Ekman & Ericson 2006), and predominantly cooperative genera are species-poor compared to their pair-breeding counterparts. Cooperatively breeding species tend to be sedentary residents, while pair-breeding species are more likely to be migratory and inhabit oceanic islands. In support of these results, high annual dispersal has recently been identified as the best predictor of phylogenetic diversification in birds (Phillimore *et al.* 2006). Sociality does not appear to accelerate speciation in other taxa, either. Social carnivores have higher extinction rates than solitary carnivores (Munoz-Duran 2002), and social insects, including termites, ants, eusocial bees and eusocial wasps, tend to have higher rates of outbreeding and slower rates of evolution than vertebrates (Wilson 1992). Thus, rather than accelerate speciation, sociality may constrain speciation.

As noted previously, the most commonly invoked behavioural cause for high rates of speciation is sexual selection (Dominey 1984, Ringo 1997, Price 1998, Edwards *et al.* 2005). While several comparative analyses of birds using degree of sexual dimorphism (Barraclough *et al.* 1995, Barraclough *et al.* 1998, Møller & Cuervo 1998, Owens *et al.* 1999b) or mating system (Mitra *et al.* 1996) to predict species richness have supported this claim, more recent studies using sexual size dimorphism, sexual dichromatism, or relative testis size and improved methods have failed to find any relationship to taxonomic diversity in birds, mammals or fishes (Gage *et al.* 2002, Morrow *et al.* 2003, Ritchie *et al.* 2005). One possible reason for failing to detect such a correlation is that sexual selection may also accelerate extinction rates (Morrow & Pitcher 2003). Resolution of this issue likely will require focused studies on groups of organisms where traits that are known to influence reproductive isolation can be measured and their evolutionary rates compared (e.g. Mendelson & Shaw 2005).

19.7 Conclusions and future directions

The process of speciation is arguably one of the most active areas of research in evolutionary biology. Considerable interest focuses on understanding how sexual selection, acting both before and after mating, may either accelerate or retard the speciation process. In addition, unravelling the temporal sequence of events that has led to divergence in traits that affect fertilisation success is critical for identifying the factors that cause, rather than correlate with, reproductive isolation. Despite intense interest in this topic, clear examples of sexual selection driving speciation are not widespread. One of the most dramatic examples of rapid speciation in birds involves sexual imprinting. This observation suggests that more study of cases where cultural transmission is involved in mate recognition is warranted.

A related challenge remains to assess the general importance of sexual conflict in driving speciation. While studies from a variety of taxa suggest that rapid amino-acid sequence divergence of sex-related proteins is likely caused by sexually antagonistic coevolution, the relationship between such protein change and reproductive isolation remains poorly understood in most taxa. Given that sexual conflict also has the potential to increase gene flow and oppose speciation whenever males control mating decisions, resolution of this issue will depend critically on understanding how mating is influenced by male and female behaviour.

The development of new and increasingly less expensive technologies for identifying genetic variants on a genome-wide scale can be predicted to advance understanding of the genetic basis of prezygotic reproductive isolation in a variety of organisms. Because most genetic studies of speciation to date have focused on postzygotic isolation in *Drosophila*, at this point it is difficult to know if general patterns will be uncovered. Certainly, additional fine-scale genetic mapping experiments should reveal if recognition cues and mate preferences share a common genetic basis or exhibit close genetic linkage in butterflies or any other taxa. Perhaps more interesting, though, will be genome scans that reveal previously uncharacterised regions that have undergone recent divergence. Such discovery-based study has the potential to identify new candidate genes whose role in speciation and possibly mate recognition can then be explored through experimental and association studies. By studying groups of closely related species, the temporal sequence of genetic events that have resulted in reproductive isolation can also be deduced. While such insights undoubtedly will require effort, revealing the origin of species has never been more attainable.

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