

# The role of mating preferences in shaping interspecific divergence in mating signals in vertebrates

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## Abstract

Vertebrates represent one of the best-studied groups in terms of the role that mating preferences have played in the evolution of exaggerated secondary sexual characters and mating behaviours within species. Vertebrate species however, also exhibit enormous interspecific diversity in features of mating signals that has potentially led to reproductive isolation and speciation in many groups. The role that sexual selection has played in interspecific divergence in mating signals has been less fully explored. This review summarizes our current knowledge of how mating preferences within species have shaped interspecific divergence in mate recognition signals among the major vertebrate groups. Certain signal modalities appear to characterize mating signal diversification among different vertebrate taxa. Acoustic signals play an important role in mating decisions in anuran amphibians and birds. Here, different properties of the signal may convey information regarding individual, neighbor and species recognition. Mating preferences for particular features of the acoustic signal have led to interspecific divergence in calls and songs. Divergence in morphological traits such as colouration or ornamentation appears to be important in interspecific diversity in certain groups of fishes and birds. Pheromonal signals serve as the primary basis for species-specific mating cues in many salamander species, most mammals and even some fishes. The evolution of interspecific divergence in elaborate courtship displays may have played an important role in speciation of lizards, and particular groups of fishes, salamanders, birds and mammals. While much research has focused on the importance of mating preferences in shaping the evolution of these types of mating signals within species, the link between intraspecific preferences and interspecific divergence and speciation remains to be more fully tested. Future studies should focus on identifying how variation in mating preferences within a species shapes interspecific diversity in features of mating signals in order to better understand how sexual selection may have led to speciation in vertebrates. © 2000 Published by Elsevier Science B.V. All rights reserved.

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## 1. Introduction

One of the critical components to understanding the process of speciation is determining which

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factors promote and maintain divergence in mate recognition systems. For species where mate recognition occurs primarily through non-behavioural mechanisms, such as in broadcast-spawning marine invertebrates (reviewed in Palumbi, 1994), selection favors gamete compatibility signals designed to avoid wasted matings between heterospecific gametes. The species-specific recognition between sperm binding or lysin proteins and conspecific egg membranes is a good example of such a mating signal (Minor et al., 1989; Vacquier et al., 1990; Glabe and Clark, 1991; Lee et al., 1995; Swanson and Vacquier, 1995; Metz and Palumbi, 1996). In species with this type of mating system, species recognition signals evolve primarily as a result of intrasexual selection (sperm competition) for gamete recognition and possibly natural selection against hybrid offspring that result from heterogametic pairings (Palumbi, 1994). However, in species where mate recognition occurs primarily through premating courtship signals, mating preferences in one sex (female mate choice) can strongly influence the evolution of mating signals in the opposite sex, resulting in intersexual selection promoting divergence in mate recognition signals.

Evolutionary biologists have long been interested in how female mating preferences shape the evolution of male mating signals (Andersson, 1994). Studies however, have often focused either on the evolution of signal properties that serve as species isolating cues (species recognition) or properties of mating signals that indicate male quality within a species (intersexual selection) (Ryan and Rand, 1993a and citations therein). Few studies have focused on the interrelation between sexual selection and species recognition (but see Wiernasz, 1989; Wiernasz and Kingsolver, 1992; Boake et al., 1997). The traditional view of mating signal evolution suggests that certain features of the mating signal serve for species recognition; stabilizing selection decreases variance in these properties making them reliable species indicators (Waage, 1975; Kyriacou and Hall, 1982; Claridge et al., 1984; Butlin et al., 1985; Gerhardt, 1991; Barlow and Siri, 1997). Females use a different set of components of the mating signal when making intraspecific mating

decisions and strong directional selection often shapes the evolution of these properties (Møller, 1988; Andersson, 1989; Zuk et al., 1990; Reynolds and Gross, 1992; Ryan and Keddy-Hector, 1992; Thompson et al., 1997). While this distinction in how selection shapes the evolution of different properties of a mating signal may be true for many multivariate signals (Pfennig, 1998), it implies that mate choice operates as a two step process. In the first step, a decision is made about species identity and the second step then involves a decision about mate quality. This distinction between interspecific mate recognition and intraspecific mate recognition however, is not likely to be a realistic process when females assess a potential mate. A more realistic view of mate choice argues that female mating preferences evolve as a direct consequence of selection of the 'best' mate among the available choices. Certainly, being a conspecific is one important aspect of being the best mate, but the process of mate choice is the same at all levels of discrimination (both intraspecific and interspecific) and thus, species recognition is a consequence of finding the best mate (Littlejohn, 1999). In this context, divergence in species recognition properties of mating signals may merely be an epi-phenomenon of intraspecific sexual selection (Gerhardt, 1982).

This continuum between sexual selection and species recognition is becoming the focus of more recent studies (Wiernasz and Kingsolver, 1992; Boake et al., 1997; Ptacek, 1998; Verrell, 1999). A number of authors have argued that sexual selection and species recognition are both essentially problems in animal communication (Verrell, 1988; Ryan and Rand, 1993a; Endler and Houde, 1995; Boake et al., 1997; Littlejohn, 1999). This implies that the same forces of evolution that influence signal properties used in species recognition also influence features of the signal that make the signaler a more attractive mate and that these signal features are not mutually exclusive. Thus mating preferences for certain features of a mating signal can promote divergence at both the intra- and interspecific levels. Divergence in mate recognition signals among populations within a species can lead ultimately to reproductive isolation and speciation (Lande, 1981; Thornhill and Alcock, 1983; West-Eberhard, 1983, 1984;

Kaneshiro and Boake, 1987; Iwasa and Pomiankowski, 1995; Payne and Krakauer, 1997).

In order to demonstrate a link between mating preferences and species recognition, studies must ask whether the same male traits that are preferred by females within a species also function to distinguish conspecific from heterospecific males (i.e. traits that confer high mating success also confer a high degree of sexual incompatibility). Only a few studies have directly tested this hypothesis (Wiernasz, 1989; Wiernasz and Kingsolver, 1992; Boake et al., 1997). Wiernasz (1989) demonstrated in *Pieris* butterflies that females of *P. occidentalis* use the same male character, dorsal forewing melanin pattern, to discriminate between potential conspecific mates and between conspecific and heterospecific males. In contrast, Boake et al. (1997) found that females of the stalk-eyed fly *Drosophila heteroneura* preferred males with broader heads, but did not use this trait when distinguishing between conspecific males and males of *D. silvestris*.

Mating signals are often complex traits where different components of the signal provide information to the receiver concerning species identity, gender, readiness to mate, individual identity and even mate quality (e.g. Crapon de Caprona and Ryan, 1990; Barlow, 1992; Rand et al., 1992; Gerhardt, 1994a; McLennan and Ryan, 1997, 1999). Determining the message and meaning of a mating signal and how mating preferences have shaped various components of the signal is necessary for us to better understand the relationship between intra- and interspecific mate choice.

In this review I explore how intraspecific mating preferences have shaped interspecific divergence in properties of mating signals in major groups of vertebrate taxa. While a number of studies have focused on mating preferences within species or on how mating signals function in species recognition (recently reviewed by Andersson, 1994), fewer have explored the role of mating preferences in the simultaneous divergence of both intra- and interspecific signal properties. First, I outline studies in different vertebrate groups that have focused on how mating preferences have shaped the evolution of interspecific divergence in mating signals. These include stud-

ies that have examined mating preferences for traits that reduce the possibility of heterospecific matings and studies in which traits that are the basis of mating preferences within species also function as species recognition signals. Second, I discuss how geographic variation in mating preferences among conspecific populations can potentially shape divergence of mate recognition signals and the potential role of such mating preferences in leading to speciation. I illustrate this point with a specific example from my own work on the poeciliid fishes commonly known as mollies.

## 2. Fishes

Teleost fishes represent one of the most species-rich vertebrate taxa, yet studies of mating preferences have concentrated on only a few groups (poeciliids: Crapon de Caprona and Ryan, 1990; Endler and Houde, 1995; Magurran et al., 1996; Warburton and Lees, 1996; McLennan and Ryan, 1997, 1999; Ptacek, 1998, cichlids: Barlow et al., 1990; Barlow and Siri, 1997; Karino, 1997; Seehausen et al., 1997a; Seehausen and van Alphen, 1998; Seehausen et al., 1999; hamlets: Fischer, 1980; Domeier, 1994; sticklebacks: Baube et al., 1995; Ziuganov, 1995; McLennan, 1996; Rundle and Schluter, 1998, butterflyfishes: McMillan et al., 1999, pupfishes: Strecker and Kodric-Brown, 1999 and mormyrid electric fishes: Kramer and Kuhn, 1994). While female mate choice can be based on a single property of the mating signal (Rosenthal et al., 1996; Kramer and Kuhn, 1994; Seehausen et al., 1997a; Seehausen and van Alphen, 1998), in most species of fishes mating preferences are based on a multivariate suite of cues. Such cues include courtship behaviours, morphological ornaments, colouration and even pheromonal signals (e.g. Crapon de Caprona and Ryan, 1990; McLennan and Ryan, 1997; Ptacek and Travis, 1997; McLennan and Ryan, 1999; Ptacek, 1998; Strecker and Kodric-Brown, 1999).

An important role of colouration in mating signal divergence among closely related species has recently been documented for haplochromine cichlids in Lake Victoria, Africa (Seehausen et al., 1997a, 1999; Seehausen and van Alphen, 1998).

This species flock of fishes is one of the best known examples of explosive speciation and until recently, at least 500 species of haplochromine cichlids were found in Lake Victoria (Greenwood, 1974; Seehausen, 1996; Seehausen et al., 1997b). Within this group of fishes, there is enormous interspecific diversity in male colouration. Female mating preferences based on male colours may explain the great diversity of male colouration as well as the explosive speciation of haplochromine cichlids (Seehausen et al., 1999). Seehausen and colleagues (Seehausen and van Alphen, 1998) performed a series of elegant female choice studies designed to explore how female mating preferences for male colouration might lead to assortative mating in these fishes. The female choice trials concentrated on two species of haplochromines where males of one species (*Haplochromis nyererei*) are predominantly red in colouration and males of the other species (undescribed *H. 'zebra nyererei'*) are blue. Females of each species showed strong mating preferences for conspecific males under white light where colour differences between the paired object males were apparent. However, when females viewed males under monochromatic light, where interspecific differences in colouration were masked, female preferences for colour were abolished and females chose non-assortatively. Results of these trials provide strong evidence that colour itself, rather than correlated characters, provides the basis for species recognition in these fishes (Seehausen and van Alphen, 1998). Seehausen et al. (1997a) conclude that the increased turbidity caused by recent eutrophication of Lake Victoria is responsible for the breakdown in reproductive isolation between closely related *Haplochromine* species whose males differ primarily in colour.

In butterflyfishes (Chaetodontidae), colour pattern evolves rapidly and is often the only morphological trait that separates closely related species (Blum, 1988). While it has been assumed that differences in colour patterns enhance species recognition in coral reef fishes (Lorenz, 1962) few direct experimental tests of this hypothesis have been conducted. McMillan et al. (1999) recently explored the association between colour pattern evolution and assortative mating in three species of butterflyfish, *Chaetodon multicinctus*, *C. pelewensis*, and *C. punctatofasciatus*.

Results of mating trials with females of all three species showed that colour pattern change and species recognition were only coupled in one species, *C. multicinctus*, while females of the other two species did not show species-specific preferences based on male colouration. These results suggest that colour pattern differences have more likely evolved in response to natural selection pressures or intrasexual selection as a result of competition within each sex for acquisition of territories. Female mating preferences for male colouration patterns are unlikely to explain species differences in at least these three taxa of butterflyfish. These results are in contrast with other coral reef fish species where mating preferences based on species-specific colour patterns have been proposed to lead to reproductive isolation among closely related species (hamlets, Fischer, 1980; Domeier, 1994 and damselfishes, Thresher and Moyer, 1983).

The above examples suggest that female mating preferences based on a single male trait, colouration, can often, but not always, maintain divergence among closely related species.

Mating decisions in many species of fishes, however, are often based upon discrimination between multiple types of male signals and mating preferences for particular types of signals may lead to interspecific differences.

Interspecific mating preferences among species of swordtails, genus *Xiphophorus*, have been studied extensively (e.g. Ryan and Wagner, 1987; Ryan and Causey, 1989; Basolo, 1990; Cragon de Caprona and Ryan, 1990; Basolo, 1995a,b; McLennan and Ryan, 1997, 1999). These studies have consistently demonstrated female preference for the sword, even in species where males are swordless (Basolo, 1990, 1995a,b). In addition, females of *X. pygmaeus* also prefer males of *X. nigrensis* based on differences in courtship displays (Ryan and Wagner, 1987; Ryan and Causey, 1989). Males of *X. nigrensis* perform courtship displays to both conspecific and heterospecific females, while males of *X. pygmaeus* do not perform a courtship display. Such patterns of asymmetry in interspecific female mating preferences, placed in a phylogenetic context, have been used as evidence for sensory exploitation

(Ryan, 1990; Ryan and Rand, 1990) or pre-existing biases (Basolo, 1990, 1995a).

Studies of female mating preferences in *Xiphophorus* have shown that male visual signals including courtship displays and presence of the sword may not provide the basis for interspecific mating preferences (Crapon de Caprona and Ryan, 1990; McLennan and Ryan, 1997, 1999). Female choice trials that provided olfactory cues through exposure to male odours found that the mating asymmetry between *X. pygmaeus* and *X. nigrensis* was not maintained. Females of *X. pygmaeus* showed a strong attraction to odours of conspecific males in terms of number of lunges, but not total time spent with conspecific males (Crapon de Caprona and Ryan, 1990). McLennan and Ryan (1997, 1999) have more recently explored the importance of olfactory cues in interspecific mate choice in three species of swordtails, *X. nigrensis*, *X. montezumae* and *X. cortezi*. When given a choice between water containing conspecific and heterospecific odours, females of all three species demonstrated a preference for the conspecific stimulus over male odours from heterospecifics. Interestingly, there appears to be a phylogenetic component to the odour preference (Meyer et al., 1994). Females of the more closely related species, *X. nigrensis* and *X. cortezi* are less likely to discriminate against odours of males of these two species than odours of males from the more distantly related *X. montezumi*. McLennan and Ryan (1997, 1999) conclude that olfactory stimuli produced by male swordtails may play an important role in mate recognition and reinforce the information provided by visual signals.

Female mating preferences in fishes are highly variable among species. Differences exist among species in the types of signals that are used for discrimination among potential mates within a species and between species. The role that mating preferences for colouration and courtship displays play in interspecific divergence in these signals is still relatively unknown, despite the large degree of interspecific diversity among males for these traits and the enormous diversity of fishes. Future research should focus on how female mating preferences promote and maintain both intraspecific and interspecific diversity in male mating signals in fishes.

### 3. Anuran amphibians

Frogs and toads communicate primarily through vocalizations given by males. The most common vocalization, termed the ‘advertisement call’ (Wells, 1977a,b), signals a male’s presence to reproductive females and in most taxa is the primary component of species recognition. Advertisement calls also function in interactions between males for acquisition and defense of territories that may contain oviposition sites (Howard, 1978; Duellman and Trueb, 1986), calling sites (Wells, 1977a,b) or diurnal retreats (Stewart and Rand, 1991). A major advantage of acoustic communication is the potential for encoding multiple messages within the same signal (Gerhardt, 1992). Variation among individuals in particular properties of anuran advertisement calls has been shown to convey information about a signaller’s species, physical condition and individual identity (e.g. Howard, 1978; Gerhardt, 1982; Wells and Taigen, 1986; Davis, 1988; Gerhardt, 1988; Ryan and Rand, 1990; Gerhardt, 1992; Ryan and Rand, 1993a; Gerhardt, 1994a; Welch et al., 1998).

Acoustic properties of male advertisement calls that influence female mating preferences are known for more than a dozen species (reviewed in Gerhardt, 1988, 1994a). Mating preferences of female anurans are most commonly assayed by using two-speaker choice tests and recording the phonotactic behaviour of females in response to synthetic calls varying in a particular property that are broadcast from each speaker. These types of choice trials are designed to identify female mating preferences for any specific properties of the advertisement call, and also to distinguish those properties that are necessary and sufficient for species recognition from those properties that are used by females to discriminate amongst conspecific males.

In most instances, results of these types of female choice tests have indicated that different properties of the advertisement call encode information used in interspecific versus intraspecific discrimination (but see Blackwell and Jennions (1993) for an alternative interpretation). A number of studies have explored the role of female

mating preferences in interspecific divergence in mating signals of anuran amphibians, especially within the hylid treefrogs (Littlejohn, 1965; Littlejohn and Loftus-Hills, 1968; Loftus-Hills and Littlejohn, 1971; Gerhardt, 1974; Fouquette, 1975; Oldham and Gerhardt, 1975; Straughan, 1975; Gerhardt, 1978, 1981a,b, 1982; Schwartz and Wells, 1984; Gerhardt, 1987; Klump and Gerhardt, 1987; Schwartz, 1987; Gerhardt, 1988; Gerhardt and Doherty, 1988; Gerhardt, 1991; Sullivan and Hinshaw, 1992; Blackwell and Jennions, 1993; Gerhardt, 1994b; Wollerman, 1998), the *Rana lessonae*/*Rana esculenta* species complex (Radwan and Schneider, 1988; Günther, 1990; Abt and Reyer, 1993), the *Physalaemus pustulosus* species complex (Ryan, 1980, 1985; Ryan et al., 1990; Ryan and Rand, 1990; Rand and Ryan, 1991; Rand et al., 1992; Ryan and Rand, 1993a,b,c, 1995; Kime et al., 1998) bufonid toads (Sullivan, 1985; Sullivan and Leek, 1987; Arak, 1988; Sullivan, 1989; Wagner and Sullivan, 1992, 1995; Gergus et al., 1997; Castellano and Giacomia, 1998) and midwife toads (Marquez, 1995; Marquez and Bosch, 1997).

An interesting example of how female mating preferences have shaped the evolution of interspecific divergence in properties of male advertisement calls is found in the gray treefrog species complex, *Hyla chrysoscelis* and *H. versicolor*.

These two species form a sibling species complex, where adults are morphologically indistinguishable but can easily be identified based upon differences in the male advertisement calls between the two species (Gerhardt and Doherty, 1988; Gerhardt, 1991). Even more unusual, these two species form a diploid-tetraploid species complex with diploid *H. chrysoscelis* ancestors giving rise to the tetraploid *H. versicolor* during multiple polyploid speciation events (Ptacek et al., 1994). Thus there is strong selection on females to distinguish between conspecific and heterospecific males in sympatric breeding choruses because mismatings result in the production of sterile triploid offspring (Johnson, 1963; Gerhardt et al., 1994b).

The advertisement calls of males of the two species differ in fine temporal structure (Fig. 1); both pulse repetition rate (pulse rate; Fig. 1A) and pulse shape (Fig. 1B) show species-specific differences. Females of both species strongly discriminate against heterospecific calls based upon the species-specific differences in pulse rate (Gerhardt, 1982; Gerhardt and Doherty, 1988; Gerhardt, 1994b). However, only females of *H. versicolor* distinguish between males of the two species based upon differences in pulse shape (Gerhardt and Doherty, 1988). Despite the species-specific differences in these properties of the advertisement calls, females of each species will respond

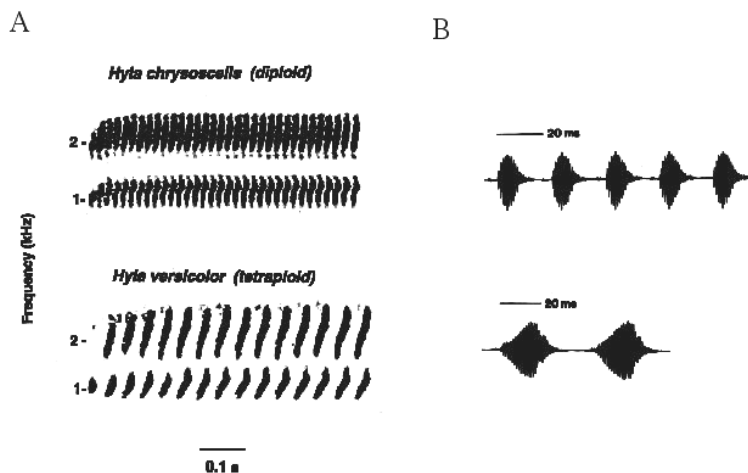


Fig. 1. (A) Narrow band sonograms of representative mating calls of *Hyla chrysoscelis* (upper trace) and *H. versicolor* (lower trace) from Missouri. The frogs were recorded at 20°C. (B) Oscillograms (expanded time base) of representative pulses from each call.

phonotactically to the heterospecific call if it is presented with no conspecific alternative (Gerhardt, 1982; Gerhardt and Doherty, 1988). In addition, females do not actively avoid calls of heterospecific males as they approach conspecific calls in sympatric choruses (Gerhardt et al., 1994a). This indicates that sometimes females treat heterospecific calls as mating signals, which argues that heterospecific properties of the signal are just one of a number of signal features that are used by females of either species during mate choice (Gerhardt, 1992; Gerhardt et al., 1994a). Blackwell and Jennions (1993) advocated a similar perspective based upon results of their female discrimination experiments with *H. ebraccata* in response to conspecific and heterospecific calls of the closely related species, *H. phlebodes* and *H. microcephala*.

Females of either gray treefrog species appear to exert strong selection pressures on the evolution of pulse rate differences both between species and among populations within a species. Females of each species prefer rates at or near the mean for their population (Gerhardt, 1988; Gerhardt and Doherty, 1988; Gerhardt, 1991), but also strongly discriminate against either the upper or lower ends of the pulse rate distribution depending upon species. Females of *H. chrysoyelis* more strongly reject alternative calls with lower-than-average pulse rates than they do those with higher-than-average pulse rates; females of *H. versicolor* show the opposite pattern (Gerhardt, 1982; Gerhardt and Doherty, 1988). Such a pattern of mating preferences should significantly reduce the possibility of mismating in sympatric choruses. Because of these unidirectional biases in mating preference for pulse rate, females of *H. chrysoyelis* avoid mating mistakes with the slower pulse rate calls of *H. versicolor*, while females of *H. versicolor* avoid mating mistakes with the faster pulse rate calls of *H. chrysoyelis*. Interestingly, Gerhardt (1994b) has shown that female mating preferences of *H. chrysoyelis* for pulse rate differences are stronger in sympatric populations than in allopatric populations. Thus, in gray treefrog species, female mating preferences have played an important role in the evolution of the male signal property that leads to species recogni-

tion. Marked divergence in mating preferences between females of the two species, especially in sympatry, has led to the rarity of interspecific hybrids (Gerhardt, 1982; Gerhardt et al., 1994b). A similar finding of stronger divergence of female mating preferences in sympatry than in allopatry for species-specific frequency differences in male advertisement calls of the midwife toads, *Alytes obstetricans* and *A. cisternasii*, was recently reported (Marquez and Bosch, 1997). These studies suggest that reproductive character displacement in female mating preferences may play an important role in the evolution of interspecific divergence in male mating signals.

Another interesting example of how female mating preferences have influenced the evolution of species-specific components of male advertisement calls is found in the Túngara frog, *Physalaemus pustulosus*, and its closely related species. This Central and South American species group of leptodactylid frogs contains four species, *P. pustulosus*, *P. petersi*, *P. coloradorum* and *P. pustulatus* (Cannatella and Duellman, 1984) and another undescribed species, *P. 'pustulatus-Peru'* (Ryan and Rand, 1993a). Males of all species produce an advertisement call that consists of a frequency-modulated component, referred to as the 'whine,' that is species-specific and necessary and sufficient for female attraction (Ryan, 1990; Ryan and Rand, 1993a). Female choice tests with *P. pustulosus* have shown that only certain parts of the whine are necessary to elicit phonotaxis (Rand et al., 1992; Wilczynski et al., 1995), but females can distinguish between the conspecific whine and those produced by males of all other species in the species group (Ryan and Rand, 1993a,b).

Males of *P. pustulosus* enhance the attractiveness of the whine by adding up to six chucks (temporally modulated pulses) at the end of the whine, yet these chucks are not sufficient by themselves for species recognition (Ryan, 1985). In some populations, *P. petersi* also adds a chuck-like suffix, but chucks are absent in all other species in the group and have not been reported in any of the other species in the genus (Ryan and Rand, 1993a). Phylogenetic relationships among members of the genus suggest that the chuck has been independently derived in *P. pustulosus* and in

certain populations of *P. petersi*, and was never present in ancestors of other species in the group (Cannatella and Duellman, 1984; Cannatella et al., 1998).

Ryan and Rand (1993b) showed that when females of *P. coloradorum* were given a choice between the whine-like call of conspecifics and the same call to which chunks from *P. pustulosus* were appended, they preferred the latter. In females of *P. pustulosus*, the addition of a prefix typical of *P. pustulatus* or the playback of doublet whines, which are sometimes produced by males of *P. coloradorum*, enhanced the relative attractiveness of conspecific whines (Ryan and Rand, 1993c). These results are consistent with the sensory exploitation hypothesis (Ryan, 1990) and suggest a broad preference for complex characters by females in this species group (Kime et al., 1998). Thus the preference by females for complex calls in the *P. pustulosus* species group is not limited to the complex characters produced by conspecific males but appears to be broad enough to include the complex characters of related species (Ryan and Rand, 1995, 1999). In this species group, such a broadly based female preference for complex calls would allow specific adornments to the male's whine to evolve along different paths in different species (Kime et al., 1998). These findings have important implications for the role of female mating preferences in promoting divergence of interspecific call differences during speciation within this group.

#### 4. Salamanders

Pheromones serve as a primary mating signal in salamanders (reviewed by Arnold and Houck, 1982; also see Houck and Reagan, 1990; Kikuyama et al., 1995). There is considerable evidence that chemical cues are important in species recognition and maintenance of reproductive isolation between sympatric species of salamanders and newts (e.g. Malacarne and Vellano, 1982; Dawley, 1984, 1986; Verrell, 1986; Cogalniceanu, 1992). Males use pheromonal cues emitted by females to locate conspecific mates (e.g. Marco et al., 1998). Species differences in female odours

have been implicated in contributing to sexual incompatibility among three sympatric species of *Plethodon* (Dawley, 1984, 1986), between sympatric *Desmognathus carolinensis* and *D. imitator* (Verrell, 1989), between *D. orestes* and *D. fuscus* (Uzendoski and Verrell, 1993) and among species of newts in the genus *Triturus* (Cogalniceanu, 1992).

Males of many salamander species also perform a complex series of courtship behaviors that involve orientation movements around the female and distinct head and tail movements (reviewed in Halliday, 1990). These displays are used to entice readiness in females to accept spermatophores deposited by males. The duration of the display varies considerably and depends in many species on the reaction of the female. During spermatophore transfer, the female follows the male, walks over the spermatophore, and if her cloaca comes in contact with it, the apical sperm mass of the spermatophore is then taken up in her cloaca. A courtship sequence in salamanders can be divided into three stages, orientation, persuasion and sperm transfer, and males exhibit both species-specific courtship elements and differences in the duration of each stage (Halliday, 1990; Uzendoski and Verrell, 1993). The role of male courtship behaviour in species recognition and reproductive isolation in salamanders has not been extensively studied (Uzendoski and Verrell, 1993; Michalak et al., 1997). In the few studies that have specifically compared male courtship behaviours during conspecific and heterospecific mating trials, some have found evidence of a primary role for courtship behaviours in species recognition (Kawamura and Sawada, 1959; Sawada, 1963; Michalak et al., 1997), while others have not (Uzendoski and Verrell, 1993).

Uzendoski and Verrell (1993) examined the importance of divergence in mate-recognition systems leading to sexual incompatibility between two species of sympatric plethodontid salamanders, *D. orestes* and *D. fuscus fuscus*. They found the two species to be highly sexually incompatible; none of 60 interspecific encounters resulted in insemination. Interestingly, detailed behavioural analyses of interspecific encounters failed to reveal any significant role for behavioural differences in

the maintenance of sexual incompatibility; males simply ignored heterospecific females. This occurred despite differences in the courtship behaviours of males of the two species in terms of both the content (certain behavioural components are species specific) and overall timing of the courtship sequence (courtship duration is shorter in one species) that were observed when males interacted with conspecific females. Thus, at least in contemporary populations, interspecific differences in courtship behaviours exist, but apparently are not currently used as the primary basis of interspecific mate choice.

Species recognition in these two species appears to be mediated by male choice of female chemical signals rather than female choice for male courtship signals. Males of both species discriminated against substrate-borne chemical cues of heterospecific females in Y-maze tests containing odours of conspecific versus heterospecific females. These results suggest that male mating preferences for female pheromones may be more important in species divergence than are male courtship behaviours. Divergence of socially significant chemical cues has been reported for several species of both *Plethodon* and *Desmognathus* (Verrell, 1989; Uzendoski and Verrell, 1993), and has been implicated as an important factor in the maintenance of sexual incompatibility among a number of other salamander species (Noble and Brady, 1930; Malacarne and Vellano, 1982; Dawley, 1986; Verrell, 1986; Dawley, 1987; Verrell, 1989; Cogalniceanu, 1992). Results of these and similar studies (Verrell, 1989, 1990) emphasize the importance of considering multiple mating signals when studying the evolution of signals that function as premating reproductive isolating mechanisms.

Behavioural isolation may play a more important role in species divergence in newts of the genus *Triturus*. Interspecific differences exist among males in both the types and degree of expression of morphological secondary sexual characters (such as the dorsal crest) and in the complex series of courtship behaviours performed by males. A recent study by Michalak et al. (1997) examined the role of male courtship behaviour patterns in sexual isolation between *T. vulgaris*

and *T. montandoni* in no choice tests using all four possible pairwise matings. Their results revealed considerable sexual isolation between *T. vulgaris* and *T. montandoni* in their courtship behaviour; 34% of all homospecific encounters progressed to successful spermatophore transfers, compared with only 4% in heterospecific encounters. They also found that mating preferences were asymmetrical, with display duration being considerably longer for heterospecific encounters with *T. montandoni* females than those for *T. vulgaris* females. Mating asymmetries such as these have recently been theoretically predicted as a consequence of divergence in male traits and female mating preferences based on those traits (Arnold et al., 1996). While results of this study cannot distinguish which elements of the courtship sequence are most important in contributing to the observed sexual isolation between these species of newts, the results do imply an important role of mating preferences in shaping interspecific divergence in courtship behaviours in *T. vulgaris* and *T. montandoni*.

## 5. Reptiles

Very few studies have attempted to examine mating preferences in reptiles, especially among snakes and crocodylians, which are often difficult experimental subjects (Tokarz, 1995). Most studies have focused on lizards, which exhibit a rich repertoire of highly conspicuous display behaviours (Carpenter and Ferguson, 1977; Jenssen, 1977; Carpenter, 1978; Martins and Lamont, 1998), and especially among *Anolis* lizards, which display a remarkable diversity in dewlap configuration including differences in size, colouration and patterning (Schwartz and Henderson, 1985). A few studies have attempted to quantify female mating preferences in lizards and have found some evidence for female mate choice based on male body size and dominance as well as on display behaviours (reviewed in Tokarz, 1995). Male display behaviours and associated morphological features such as dewlap colours and sizes have been suggested as the primary signals that may serve for species recognition in lizards.

Male lizards exhibit species-specific differences in visual displays including shifts in body posture, changes in body colour, head-bobbing, push-up movements, dewlapping and various tail movements (Carpenter, 1967, 1978, 1986). Males in the family Gekkonidae may also use vocalizations in addition to visual signals (Stamps, 1977; Carpenter, 1978) and the importance of pheromones in mate recognition by some lizard species has recently been described (Mason, 1992). Martins (1993), Martins et al. (1998) examined population differentiation in push-up displays of males in the sagebrush lizard, *Sceloporus graciosus*. These studies found that both the structure and the function of the push-up display are undergoing rapid differentiation among populations suggesting that such variation in push-up displays may be used to advertise individual, sex and species identity.

The extension of the dewlap, a large and frequently colourful fold of skin in the gular region (von Geldern, 1919; Bels, 1990), is one of the most striking features of *Anolis* lizards (Etheridge, 1960). Anoles display a remarkable diversity in dewlap configuration among species (Schwartz and Henderson, 1985), and this diversity may be the result of the many functions of the dewlap, which is used in courtship, intrasexual interactions, species recognition, and predator deterrence (Williams and Rand, 1977; Jenssen, 1978; Leal and Rodriguez-Robles, 1997).

Studies of *Anolis* lizards have suggested that female mating preferences may be based upon male display behaviour. Most anoles give a species-specific signature bob display (Stamps and Barlow, 1973; Stamps, 1977) and several workers have suggested that this display may attract females into a male's territory (Jenssen, 1970, 1971; Stamps, 1977). In addition, species-specific differences exist in dewlap configuration (i.e. colour, size and patterning) and Rand and Williams (1970) have argued that anole dewlap diversity evolved as a means of species recognition. Few studies, however, have directly examined female mating preferences in anoles (but see Jenssen, 1970; Sigmund, 1983). The importance of dewlap features and associated display behaviours in interspecific divergence in lizards has been tested

using male responses to conspecific and heterospecific displays (e.g. Macedonia et al., 1994; Macedonia and Stamps, 1994) or dewlap colour (Losos, 1985). Additionally tests of assortative mating (Jenssen, 1996) or comparative studies (Jenssen, 1978; Williams and Rand, 1977; Losos and Chu, 1998) using species that differ in dewlap features and display behaviours have been conducted. Little evidence exists for a role of dewlap size (Losos and Chu, 1998) or colour (Jenssen, 1996) in species recognition in anoles. The importance of display behaviours associated with the dewlap and the role of female mating preferences in the evolution of interspecific differences in these behaviours remains to be tested.

## 6. Birds

Song, plumage patterns and courtship displays all appear to play a role in species recognition in birds. It has been difficult to tease apart the relative importance of each of these traits in species recognition since females are seldom exposed to just one feature at a time. Additionally, studies of female mating preferences in birds have been hampered to some degree by the fact that in many temperate species, females do not sing. Very few studies of mating preferences have been conducted on species of birds that live in the tropics where both sexes do sing. Thus for temperate species, measuring female responses to male mating traits is often difficult, especially in field studies.

The role of mating preferences in promoting divergence in male secondary sex traits in birds is assumed to be important (Searcy and Yasukawa, 1996), yet understanding how females might come to use sexually selected male traits in interspecific mate choice is a more difficult problem. In birds, sexual imprinting is often of central importance in the establishment and maintenance of premating isolation (Immelmann, 1975; Laland, 1994; Irwin and Price, 1999; ten Cate and Vos, 1999). Sexual imprinting has been defined as the process by which young birds learn species-specific cues that enable them to find a conspecific mate when adult (Lorenz, 1935; Sluckin, 1964; Clayton, 1993). The

learning is usually from parents (Clayton, 1993), and cues are largely auditory and visual (e.g. Baker and Baker, 1990; Grant and Grant, 1997a,b). Imprinting itself has been suggested to evolve in order for individuals to avoid mating with kin, distantly related conspecifics or heterospecifics (McGregor and Krebs, 1982; ten Cate and Bateson, 1988).

Studies of bird song over the last 40 years have provided observational and experimental evidence that species can discriminate between conspecific and heterospecific song (e.g. Marler, 1960; Thielcke, 1962; Emlen, 1972; Gill and Murray, 1972; Becker, 1977; Marler and Peters, 1977; Thielcke et al., 1978; Becker, 1982; Grant, 1984; Ratcliffe and Grant, 1985; Grant and Grant, 1989; Nelson, 1989; Baker and Baker, 1990; Slater and Catchpole, 1990; Lynch and Baker, 1990; Searcy, 1990; Baker, 1991; Nelson and Marler, 1993; Baker, 1994; Searcy et al., 1995; Grant and Grant, 1996, 1997a,b). Mating decisions by females may be based largely on that discrimination (Eriksson and Wallin, 1986; Searcy and Brenowitz, 1988; Baker and Baker, 1990; Searcy, 1990; ten Cate et al., 1993). Vocalizations possess both species-specific characteristics and individually distinctive features (Borror, 1959; Marler, 1960; Schleidt, 1976; Becker, 1982; Falls, 1982; Nelson, 1989; Elfström, 1990; Lambrechts and Dhondt, 1995). Marler (1960) predicted that vocal features of bird song that are used to recognize species should differ from those that are used to recognize individuals within a species. To understand how song may function in species recognition, it is important to know whether or not it is learned, from whom it is learned, and if mislearning can lead to hybridization (Nicolai, 1959; Gill and Murray, 1972; Immelmann, 1975; Kroodsma, 1978; Güttinger, 1979; Böhner, 1983; Gelter, 1987; Wallin, 1987; Baptista and Morton, 1988; Alatalo et al., 1990; Böhner, 1990; Baker, 1991; Immelmann et al., 1991; Kruijt and Meeuwissen, 1991, 1993).

When learned, song is a culturally inherited trait whose characteristics can change rapidly as a result of small inconsistencies in transmission from one generation to the next (Böhner, 1983; Lynch and Baker, 1990). Such small changes in song characteristics in different geographic loca-

tions have led to the evolution of 'vocal dialects' (Thielcke, 1969; Mundinger, 1982) and in some species, females show a parallel geographic variation in mating preferences (e.g. Baker et al., 1981; Baker, 1982, 1983; Baker et al., 1987; Balaban, 1988a,b). Such divergence in female mating preferences may have shaped the evolution of species-specific features of song in birds (Irwin and Price, 1999).

The importance of cultural inheritance of song and its influence on intra- and interspecific mating preferences has been studied extensively in sympatric species of Darwin's finches (Grant, 1984; Ratcliffe and Grant, 1985; Grant and Grant, 1989, 1996, 1998). Two species, *Geospiza fortis* (medium ground finch) and *G. scandens* (cactus finch), are sympatric residents on Isla Daphne, Galapagos Islands. Song characteristics are culturally inherited from father to son in both species (Gibbs, 1990; Grant and Grant, 1996). Female mating preferences for song type also appear to be culturally inherited, with females preferring songs of the same species as their father, but not necessarily identical in song features to that of their father (Grant and Grant, 1996). This pattern of mating preferences suggests species recognition of song, but avoidance of mating with close relatives such as brothers who have learned songs from their father (Grant and Grant, 1996). The clear differences between the songs of the two species of Darwin's finches provide an opportunity for unambiguous species recognition. Heterospecific singing by males is very rare, and females almost always mate with males that sing the same song as their fathers (Grant and Grant, 1996). Occasional misimprinting has led to a low frequency of interspecific hybridization between the two species (Grant and Grant, 1997a), and hybrids backcross to the parental species to which their fathers belonged (Grant and Grant, 1997b, 1998). Thus, imprinting in Darwin's finches has served to strongly influence female mating preferences and led to the evolution of species-specific song features.

Birds are the most thoroughly studied vertebrate group with regard to conspicuous colours and other plumage characteristics (Andersson, 1994). However, the role that plumage differences

play in intra- and interspecific mating preferences remains largely untested. While closely related, sympatric species often differ dramatically in colouration and plumage patterns, little empirical evidence exists with regards to these plumage differences playing a major role in species recognition (Savalli, 1995).

One recent example has suggested the importance of interspecific mating preferences in promoting the divergence of plumage characteristics in two sympatric flycatcher species, the pied flycatcher (*Ficedula hypoleuca*) and the collared flycatcher (*F. albicollis*) (Sætre et al., 1997). These two species are widespread in Europe, and in a large area in central and eastern Europe their breeding distributions overlap (Lungberg and Alatalo, 1992; Roskaft and Järvi, 1992). Males of the collared flycatcher are distinctly black and white in colouration, but the amount of white patches on the forehead, neck and primaries varies between sympatric and allopatric populations; males in sympatry have larger patches of white (Sætre et al., 1997). Male pied flycatchers are highly variable in breeding plumage; some are conspicuously black and white, but others are a dull brown, resembling females (Roskaft et al., 1986; Lungberg and Alatalo, 1992). Males of the pied flycatcher are particularly dull where they occur in sympatry with the collared flycatcher (Roskaft et al., 1986; Lungberg and Alatalo, 1992; Roskaft and Järvi, 1992).

Sætre et al. (1997) tested whether the observed character divergence in male plumage between the two species in sympatry was related to a female preference for divergent male characteristics. They found that female collared flycatchers from a sympatric population preferred males with larger white patches to males with smaller patches. Female pied flycatchers from this same population preferred dull, brown males to black and white conspecifics. Hence, in sympatry, females of the two species show preferences for the divergent characteristics that distinguish males of the two species. Furthermore, females of the two species from allopatric populations were much less likely to discriminate against heterospecific males on the basis of plumage differences. These results suggest that reproductive character displacement in fe-

male mating preferences may have played an important role in the evolution of interspecific divergence in male plumage in sympatric populations of pied and collared flycatchers.

Elaborate courtship displays, which are often associated with extreme feather ornamentation in birds, are among the most famous examples of sexually selected traits. Such displays have been described in a variety of groups of birds, including grouse (Wing, 1946; Wiley, 1978), birds of paradise and bowerbirds (Marshall, 1954; Gilliard, 1969; Borgia, 1995), manakins (Snow, 1976), cotingas and bellbirds (Armstrong, 1965; Snow, 1976), ducks (Armstrong, 1965; Johnsgard, 1965; McKinney, 1975), tragopans (Islam and Crawford, 1998) and pheasants (Armstrong, 1965). Evidence that these traits diverge relatively rapidly is reflected in the characters used to distinguish species in these groups (e.g. Robbins et al., 1966; Gilliard, 1969; Delacour, 1970; Davis, 1972; Meyer de Schauensee and Phelps, 1978). An important role for female mating preferences in shaping the evolution of these traits within species is well known; however, the importance of these displays during interspecific mate discrimination has rarely been examined.

There is some empirical support for the idea that female mating preferences for male display characteristics in birds may lead to dramatic divergence among conspecific populations in these secondary sexual traits. Young et al. (1994) examined the phenotypic divergence of secondary sexual traits among populations of sage grouse (*Centrocercus urophasianus*). Behavioural analyses revealed that males from an isolated montane basin near Gunnison, CO, perform strut displays at a slower rate than males in two other sage grouse populations sampled. Additionally, the strut displays of males from the Gunnison population contain unique visual and acoustical aspects. Differences in the acoustical component and the slower strut rate of the Gunnison population are especially intriguing because they represent a divergence in expression of traits that correlate with mating success in other populations (Wiley, 1973; Gibson and Bradbury, 1985; Gibson et al., 1991). The authors argue that sexual selection through female mating preferences is the

most likely explanation for this divergence (Young et al., 1994), although they offer no direct test of this hypothesis.

The vast number of bird species that differ in song, plumage and display behaviours argues strongly for an important role for mating preferences in shaping the evolution of this diversity. Further research is needed to determine the role that different mating signals play in species recognition in birds and how female mating preferences may shape divergence in these traits.

## 7. Mammals

Communication among mammals usually entails olfactory, acoustic, visual and tactile signals. Scent plays a major role in social communication in mammals (e.g. Doty, 1976; Brown and MacDonald, 1985; Alberts, 1992), and the importance of olfactory perception for precopulatory recognition between members of the same and related species, especially in rodents, has been suggested by a number of studies (e.g. Parkes and Bruce, 1961; Moore, 1965; Smith, 1965; Bowers and Alexander, 1967; Doty, 1973; Nevo et al., 1976; Nevo and Heth, 1976; Cox, 1984; Pillay et al., 1995; Theiler and Blanco, 1996; Laukaitis et al., 1997). Males in many mammal species produce a larger amount and wider repertoire of odours, and scent mark more than females do (e.g. Stoddard, 1974; Thiessen and Rice, 1976; Bell, 1983; Brown and MacDonald, 1985; Jannett, 1986). Thus, species-specific differences in male odours may serve as an important signal to females in interspecific mate choice.

Several studies have demonstrated that female mating preferences for conspecific male odours play an important role in pre-mating reproductive isolation between closely related species in areas of geographic contact. The South American murid rodent *Graomys griseoflavus* shows a high degree of chromosomal polymorphism leading to the formation of distinct chromosomal races or cytotypes (Ortells et al., 1989; Zambelli et al., 1994). Results of female discrimination trials (Theiler and Blanco, 1996) show that females are able to recognize olfactory stimuli from males of

compatible chromosome complement and those from males with whom they would not produce viable descendants or would produce sterile hybrids. Furthermore, this discrimination ability is only evident during the estrus phase, suggesting that odour differences between males of the two chromosome races may serve as an important species recognition signal leading to pre-mating reproductive isolation.

In a similar study, Laukaitis et al. (1997) recently showed females of *Mus musculus musculus* and *M. m. domesticus* can distinguish homotypic from heterotypic males based upon a fixed allelic difference at the salivary androgen binding protein (ABP) locus. Males apply the ABP protein while licking their pelts and then deposit the protein on their surroundings within their territory. Females show a strong preference (> 2:1) to associate and mate with males of their own ABP type. In addition, females can differentiate between the territories of the two subspecies of males, even when the males have been removed, implying that the territories themselves are marked with the ABP-specific protein. ABP-assortative mate selection, although perhaps derived secondarily at contact zones, appears to play an important role in pre-mating isolation between *M. m. musculus* and *M. m. domesticus*.

Behavioural differences have been suggested to function in species recognition among species of African gerbils (*Gerbillurus* spp. and *Tatera brantsii*) (Dempster et al., 1992, 1993). These species also have species-specific ultrasonic vocalizations that are more frequently associated with sexual and contact-promoting behaviour than with solitary or agonistic behaviour (Dempster et al., 1991), and acoustic communication is believed to be an important component of species identification in gerbil species as well (Dempster et al., 1992). Parapatric and sympatric species of gerbils show more pronounced differences in communication, both in visually identifiable signals and in acoustic communication, than is exhibited between allopatric species (Dempster and Perrin, 1991; Dempster et al., 1992, 1993). The importance of female mating preferences in shaping divergence among parapatric or sympatric species in male behaviours or vocalizations has not been tested.

Differences in songflight calls between two phonic types of the vespertilionid bat *Pipistrellus pipistrellus* have recently been implicated as a potential mechanism of premating reproductive isolation (Barlow and Jones, 1997). The pipistrelle occurs as two phonic types in Britain, its echolocation calls falling into two distinct frequency bands with mean frequencies of maximum energy at 55 and 46 kHz. During the mating season, males perform songflights, often following a fixed path near the roost and repeating the songflight call. This call has been suggested to serve as an advertisement signal to attract females to the roost (Lundberg and Gerell, 1986; Gerell-Lundberg and Gerell, 1994). Males and females of the same phonic type are more often found roosting together than are males and females of mixed phonic types (Park et al., 1998). At present, however, there is no experimental evidence that songflight calls are used in mate choice in this species of bat (Barlow and Jones, 1997).

Although mammals exhibit a wide variety of interspecific differences in olfactory, acoustic and visual mating signals, very few studies have tested whether or not mating preferences play an important role in the evolution of these traits. Further work is needed in order to assess the importance of mating preferences in the evolution of species-specific mating signals in mammals.

## 8. Mating preferences, population divergence and speciation

An important role for mating preferences in shaping phenotypic trait distributions within species has considerable empirical support and is a major focus of many studies of sexual selection (reviewed by Andersson, 1994). However, the importance of sexual selection as an evolutionary force leading to speciation is still a subject of debate among evolutionary biologists. It has been theoretically demonstrated that sexual selection can lead to speciation when premating reproductive isolation develops in parallel with the divergence of sexually selected traits (Lande, 1981; Thornhill and Alcock, 1983; West-Eberhard, 1983, 1984; Kaneshiro and Boake, 1987; Iwasa

and Pomiankowski, 1995; Payne and Krakauer, 1997). However, how often parallel divergence of female mating preferences and male mating signals leads to reproductive isolation between populations and eventual speciation is unclear.

A number of studies have demonstrated that geographic variation in morphological traits and behaviours can be correlated with parallel differences in mating preferences among populations (e.g. frogs: Ryan and Wilczynski, 1991; Ryan et al., 1992; Wilczynski and Ryan, 1999, poeciliid fishes: Endler and Houde, 1995; Ptacek and Travis, 1997; salamanders: Uzendoski and Verrell, 1993; birds: Young et al., 1994, mammals: Pillay et al., 1995). Far fewer studies however, have examined whether or not the same varying traits that are the targets of sexual selection within a species are also important signals for species recognition. Models of sexual selection that act through Fisherian 'runaway' processes require a genetic correlation between female preference and male mating signal (Fisher, 1930), hence in order for reproductive isolation to result, the same male traits must be the basis of both intra- and interspecific mating preferences (Lande, 1981; West-Eberhard, 1983). If we assume that species recognition is merely an extension of intraspecific mate choice (e.g. Gerhardt, 1982; Verrell, 1988; Ryan and Rand, 1993a; Endler and Houde, 1995; Littlejohn, 1999), then it is easy to see how female mating preferences could shape the evolution of male signals that in turn, function in species recognition. Divergence in signals and responses among conspecific populations has been suggested as the first step in speciation (Verrell, 1999). Such a continuum between sexual selection and species recognition has been proposed by a number of authors (West-Eberhard, 1983; Verrell, 1988; Blackwell and Jennions, 1993; Ryan and Rand, 1993a; Gerhardt, 1994a; Endler and Houde, 1995; Boake et al., 1997; Zahavi and Zahavi, 1997; Pfennig, 1998; Ptacek, 1998; Verrell, 1999). Few studies in vertebrates however, have directly tested whether or not females use the same properties of male mating signals for both intra- and interspecific discrimination.

Indirect evidence suggests an important role for female mating preferences in promoting diver-

gence in mate recognition signals that have potentially led to speciation in the group of poeciliid fishes commonly known as mollies (Ptacek, 1998). Mollies have been divided taxonomically into two species group, sailfins and shortfins (Hubbs, 1933; Miller, 1975). Males of these two species complexes differ dramatically in both morphological and behavioural traits. Sailfin species are characterized by a sexual dimorphism in which males possess a greatly enlarged dorsal fin (Regan, 1913; Hubbs, 1933; Parzefall, 1969). This 'sail' fin is erected and presented to the female in a courtship display (Parzefall, 1969, 1979; Farr et al., 1986), thought to be an attempt to elicit female cooperation in mating. Shortfin species do not show sexual dimorphism in fin morphology and in species in which male mating behaviour has been examined, little evidence of courtship display behaviour has been observed (Parzefall, 1969, 1979; Brett and Grosse, 1982; Balsano et al., 1985; Woodhead and Armstrong, 1985; Ptacek, 1998).

Experimental studies have demonstrated female choice in at least one of the sailfin species, *P. latipinna* (Ptacek and Travis, 1997). Variation exists in the pattern of female mating preferences among conspecific populations, with females preferring native males to foreign males in some population comparisons. While the exact male signal that is the basis for this discrimination is not known, males vary among conspecific populations in rates of courtship displays (Ptacek and Travis, 1996) and in size and shape of the dorsal fin (Travis et al. unpubl. data). These same morphological and behavioural traits clearly distinguish males of this sailfin species from males of shortfin species (Ptacek, 1998). Furthermore, females of *P. latipinna* prefer conspecific males to males of two different shortfin species, *P. mexicana* or *P. orri* (Ptacek, 1998). These results strongly suggest that the same male traits that females of *P. latipinna* use when distinguishing males from native and foreign populations function in interspecific mate choice as well. This implies an active role for sexual selection during speciation of sailfins from shortfin molly ancestors (Ptacek and Breden, 1998).

## 9. Conclusions

Mating preferences within species of vertebrates have been shown to lead to a wide variety of acoustic, visual, olfactory and tactile signals, many of which have important functions in species recognition. This implies an important role for sexual selection in signal divergence and speciation in vertebrates. More work is needed in order to fully understand the basis for mating preferences in many vertebrate species. As we begin to further explore the relationship between mating preferences and species recognition, future studies should focus on how mating preferences shape various components of mating signals and in turn, how divergence in mating signal properties can lead to reproductive isolation.

Comparative studies are needed with emphasis placed on geographic variation among conspecific populations in both signal properties and mating preferences. These studies need to be examined in a phylogenetic context in order to disentangle the independent evolutionary origins of signal traits and mating preferences from historical effects arising from common ancestry. Molecular techniques are available that enable us to reconstruct phylogenetic relationships, both among species and among conspecific populations. In this manner, we can reconstruct ancestral signal properties and mating preferences and begin to understand how changes in both properties of signalers and receivers have influenced population divergence. Only by identifying how variation in mating preferences shapes the evolution of intra- and interspecific mate recognition signals can we ever hope to understand how sexual selection can be an important evolutionary force leading to speciation.

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