

REVIEW

The genetic architecture of insect courtship behavior and premating isolation

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The genetic architecture underlying reproductively isolating traits may have substantial impacts on the likelihood and pace of speciation. Recent studies of a key premating barrier, courtship, provide sufficient data to assess the degree to which behaviorally isolating traits are controlled by many or few loci, and help to investigate whether the same loci underlie both intraspecific and interspecific behavioral differences. Of the behavioral courtship traits examined, 69% (25 of 36) were found to be mediated by few loci of relatively large effect. This apparent prevalence of major loci suggests that changes in courtship behavior may

often evolve quickly, which in turn may drive rapid speciation through premating isolation. Although both intraspecific and interspecific courtship differences are commonly controlled by major loci, intraspecific and interspecific differences usually involve different loci or traits. This finding provides evidence that different sets of processes and genetic changes characterize microevolutionary change in courtship-related traits, in contrast to change during speciation.

Heredity (2009) **103**, 15–22; doi:10.1038/hdy.2009.22; published online 4 March 2009

Keywords: mating behavior; behavioral isolation; genetic architecture; speciation; sexual selection; species recognition

Introduction

Courtship behavior plays a central role in isolation between many species (for example, Hoikkala *et al.*, 2000; Williams *et al.*, 2001; Gleason *et al.*, 2002; Gleason and Ritchie, 2004; Mackay *et al.*, 2005), and the genetic architecture of such behavior may have important implications for the process of speciation (Coyne and Orr, 1989, 1997, 2004; Gavrillets and Boake, 1998; Via and Hawthorne, 1998; Henry *et al.*, 2002). Recent models have suggested that divergence among populations, and consequent speciation, may be more likely when traits are controlled by few loci (Arnegard and Kondrashov, 2004; Gavrillets and Vose, 2007; Gavrillets *et al.*, 2007; Hayashi *et al.*, 2007), and that speciation may also occur more rapidly under such genetic architecture (Gavrillets and Vose, 2007).

Earlier laboratory studies have led some researchers to conclude that the interspecific differences in phenotypes that cause reproductive isolation are most commonly polygenic (for example, Beukeboom and van den Assem, 2001; for review, see Coyne and Orr, 1998), and that mating behaviors represent complex traits controlled by many loci of small effect (Mackay *et al.*, 2005). In the most recent review of the genetics of different mating signals that lead to reproductive isolation, Ritchie and Phillips (1998) concluded that song differences are polygenic, whereas few genes of major effect usually control pheromone profiles; they also proposed that quantitative differences are usually polygenic, whereas qualitative differences are mediated by effects of major genes.

However, these authors, as well as Coyne and Orr (1998), also concluded that there were not enough data for robust cross-taxon generalizations regarding the genetics underlying premating isolation.

Since 1998, a considerable amount of data on the genetic architecture of courtship has accumulated, enough to warrant a re-evaluation of this key question. In this review, I assess available data on the number and effect size of loci underlying behavioral courtship traits, mainly for traits involving auditory phenotypes in *Drosophila* and other insects. I also assess whether the same or different loci and traits underlie species recognition and intraspecific mate choice to help determine if the processes involved in intraspecific mate choice also influence the evolution of reproductive isolation (Lande, 1981; Turner and Burrows, 1995; Boake *et al.*, 1997; Blows and Higgie, 2002; Gleason and Ritchie, 2004).

Methods

Selection of traits

Courtship can be treated as a single phenotypic trait or a combination of several individual characters (Etges *et al.*, 2006). To draw meaningful conclusions about reproductive isolation, one must reliably identify which particular traits are acting as reproductive barriers (Via and Hawthorne, 1998; Etges *et al.*, 2007); determining that a character is species specific is not equivalent to determining its role in isolation. Some researchers have measured the courtship phenotype as a whole by quantifying attractiveness to the opposite sex (for example, Henry *et al.*, 2002; Moehring *et al.*, 2004; Klappert *et al.*, 2007). Anholt and Mackay (2004) suggest that one can quantify courtship by simply measuring latency to courtship and copulation. Although such

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Received 16 November 2008; revised 6 January 2009; accepted 7 January 2009; published online 4 March 2009

measures are useful in quantifying premating isolation as a whole, they integrate a large collection of traits, including male activity, mate recognition, male choice, female resistance, female choice, and the complexity of courtship, making these measures relatively uninformative about what specific traits underlie isolation. Moreover, as pointed out by Boake *et al.* (1998), as such summary traits likely represent several characters, they are predisposed to reveal a polygenic architecture, biasing studies of the genetics of reproductive isolation towards detection of such effects. In this review, I thus concentrate on the genetic bases of the specific phenotypic traits involved in courtship and reproductive isolation.

Major loci versus polygenic effects

Major-locus and polygenic effects represent ends of a continuum (Falconer and Mackay, 1996), and authors vary in their criteria for concluding either simple or complex genetic architecture. Some studies make a distinction between major-locus and polygenic distinction by determining the percent of phenotypic variance explained by target loci (for example, Hoikkala *et al.*, 2000; Gleason *et al.*, 2002); by contrast, other studies base their conclusions on the number of loci underlying a trait relative to genome size, or the distribution of loci throughout the genome (for example, Yeh *et al.*, 2006; Klappert *et al.*, 2007). In this review, I describe the criteria used by different authors for such conclusions alongside the results, and present both the conclusions of the authors and the percent of phenotypic variance explained.

Regardless of the criteria used to determine simple versus complex genetic architecture, most genetic methods show a bias towards detecting loci of large effect, as with quantitative trait loci studies (Via and Hawthorne, 1998). Furthermore, Orr's (1998) theoretical models predict that we should find a mixed (exponential) distribution of genetic effect sizes, meaning that there should be few loci of large effect, many loci of intermediate effect, and many more loci of small effect. Given that genetic methods are limited in their ability to detect loci of small effect, there is an expected bias to the detection of loci of large and intermediate effect, whereas the many loci of small effect may go undetected. It is therefore important to consider these methodological biases when interpreting the results of the available data on the genetic architecture of courtship.

Literature surveyed

This review focuses on courtship-related signals, mainly in auditory traits in *Drosophila*, which represents the primary source of information in the literature. As genetic analyses of courtship extend to non-insects, and a diversity of traits, the generality of the patterns inferred here can be evaluated. The term 'genetic architecture' refers here to the number and locations of loci underlying courtship traits. This scale of analysis allows conclusions to be drawn regarding genomic regions, rather than specific genes; such regions may vary considerably in size (Paterson *et al.*, 1988), and a locus originally recognized initially to be of large effect may actually comprise several genes of relatively small effect (for example, Perez *et al.*, 1993; Perez and Wu, 1995).

However, the literature pertaining to genetic architecture is dominated by analysis of loci, making this the optimal level of analysis in which to make conclusions on the evolutionary dynamics of courtship traits and premating isolation.

To be included in this review, a study had to either (i) make an inference about the genetic architecture of a behavior involved in courtship or (ii) provide an estimated number of loci involved in a courtship behavior. A list of related references, which were not included in this review are provided in the Supplementary Information section.

Results

How many loci control courtship differences?

The results from 20 studies, representing 33 characters and 24 species, are summarized in Table 1. Of the traits in which a genetic architecture was inferred by the authors (authors' criteria for these observations are summarized in column 7 of Table 1), 25 of 36 (69%) was considered to be influenced by few loci of large effect. Percent of phenotypic variance explained by one locus ranged from 9 to 40% (average 23%) in those studies that present this information. Of those traits concluded to be under simple genetic control, the variance explained ranged from 19 to 40% (average 30%), whereas those traits concluded to be polygenic ranged from 9 to 14% (average 10%).

Some data that did not meet all of the criteria to be included in Table 1 (because they measured isolation as a whole rather than a behavior, did not make an inference regarding genetic architecture, or did not present the number of loci) are also relevant to this compilation. Few loci (2 or 3, depending on the backcross used) of large effect were found to be responsible for sexual isolation, measured as copulation occurrence, in *Drosophila yakuba* and *Drosophila santomea* (Moehring *et al.*, 2006). Similarly, Noor *et al.* (2001) concluded that sexual isolation (through courtship dysfunction of hybrids) between *Drosophila pseudoobscura* and *Drosophila persimilis* was mediated by three loci of large effect. By contrast, Jia *et al.* (2000) found that many loci control sexually selected characters (components of male ultrasonic signals) in the wax moth *Achroia grisella*, and Mackay *et al.* (2005) have suggested that up to 21% of the genome may be involved in the mating speed of *Drosophila*. Considered together with the studies in Table 1, this evaluation of the genetic basis of traits involved in premating isolation indicates that large effects of few loci underlie variation in over two-thirds of the traits examined.

In some species pairs (*Drosophila ananassae/pallidosa*, *Chrysoperla plorabunda/johnsoni*, *Chorothippus albomarginatus/oschei*, *Chorothippus brunneus/jacobsi*, and *Laupala paranigra/kohalensis*), reproductive isolation has been considered to evolve quickly through changes in behavior alone, as there is a lack of postzygotic isolation, and ecology and morphology may be identical between species (Henry *et al.*, 2002; Yamada *et al.*, 2002; Saldamando *et al.*, 2005; Shaw *et al.*, 2007; Vedenina *et al.*, 2007). When this subset of species pairs for which behavioral isolation represents the only reproductive barrier, or for which speciation is known to be rapid, is considered, a similar proportion, five of the nine traits

Table 1 Traits involved in courtship behavior

<i>Taxon and species</i>	<i>Trait</i>	<i>Selected during mate choice?^a</i>	<i>Method</i>	<i>Loci number</i>	<i>Maximum effect^b</i>	<i>Polygenic or major loci^c</i>	<i>Reference</i>
<i>Drosophila melanogaster</i>	Interpulse interval	Y	Chromosome replacement			Major loci ¹	Colegrave <i>et al.</i> (2000)
<i>D. mojavensis</i>	Interpulse interval	Y	QTL	3	24.9	Major loci ²	Gleason <i>et al.</i> (2002)
	Interpulse interval	Y	Breeding experiment			Polygenic ¹	Etges <i>et al.</i> (2006)
	Long interpulse interval	Y	QTL	3			Etges <i>et al.</i> (2007)
	Short interpulse interval	N	QTL	1			Etges <i>et al.</i> (2007)
	Burst duration	? (Y for <i>D. arizonae</i>)	Breeding experiment			Polygenic ¹	Etges <i>et al.</i> (2006)
<i>D. virilis</i>	Pulse number	Y	QTL	3	13.8	Polygenic ^{1,2}	Etges <i>et al.</i> (2007)
		?	QTL	13			
<i>D. elegans/gunungcola</i>	Pulse train length	?	QTL	8	9	Polygenic ^{1,2}	Huttunen <i>et al.</i> (2004)
	Male courtship	?	Crosses+genotyping	'Many'		Polygenic ¹	Yeh <i>et al.</i> (2006)
	Wing display	?	Crosses+genotyping	'Few'		Major loci ¹	Yeh <i>et al.</i> (2006)
	Body shaking	?	Crosses+genotyping	'Few'		Major loci ¹	Yeh <i>et al.</i> (2006)
<i>D. ananassae/pallidosa</i>	Song characters chosen by females	?	Crosses+genotyping	'Few'		Major loci ¹	Yeh <i>et al.</i> (2006)
		Y	Chromosome substitution crosses			Major loci ¹	Yamada <i>et al.</i> (2002)
<i>D. pseudoobscura/persimilis</i>	Interpulse interval	Y	msat, RFLP	≥3	19	Major loci ^{1,2}	Williams <i>et al.</i> (2001)
	Intrapulse frequency	Y	msat, RFLP	≥2	24	Major loci ^{1,2}	Williams <i>et al.</i> (2001)
<i>D. simulans/sechellia</i>	Interpulse interval	Y	QTL	6	9.4	Polygenic ^{1,2}	Gleason and Ritchie (2004)
<i>D. simulans/mauritiana</i>	Male traits being selected by females	Y	QTL	3		Major loci ¹	Moehring <i>et al.</i> (2004)
	Interpulse interval	Y	Breeding experiment and chromosome markers			Polygenic ¹	Pugh and Ritchie (1996)
<i>D. virilis/littoralis</i>	Pulse length	?	Breeding experiment and chromosome markers	5	39	Major loci ^{1,2}	Hoikkala <i>et al.</i> (2000)
	Pulse train length	?	Breeding experiment and chromosome markers	2	30.6	Major loci ^{1,2}	Hoikkala <i>et al.</i> (2000)
	Song pause	?	Breeding experiment and chromosome markers	6	40.4	Major loci ^{1,2}	Hoikkala <i>et al.</i> (2000)
	Pulse number	?	Breeding experiment and chromosome markers	3	21.7	Major loci ^{1,2}	Hoikkala <i>et al.</i> (2000)
	Cycle number	?	Breeding experiment and chromosome markers	4	36.6	Major loci ^{1,2}	Hoikkala <i>et al.</i> (2000)
<i>Neuroptera Chrysoperla plorabunda/johnsoni</i>	First principle component of selected song traits	Y	Breeding experiment	2–7		Major loci ¹	Henry <i>et al.</i> (2002)

Table 1 (Continued)

<i>Taxon and species</i>	<i>Trait</i>	<i>Selected during mate choice?^a</i>	<i>Method</i>	<i>Loci number</i>	<i>Maximum effect^b</i>	<i>Polygenic or major loci^c</i>	<i>Reference</i>
<i>Orthoptera</i>							
<i>Teleogryllus oceanicus</i>	Presence/absence of courtship song	Y	Breeding experiment	1		Major loci ¹	Tinghitella (2008)
<i>Chorthippus biguttulus</i>	Male song attractiveness	Y	AFLP	2		Major loci ¹	Klappert <i>et al.</i> (2007)
<i>C. albomarginatus/oschei</i>	Song amplitude	? (Y for song as a whole)	Breeding experiment	'Many'		Polygenic ¹	Vedenina <i>et al.</i> (2007)
	Song duration	? (Y for song as a whole)	Breeding experiment	'Many'		Polygenic ¹	Vedenina <i>et al.</i> (2007)
<i>C. brunneus/jacobsi</i>	Tibia strokes	?	Breeding experiment	1		Major loci ¹	Vedenina <i>et al.</i> (2007)
	Song syllables	Y	Breeding experiment	'Few'		Major loci ¹	Saldamando <i>et al.</i> (2005)
	Phrase length	Y	Breeding experiment	'Few'		Major loci ¹	Saldamando <i>et al.</i> (2005)
	Echeme length	Y	Breeding experiment	'Many'		Polygenic ¹	Saldamando <i>et al.</i> (2005)
<i>Laupala paranigra/kohalensis</i>	Song pulse rate	Y	QTL	8	9.6	Polygenic ^{1,2}	Shaw <i>et al.</i> (2007)
<i>Homoptera</i>							
<i>Nilaparvata lugens</i> : rice versus <i>Leersia</i> feeding populations	Pulse repetition frequency	Y	Breeding experiment	4 or 5		Major loci ¹	Butlin (1996)
<i>Nilaparvata lugens</i> : India versus Australia rice feeding populations	Pulse repetition frequency	Y	Breeding experiment	1.5–2		Major loci ¹	Butlin (1996)

Abbreviations: AFLP, amplified fragment length polymorphism; msat, microsatellite; QTL, quantitative trait loci; RFLP, restriction fragment length polymorphism.

^a'Y' denotes that authors claim trait is important in isolation. 'N' denotes that authors claim trait is not important in isolation. '?' denotes that authors make no claim about the trait's impact on isolation.

^bMaximum percentage of phenotypic variance explained by one locus.

^cAuthors' conclusion of genetic architecture. Superscripts denote the basis of authors' definitions of major loci versus polygenic architecture: ¹number of loci relative to total genome size, ²percent phenotypic variance explained by a single locus.

Table 2 Genetic mechanisms controlling courtship differences within and between *Drosophila* species

Comparison	Species	Trait	Locus ^a	Locus overlap?	Comments	Reference
Intraspecific	<i>D. melanogaster</i>	Interpulse interval (IPI)	2 (L)–1 3 (L)–2	N	Intraspecific differences through few loci	Gleason and Ritchie (2004)
Interspecific	<i>D. simulans</i> / <i>sechellia</i>		2 (R)–4 3 (R)–2		Interspecific differences through many loci	
Intraspecific	<i>D. melanogaster</i>	IPI	2 (L)–1 3 (L)–2	N	<i>D. pseudoobscura</i> and <i>persimilis</i> use different signals during mate choice.	Williams <i>et al.</i> (2001)
Interspecific	<i>D. pseudoobscura</i> / <i>persimilis</i>		X–2 2–1			
Intraspecific	<i>D. montana</i>	Song traits	Autosomes	N		Hoikkala <i>et al.</i> (2005)
Interspecific	<i>D. montana</i> subgroup		Autosome–≥1 X–many			
Intraspecific	<i>D. virilis</i>	Pulse number (PN)	Autosomes Y	?	Possible overlap of autosomal loci yet to be done	Huttunen and Aspi (2003)
Interspecific	<i>D. virilis/lummei</i>		Autosomes			
Intraspecific	<i>D. virilis</i>	PN	X–1 2–1 3–5 4–1	N	No autosomal loci involved in interspecific differences.	Huttunen <i>et al.</i> (2004)
		Pulse train length (PTL)	3–4			
Interspecific	<i>D. virilis/littoralis</i>	PN PTL	X (proximal end)			

^aFormat is as follows: chromosome (arm or region of chromosome)–number of loci in this region.

(56%), were controlled by major loci, whereas the other four were polygenic.

Intra- versus interspecific changes in courtship

From Table 1, nine of 13 differences (69%) within species are mediated by few loci of large effect, whereas 16 of 23 differences (70%) between species are through few loci of large effect. The majority of both intraspecific and interspecific differences in courtship traits are thus mediated by few loci of large effect. Similar genetic architecture underlying the two comparisons does not, however, mean that the same mechanisms underlie each. In fact, the majority of studies that discuss intraspecific versus interspecific differences conclude that they do not involve the same traits. For example, intraspecific differences in the interpulse intervals of *Drosophila melanogaster* are underlain by few loci of major effect, whereas interspecific differences in interpulse intervals of *Drosophila simulans* and *Drosophila sechellia* have apparently evolved through many loci of small effect, which indicates that sexual selection and species recognition do not represent a continuum in these species (Gleason and Ritchie, 2004). A similar pattern is seen for species in the *Drosophila virilis* and *Drosophila montana* groups, as well as the observation that intraspecific differences involve autosomes, whereas interspecific differences are largely influenced by the X chromosome (Hoikkala *et al.*, 2005). Lastly, Carracedo *et al.* (2000) determined that *D. melanogaster*, *D. simulans*, and *Drosophila mauritiana* all use different discrimination mechanisms when interacting with heterospecifics versus conspecifics, and that interspecific genetic differences in sexually isolating traits originate after speciation.

Many additional studies have found that the loci responsible for intraspecific differences are located on different chromosomal arms or different chromosomes altogether than loci responsible for interspecific differences in courtship behavior (Table 2). When analyzed at the behavioral level, Boake *et al.* (1997) concluded that sexual selection and species recognition do not represent a continuum in the species pair *Drosophila silvestris* and *Drosophila heteroneura*. Therefore, although similar genetic patterns may underlie both intraspecific mate choice and species recognition, most evidence suggests that the two processes are not driven by the same traits.

Discussion

Behavioral signaling, which plays a key role in courtship and premating isolation, has been earlier thought to be mediated predominantly by many loci of small effect (for example, Coyne and Orr, 1998; Beukeboom and van den Assem, 2001; Mackay *et al.*, 2005). The primary conclusion of this review is that the majority of traits influencing premating isolation measured to date show a genetic architecture of few loci of major effect. Furthermore, the percentage of phenotypic variance explained is often large enough for natural or sexual selection to act on through change in a single locus. However, this pattern of mating signals controlled by few loci is far from universal and in no way can it be considered a rule, as approximately 30% of traits are found to be under polygenic control.

One important implication of a pattern of major loci underpinning the genetic basis of courtship is that several recent models have suggested that speciation may be more likely (Arnegard and Kondrashov, 2004;

Gavrilets and Vose, 2007; Gavrilets *et al.*, 2007; Hayashi *et al.*, 2007), and divergence faster (Gavrilets and Vose, 2007), when adaptive or reproductive traits are underlain by such simple genetic architectures. For example, in simulations by Gavrilets and Vose (2007), ecological traits controlled by four loci promoted speciation more often, and faster, than simulations in which traits were controlled by eight or 16 loci, even when all selective and ecological forces were kept constant. Therefore, this study's results suggest that changes in courtship behavior and premating isolation may often evolve quickly, which in turn may contribute to the importance of behavior early in the speciation process. Such theoretical predictions are consistent with observations of rapid courtship divergence among some insect lineages (Ritchie and Gleason, 1995; Etges *et al.*, 2006), although robust tests of the assumptions and predictions of such models require additional studies. A possible further test of the role of genetic architecture in speciation would involve comparing traits causing reproductive isolation with otherwise comparable behavioral traits that do not influence isolation, to determine if isolation-related traits are more commonly controlled by few major loci.

Henry *et al.* (2002) suggested that changes through few loci (which are capable of relatively large leaps in phenotype) should be characteristic of differences predominantly in sexually selected traits that are arbitrary with respect to natural selection, but changes through many loci (which are generally more gradual) may indicate that environmental adaptation accompanies sexual selection, making speciation adaptive, as in conditions underlying ecological speciation (Schluter, 2001; Rundle and Nosil, 2005). The data reviewed here, however, indicate that some species pairs that have diverged recently, in which behavior represents the only barrier to reproduction, exhibit polygenic architecture for isolating traits (for example, Saldamando *et al.*, 2005; Shaw *et al.*, 2007; Vedenina *et al.*, 2007), which run counter to the predictions of Henry's (2002) hypothesis. Additional data are needed, however, for quantitative evaluation of the degree to which ecological versus non-ecological speciation are underlain by different patterns of genetic change.

Interpretation of the results presented here regarding the genetic architecture of premating isolation is subject to several important caveats. First, the apparent prevalence of major loci may, in part, reflect methodological biases, given the precision of genetic analyses and their power to detect loci of small effects; for example, some quantitative trait loci methods can exhibit biases towards detection of loci of large effect (Via and Hawthorne, 1998). However, there is no reason to expect systematic biases specific to courtship-related traits. Furthermore, the studies in Table 1 show no evidence of association between genetic architecture and ascertainment method: 68% of traits studied through crossing and breeding experiments are controlled by major loci, whereas 64% of quantitative trait loci analyses showed traits to be controlled by major loci.

Second, the choice of traits to examine may also influence the nature of genetic inferences, as courtship often comprises multiple behavioral components. For example, when considered a single phenotype, courtship differences between *Drosophila elegans* and *Drosophila gunungcola* are polygenic (Yeh *et al.*, 2006), but when each

component of courtship is considered separately, they are each apparently under the control of a few major loci (Table 1), with wing display, body shaking, and circling mediated by effects of loci on different chromosomes. Such results show the importance of determining which traits underlie reproductive isolation.

Third, courtship need not mediate sexual selection within species, or reproductive isolation among them (for example, Boake and Hoikkala, 1995; Price and Boake, 1995; Boake and Poulsen, 1997; Saarikettu *et al.*, 2005). However, the majority of traits in Table 1 have been shown to be important in mate choice. When considering only those traits with demonstrated direct relevance to mate choice, 14 of 19 (74%) traits are underlain by major loci. Therefore, this examination of genetic architecture of courtship is pertinent to our understanding of the evolution of reproductive isolation.

Finally, intraspecific versus interspecific locus comparisons sometimes involve intraspecific signals of *D. melanogaster*, contrasted with interspecific processes as measured in separate *Drosophila* species pairs. To conclude whether the same or different traits underlie intraspecific mate choice and interspecific reproductive isolation at the genetic level, it is necessary to identify the loci influencing sexually selected traits in one species, and to determine whether there is overlap with loci causing reproductive isolation between this focal species and a sister species.

A second primary conclusion of this review is that studies of both intraspecific and interspecific differences in behavioral signaling show a prevalence of major-locus effects on variation, but that the loci involved seldom overlap. These results suggest that sexual selection and species recognition are not mediated through the same loci and traits, which implies that these two processes do not represent two ends of a continuum, at least at the level of genetic architecture. This inference does not imply that sexual selection does not drive processes of speciation in these organisms; conclusions as to the mode of speciation cannot be drawn simply from looking at the genes underlying isolation. What these data do suggest is that the same loci and traits do not underlie isolation at both the within- and between-species levels. Speciation may thus represent less a continuous process in which one isolating mechanism initiates and completes reproductive isolation than a process involving the accumulation, or replacement, of novel isolating mechanisms and traits during and after the speciation process (Boake *et al.*, 1997; Carracedo *et al.*, 2000).

Evidence on the interrelatedness of sexual selection and speciation remains sparse, and perhaps insufficient to draw any general conclusions. Indeed, Price (2002) points out that 'the genetics of species differences is not the genetics of speciation,' given that species differences likely accumulate after speciation and processes causing isolation now may not have caused isolation during speciation. Comparative studies that integrate behavioral data on courtship and prezygotic isolation with information on genomic architecture, for specific clades with species at variable stages of divergence, may be most useful for assessing the genetic bases of the speciation process.

Overall, there is a prevalence of major loci in the available data for both intra- and interspecific differences in behavioral mate signaling, though approximately 30%

of the traits included are under polygenic control. This data complements two other important conclusions from earlier work. First, premating isolation often evolves quickly (for example, Coyne and Orr, 1989, 1997; Grant and Grant, 1997), making it important in the early stages of speciation. Second, some recent models predict that speciation is more probable and progresses more quickly when isolating traits are through few loci (Gavrilets and Vose, 2007; Gavrilets *et al.*, 2007; Hayashi *et al.*, 2007). The empirical evidence presented here for the genetic control of courtship is thus generally concordant with earlier empirical and theoretical work on the patterns of isolation and speciation. Courtship is often controlled by few loci, which may predispose it to fast divergence, which in turn may drive rapid speciation through premating isolation.

Acknowledgements

I thank Felix Breden for introducing me to questions about genetic architecture and evolution. BJ Crespi and F Breden provided extensive feedback and revisions for this paper. This work was funded by a NSERC CGS-M scholarship to DA and a NSERC Discovery Grant to BJ Crespi.

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