

# Polymorphic signals of harassed female odonates and the males that learn them support a novel frequency-dependent model

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For mate-searching species, the learned mate recognition (LMR) hypothesis assumes that sexual harassment favours signal variation among females, which exploits the receiver ability of males. The model predicts that coevolving males have responded to the female sexual foil by learning to recognize female variants as potential mates. I translate the LMR hypothesis into the language of signal detection theory to explain its novelty as a dynamic, coevolutionary, negative frequency-dependent selection model. Due to gene–environment interactions, males cueing to the morph detected most often should generate positive but often asymmetrical, detection-dependent harassment towards females. Females are expected to sort to an ideal free distribution where harassment costs are equal. At equilibrium, morph fitness, but not necessarily morph frequency, is predicted to be equal. The LMR hypothesis is consistent with recent experimental data and the distribution of colour polymorphisms in the Odonata, predicts general conditions favouring variation in sexual signals, and provides a novel mechanism for speciation via sexual signalling.

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Humans are notably good at detecting cheaters (Cosmides & Tooby 1992). Our predisposition for grasping the concept of deception may be one reason that mimicry polymorphisms have featured so prominently in models of natural selection (e.g. Wallace 1865; Darwin 1871; Ford 1964). Signal deception has been modelled predominantly in terms of predators locating cryptic prey, but is equally applicable to sexual deception, most notably in sneaker males that benefit from looking or acting like females (e.g. Forsyth & Alcock 1990; Radwan 1993; Hews et al. 1994). Among males, intrasexual signal deception is not uncommon and is generally accepted as a type of alternative mating strategy (reviewed by Gross 1996). Deceptive colour polymorphisms in adult females are less common, and in some species may be antipredator adaptations (Stamps & Gon 1983). That explanation is insufficient, however, for female-specific polymorphisms that are a prominent characteristic of a few families in the Odonata, whose predators are cued more often by motion than colour (Fincke 1994a). As I here suggest, understanding how selection maintains these obvious female variants

offers insights into the maintenance of more subtle variation in sexual signalling by either sex.

In damselflies (Zygoptera) and dragonflies (Anisoptera), andromorphic females are similar to males in colour and pattern, whereas heteromorphic females are more distinct from males in coloration (Johnson 1975). In many dragonflies, the dichotomy is less clear due to intermediate patterns. For these species, andromorph refers to the extreme case and all other types are considered heteromorphs (e.g. Walker 1953). The morphs appear to result from one to two Mendelian genes (*Ischnura*, Johnson 1964, 1966; Cordero 1990; *Ceriatrion*, Andrés & Cordero 1999). In genera such as *Ischnura*, andromorphs are usually brightly coloured, nearly identical to males in colour pattern, and may mimic male behaviour. Males may then have a harder time recognizing andromorphs as potential mates (Robertson 1985; Cordero 1989; *Ceriatrion*, Andrés et al. 2002) compared with genera whose andromorphs are less bright than males and show female-specific, dark abdominal dorsa that cue their sex to males (*Coenagrion*, Gorb 1998; *Enallagma*, Fincke 1994a; Miller & Fincke 1999). Despite such differences in detail, colour polymorphisms have been viewed consistently in the context of sexual conflict (Fincke 1997) as a way for females to avoid harassment, either from heterospecific

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**Table 1.** The five hypotheses for the maintenance of female colour polymorphisms in odonates. The last hypothesis is unique in its assumption that a male's pre-existing bias for sex or species characters does not include any morph-specific character

Hypothesis			Source
(1) Fitness trade-offs (sexual isolation versus predation)	<b>Benefit to 'male mimic'</b> Fewer heterospecific matings	<b>Morph-specific cost</b> Greater predation risk	Johnson 1975
(2) Negative frequency-dependent selection on andromorphs only	Frequency dependent; fewer unwanted matings with conspecific males	Frequency-independent risk (e.g. predation)	Robertson 1985
(3) Density-dependent selection	Fewer unwanted conspecific matings at high density	Greater mating failure at low density	Hinnekin 1987
(4) Negative frequency-dependent selection on andromorphs only	Fewer unwanted conspecific matings at low frequency (heteromorphs always recognized as 'female')	More unwanted matings for andromorphs at high frequency	Sherratt 2001
(5) Negative frequency-dependent selection on both morphs	<b>Benefit to rare morph</b> Lower harassment (from conspecific and heterospecific males)	<b>Cost to common morph</b> Positive detection-dependent harassment	Miller & Fincke 1999; this study

males, conspecific males, or both (Table 1; see also Forbes 1991). Nevertheless, consensus on how female morphs are maintained by selection has been stymied for several reasons.

First, an overemphasis on sexual coercion (Clutton-Brock & Parker 1995) as the outcome of sexual conflict has resulted in a reluctance to acknowledge that females of both morphs are equally successful in avoiding unwanted matings, even if they use different tactics to do so (Table 2). For example, coercive copulations, although not essential for any of the proposed selective mechanisms, have been repeatedly assumed to be a major fitness cost of male harassment towards females (Table 1; see also Cordero Rivera & Egido Pérez 1998; Andrés et al. 2002). This view has persisted in spite of evidence that lifetime mating frequencies for both morphs are low and females rarely mate more than once per day (Fincke 1997; Andrés et al. 2002), data that suggest more subtle, but possibly significant, costs of lost time. To avoid supernumerary matings, females must interrupt what they are doing, such as resting, thermoregulating, foraging, or ovipositing. Harassment costs to female morphs should be equal at field equilibria (Table 2), and hence, more readily detected by measuring female fitness correlates under nonequilibrium conditions, while controlling for other variables. Results of the only such experiment to date (Sirot & Brockman 2001) suggest that morphs differ physiologically in their responses to harassment.

Second, the deception advantage of a male-like morph, intuitively attractive as it is, has been overemphasized to the exclusion of other features relevant to mate recognition. Indeed, all but one of the explanatory hypotheses assume that the andromorph functions as a male mimic that is invariably more difficult to recognize as a potential mate than is the heteromorph (Table 1; see also Conrad & Pritchard 1989). However, signal intensity relative to background noise (e.g. Bick & Bick 1965), and any similarity among sympatric, congeneric individuals (of both morph and sex types), which can be nearly identical in appearance (see Dunkle 1990), pose additional problems for mate-searching males while simultaneously providing

females with multiple ways of confounding males. Moreover, as was first suggested by an analysis of comparative data (Fincke 1994a) and subsequently demonstrated experimentally (*Enallagma*, Miller & Fincke 1999; *Ischnura*, Van Gossum et al. 2001a), a male's sexual reaction towards morphs depends on his experience with them in a manner consistent with learning (see Papaj & Prokopy 1989). His temporary morph preference does not depend on copulation; under field conditions, marked males mate randomly with respect to morph type (Fincke 1982; Conrad & Pritchard 1989; Cordero 1992; Fincke 1994a).

Empirical evidence for equality among morphs in their control over mating decisions, and for plasticity in a male's sexual response, spurred the learned mate recognition (LMR) hypothesis of Miller & Fincke (1999). These authors proposed that, given sufficient costs of male harassment towards single females, selection favours polymorphic females whose colour variation makes it more difficult for a mate-searching male to cue to any given female type. In response to this sexual foil, males are predicted to increase efficiency in recognizing females as potential mates (i.e. detecting them) by cueing to the morph recognized most often. Such males exert positive detection-dependent harassment towards female morphs, resulting in negative frequency-dependent selection on females that maintains multiple morph types. Evidence supporting predictions of the LMR hypothesis as it applies to mate-searching species is summarized in Table 2.

Some authors (e.g. Andrés et al. 2000; Sherratt 2001) have assumed that the LMR model invariably predicts equal morph frequencies at equilibrium. Others (Cordero Rivera & Andrés 2001; Andrés et al. 2002) have overlooked the fact that a bias towards the majority morph in a preference test would be expected only if morph frequencies as measured in the field were indicative of the tested male's actual experience with females. Such misunderstandings and other incorrect predictions attributed to the LMR hypothesis (e.g. Sherratt 2001; Sirot et al. 2003) prompted this analysis of the model in terms of a signal detection problem to justify its predictions and to illustrate more convincingly its novel and general features

**Table 2.** Predictions arising from the learned mate recognition hypothesis as applied to mate-searching species and the odonate species for which data are consistent with the prediction

Prediction	Species	Source
<b>Within-species</b>		
Lifetime mating frequency, survivorship and fecundity of morphs are equal at equilibrium	<i>Coenagrion puella</i>	Banks & Thompson 1985; Thompson 1989
	<i>Enallagma hageni</i>	Fincke 1982, 1986
	<i>E. boreale</i>	Fincke 1994a
	<i>Ischnura graellsii</i>	Cordero 1992; Fincke 1994b
	<i>I. ramburi</i>	Sirost et al. 2003
	<i>I. elegans</i>	Van Gossum et al. 2001b
Females of each morph are equally able to reject males		
Males display false alarms towards:		
(1) Other males (especially when $d_{\text{male}}$ is low)	<i>I. ramburi</i>	Robertson 1985
	<i>I. graellsii</i>	Cordero 1989
(2) Heterospecific females (especially when $d_{\text{het}}$ is low)	<i>Argia</i> , <i>Coenagrion</i> , <i>Enallagma</i> , <i>Ischnura</i> , <i>Nehalenni</i> , <i>Pseudagrion</i> , <i>Xanthocnemis</i>	Bick & Bick 1981
	<i>E. civile</i>	Miller & Fincke, in press
	<i>E. boreale</i>	Forbes 1991
	<i>Aeshna cyanea</i>	Kaiser 1985
	<i>E. civile</i>	Miller & Fincke 1999
When male attention is desired, females signal their presence opportunistically		
A morph can decrease her detectability by:		
(1) Mimicking male behaviour	<i>I. ramburi</i>	Robertson 1985; Sirot et al. 2003
	<i>I. graellsii</i>	Cordero 1989
(2) Frequenting microhabitats where distractor density is high	<i>Erythrodiplax umbrata</i>	Paulson 1998
(3) Hiding in vegetation	<i>Nehalennia irene</i>	Forbes et al. 1995
Males switch from a natural preference for the majority morph to a preference for the minority morph after experiencing only the latter	<i>I. elegans</i>	Van Gossum et al. 2001b
Andromorphs may be the majority morph in some populations	<i>Enallagma civile</i>	Miller & Fincke 1999
	<i>I. elegans</i>	Van Gossum et al. 2001a
	<i>Argia vivida</i>	Conrad & Pritchard 1989
	<i>Ceriagrion tenellum</i>	R. Jödicke, personal communication
	<i>E. boreale</i>	Forbes 1994
	<i>I. elegans</i>	Cordero Rivera & Andrés 2001
	<i>I. ramburi</i>	Sirost et al. 2003
	<i>C. tenellum</i>	Andrés et al. 2002
	<i>I. graellsii</i>	Cordero Rivera & Egido Pérez 1998
	<i>I. elegans</i>	Hinnekin 1987
	<i>Nehalennia irene</i>	Forbes et al. 1995
	<i>I. graellsii</i> (?)	
Mean per capita harassment towards females is higher in populations with more than two female morphs than in populations with only two morphs		
Plasticity in morph expression is mediated by gene–environment interaction at the larval stage	<i>E. civile</i> (?)	
<b>Between-species</b>		
Mean per capita harassment towards single females is higher in polymorphic than in monomorphic populations		Table 4, this study
Female signal polymorphisms are more common in species whose males search for mates than in species whose receptive males remain localized		Table 4, this study

as a negative frequency-dependent model. Learned mate recognition is also relevant for sire-seeking females of territorial species, but for brevity's sake I here focus on its application to mate-searching males. In Part 1, I analyse the conditions favouring signal variation in females and learning by males. In Part 2, I analyse comparative data from the Odonata to test the model's underlying assumption and its predictions about conditions that favour female signal variation or otherwise constrain its evolution. Finally, I discuss the broad implications of learned mate recognition for sexual conflict and cooperation, and as a mechanism for speciation via learning sexual signals.

## PART 1: METHODS AND RESULTS

### Learning as a Way to Maximize Efficiency in Signal Detection: Terminology

Duda & Hart (1973) present the statistical theory of signal detection, developed originally for radar discrimination between friendly and enemy aircraft. They outline how a receiver's 'optimality criterion' can be derived to optimize its performance in discriminating among hypotheses (i.e. what signal is present). The signal detection task for a mate-searching damselfly male is to distinguish between 'desired' signals of conspecific females and

‘distractor’ signals such as those of conspecific males and co-occurring heterospecific individuals of both sexes. A male’s performance at this task depends in part on the signal-to-noise ratio that results in some probabilistic distribution of observer error around the signal means, due to confusing backgrounds. Another source of difficulty occurs when two signals appear very similar due to low  $d_x$ , the ‘vector distance’ between a desired signal and a given distractor signal,  $x$ . Both of these frequency-independent factors contribute to a female’s crypsis,  $s$  (Staddon & Gendron 1983). Frequency-dependent factors that affect a receiver’s performance are the a priori probabilities that each possible signal is actually the one present, here proportional to the density of conspecific females ( $D$ ), conspecific males ( $N$ ) and heterospecific distractors ( $H$ ). Finally, a male’s performance depends on the optimality criterion or decision rule, a product of the male’s neurophysiology, which is designed by natural selection.

The receiver optimality criterion appropriate for a damselfly male is a Bayesian one, which incorporates the net benefits of an action (Table 3). The optimal strategy for a male damselfly is to minimize his Bayesian risk. This is the statistically averaged cost of a ‘miss’,  $v_m$ , or failing to detect a desired signal when one is present, and the cost of a ‘false alarm’,  $U_m$ , or attempting to mate with a distractor, offset by the benefits gained of a ‘hit’ ( $B_m$ ), or detecting a conspecific female when one is present. In keeping with other biological signal detection models (e.g. Staddon & Gendron 1983; Sherratt 2001), I here use the term ‘encounter’ in the sense independent of detection. Thus, a male may encounter a female without detecting (i.e. recognizing) her as a potential mate. I use the term ‘cue’ to refer to the action resulting from a temporary sensory bias for a specific stimulus; ‘template’ refers to a more permanent neurological bias for key features of a stimulus against which unknown signals can be compared.

In the absence of precise statistical characterization of vector distances between signals and precise noise distributions, the performance of a receiver can approach optimality with statistical learning. ‘Supervised learning’ in which trial signals are correctly labelled with identifying ‘tags’ yields better results than ‘unsupervised learning’ from unlabelled data, when the receiver learns without sure knowledge of actual fact (Duda & Hart 1973). The ability of a biological receiver to learn about morph-specific signals depends on  $a_x$ , the per capita rate of encounter with morph  $x$ . Given the importance of a female as a reproductive resource, I expect natural selection has favoured some pre-existing template for

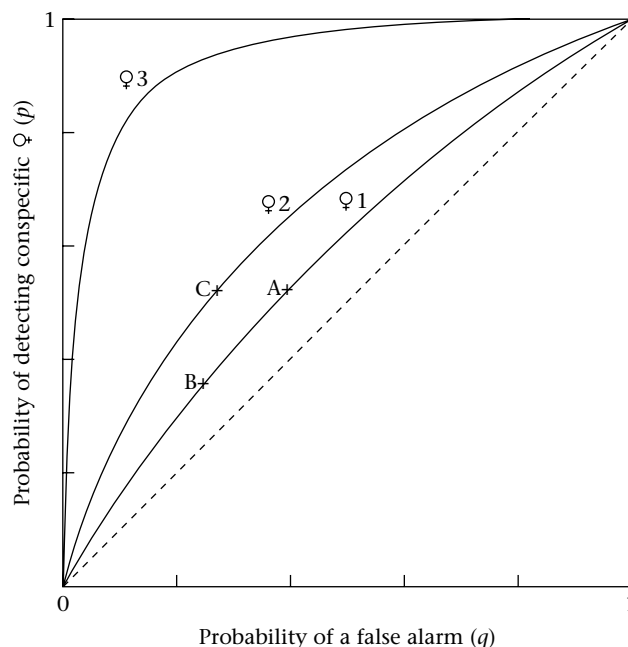
**Table 3.** Possible outcomes of a male’s encounter and its consequences to the male receiver ( $m$ ), female emitter ( $f$ ) and conspecific male distractor ( $m_{dis}$ )

Conspecific female	Conspecific male does not attempt to mate	Conspecific male attempts to mate	Heterospecific male attempts to mate
Present	$v_m, v_f$	$B_m, B_f$	$U_f$
Absent	0	$U_m, U_{m_{dis}}$	0

B: benefit gained;  $v$ : cost of a miss;  $U$ : cost of a false alarm.

‘conspecific femaleness’ (a ‘tag’). Because most females possess sex- and species-specific features (but see Paulson 1974), a male with sufficient time for inspection should nearly always detect a conspecific female as a potential mate and do so more quickly when it benefits both sexes.

However, efficient identification is a premium when males searching for potential mates must compete for relatively few matings. The receiver operating characteristic (ROC) curves for a male faced with variable signals from females whose identities are uncertain illustrate the limitations under which a male operates (Fig. 1). A male that attempts to mate with anything remotely resembling a conspecific female would rarely miss reacting to any potential mate that is encountered, but he would also make many mistakes. A more cautious male decreases  $q$ , the probability of attempting to mate with a distractor given an encounter with one, but also reduces  $p$ , the probability of detecting a conspecific female given an encounter with one. The relationship between the two probabilities is approximated by  $p = q^s$ , where  $s$  is a measure of crypsis (Staddon & Gendron 1983). By using the decision rule ‘cue to the morph detected most often’, a male can gain efficiency because learning effectively shifts the curve towards the Y axis, decreasing  $q$  without



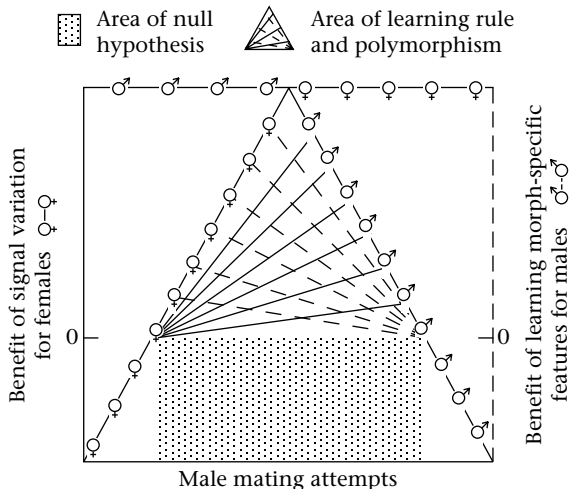
**Figure 1.** Hypothetical receiver operating characteristic (ROC) curves for a male faced with multiple signals from conspecific females of uncertain identities. Each curve is approximated as  $p = q^s$ , where  $s$  is a measure of crypsis, maximal when  $s = 1$  (i.e. dotted line, Staddon & Gendron 1983). Mimicry models assume that a heteromorph is always more readily recognizable to a male as a potential mate than is an andromorph (e.g. ♀3 and ♀1, respectively). In static models, a receiver reduces the rate of false alarms by lowering his criterion (e.g. from A to B). The dynamic LMR model predicts that a male gains a more efficient  $p/q$  by learning, effectively shifting any criterion point towards the Y axis (e.g. from A to C). A female can behaviourally affect the detectability of her signal ( $1/s$ ), effectively shifting the curve to her advantage (e.g. from signal 2 to 3 if sperm are needed, from 2 to 1 if not).

a concomitant reduction in  $p$ . Males may be taking more time to inspect females (Guilford & Dawkins 1987) or they may be learning a specific morph feature (Reid & Shettleworth 1992). Either or both may occur, depending on the sex ratio and density during training. Regardless, the LMR hypothesis predicts that  $p/q$  increases with a male's experience. Mate-searching males are expected to use a sort of Bayesian updating (McNamara & Houston 1980) to modify an internal template, not unlike birds learning about patch quality over time (Getty & Krebs 1985), or abiotic receivers designed with 'neural networks' (Bishop 1995).

### Effects of OSR and Population Density on Female Signal Variation and Male Learning

*When is it advantageous for females to confuse males?*

The LMR hypothesis is best described as a bounded negative frequency-dependent selection model. When applied to mate-searching males, it predicts that female morph frequencies will vary from 0 to 100%, in part depending on the relationship between  $v_f$  and  $v_m$ , which depends on the level of male attention towards females (Fig. 2). Because it is difficult to interpret a male's approach to a female if there is no subsequent action by



**Figure 2.** The multidimensional learned mate recognition (LMR) model for the two-morph case, depicted here in two dimensions, and with straight lines, for simplicity. Female and male interests set the boundaries within which, respectively, the presence of a second morph increases female fitness by reducing per capita harassment (i.e.  $v_{f2} < 0$ ) and cueing to morph-specific features increases a male's detection efficiency (i.e.  $v_m > U_m$ ). Then, at any level of harassment, the predicted frequency of a second female morph is that at which her harassment costs (solid lines) equal those of the first morph (dashed lines). Morph–environment interactions lead to asymmetrical equilibrium frequencies (see Fig. 5). Benefits become negative and selection favours monomorphic females at very low and very high male mating attempts when, respectively, females benefit by being more conspicuous (clear triangle, bottom left) and males benefit by cueing to female-specific features, constraining any benefit of a polymorphic female ruse (bottom right).

either individual, mating attempts (regardless of ensuing copula) per female offers a practical measure of male attention. Whether or not male attention benefits a female depends on his species, her age, and the quantity (and quality) of her sperm reserves. For example, the juvenile colour form that is characteristic of many female coenagrionids (see Dunkle 1990) may signal a female's sexual immaturity and usually her lack of receptivity (e.g. Fincke 1987; but see Van Gossum et al. 2001c; Sirot et al. 2003). For a sexually receptive female, the combination of low operational sex ratio (OSR, males:females) and low population density should cause a male's missed mating opportunity to be at least as costly to her as it is to him ( $v_f \geq v_m > 0$ ). Then, colour polymorphism provides no net advantage to females, and selection should favour a mother producing a single morph type (monomorphism, Fig. 2). The lowest levels of male attention should favour fixation of a conspicuous, easily detected morph (e.g. heteromorphs with high  $d_{\text{male}}$  in a habitat with low noise). As male attention rises to become sexual harassment, here defined as undesired attention from a mate-seeking individual ( $v_f < 0$ ), a less conspicuous female type should be fixed.

A female benefits by producing a second morph type among her female offspring when  $v_{f2}$  is less than zero for the second female type as well (Fig. 2). The presence of a second morph adds a negative frequency-dependent component to the model while decreasing  $D_1$ , the density of the first morph. All else being equal, as morph frequencies approach equality, and the number of variants increases, the more difficult it becomes for a male to detect a conspecific female. The number of variants is limited, if not by genetic constraints then by the concomitant decrease in  $D_x$ . If males rarely encounter a morph, they may not learn to recognize it. Then, a female's cost of searching for sperm overrides any benefit of her ruse ( $v_{fx} > 0$ ).

Depending on a species' ancestral colour state and phylogenetic constraints on the colour patterns possible, a female's signal may be similar to those of conspecific males (low  $d_{\text{male}}$ ) or heterospecific females (low  $d_{\text{het}}$ ). Either type of distractor should cause a conspecific male to make mistakes and is known to do so (Table 2). As conspecific OSR rises and/or  $d_{\text{male}}$  of andromorphs decreases, andromorphs should enjoy an asymmetrically lower cost of harassment relative to heteromorphs, because of the disproportional increase in signal distractors. Such morph–environment interaction may explain some experimental results previously interpreted as being inconsistent with the LMR hypothesis (e.g. Van Gossum et al. 2001b). In sympatry, the advantage of low  $d_{\text{het}}$  depends on the density and OSR of heterospecifics, which determines whether the advantage of distractors outweighs  $U_f$ , the cost to a female of harassment from heterospecific males.

Females make it more difficult for males to detect them by mimicking male behaviour (Table 2). Independent of their frequency, morphs can affect a male's encounter rate with them ( $a_x$ ) by being less active or assorting non-randomly to microhabitats where male attention is minimized by distractors or background noise. For example,

andromorphic *Nehalennia* frequent areas with a high concentration of male distractors (Table 2), presumably until the increasing density of andromorphs is countered by males learning their true identity.

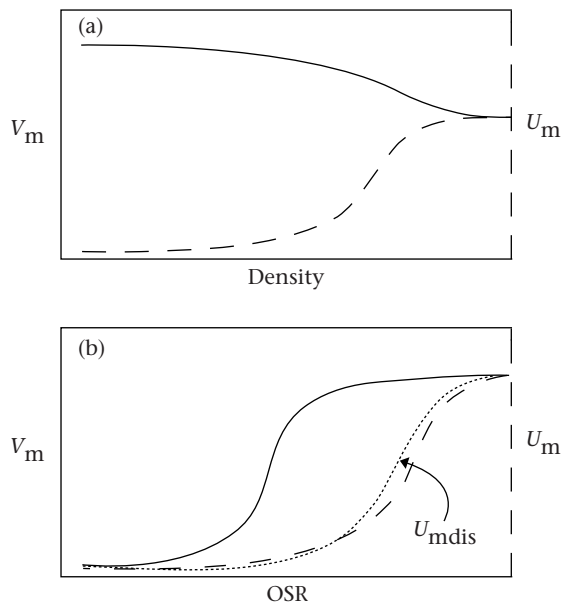
#### When is it advantageous for males to pay attention to female variation?

The boundary below which learning morph-specific details optimizes a male's signal detection efficiency depends on the cost of a miss relative to the cost of a false alarm. Given that 20–50% of mate-searching coenagrionid males are known to fail to mate at all during their lifetimes (Fincke 1982; Banks & Thompson 1985), overlooking a potential mate is as costly to some males as the failure to mate at least once is to a female. The cost of a missed detection ( $v_m$ ) is a selective pressure that should favour the evolution of learning in males. This opportunity cost is not automatically taken into account by  $B_m$ , which is best measured as the probability of mating, given that a conspecific female is detected by a male. Hence,  $B_m$  is in part determined by  $B_f$ , the value of the mating to the female; a female does not automatically mate with any male that takes her in tandem (see Fincke 1997).

The cost of a false alarm,  $U_m$ , should be significant when males can incur physical damage by mistaking a male for a female or waste sperm by mistaking a heterospecific female for a potential mate, as occurs in some territorial congeners (Oppenheimer & Waage 1987). In mate-searching species, agonistic encounters are generally low for single males. Their risk of sperm wastage is also low because females taken in tandem by heterospecifics can discriminate against them before copula (Robertson & Paterson 1982). Usually,  $U_m$  would be the time and energy lost by trying to mate with a distractor, although physical risk might occur, depending on the suite and density of distractors (e.g. some *Ischnura* females prey on *Enallagma*, Fincke 1987; Dunkle 1990). Perhaps a more significant cost is that of false alarms to males as distractors,  $U_{mdis}$ , when they are mistaken for potential mates (i.e. sexual harassment towards males).

Population density and OSR of conspecifics and heterospecific distractors have independent effects on a male's performance in detecting potential mates. The density of conspecific females ( $D$ ) affects the number of mating opportunities available and hence the cost of a miss, whereas the density of males ( $N$ ) and heterospecifics ( $H$ ) affects the potential for false alarms. At low population density, the cost of a miss is maximal, as it could be the only opportunity a male gets to mate. But then, effectiveness of the learning rule is limited by the duration of a male's temporary sensory bias, which may be less than a day and at times shorter than his encounter rate with females (Miller & Fincke, in press). As competition from other males decreases, a male has more time to carefully inspect females. Thus, at low male density and OSR, the probability of a false alarm should approach zero, whereas that of a hit should remain relatively high.

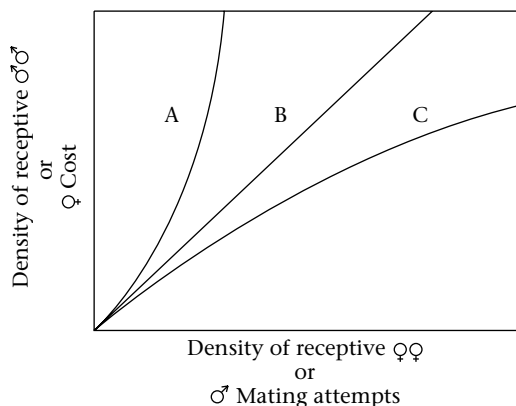
As density increases,  $v_m$  should decrease and  $U_m$  should increase (Fig. 3a). OSR determines the degree of competition among conspecific mate-searching males and the



**Figure 3.** Hypothetical relationship between the costs of a miss ( $v_m$ , solid line) and a false alarm ( $U_m$ , dotted line) to mate-searching male receivers as a function of (a) population density and (b) operational sex ratio (OSR). The cost of sexual harassment towards conspecific males,  $U_{mdis}$ , may rise faster than  $U_m$  in some species.

cost of time lost to a false alarm. Although both  $v_m$  and  $U_m$  increase with rising OSR,  $v_m$  is expected to increase faster than  $U_m$ , before reaching a plateau (Fig. 3b). If  $U_{mdis}$  rises faster than  $U_m$ , males should diverge generally from female coloration, which may explain the greater sexual dimorphism of andromorphic *Coenagrion* and *Enallagma*, relative to andromorphic *Ischnura*. OSR is affected by the time required for both sexes to cycle to receptivity and may remain constant, rise, or decrease as density rises (Fig. 4; e.g. Andrés et al. 2002; Miller & Fincke, in press).

At the density and OSR at which  $U_m$  equals  $v_m$ , the benefit of a high but less discriminating attack rate



**Figure 4.** Possible relationships between density of receptive males and females, or between female cost per mating attempt and male mating attempts. As density increases, operational sex ratio (OSR) or female cost/harassment, respectively: (A) increases, (B) remains the same, or (C) decreases. Conditions such as C and A contribute to interaction effects.

prevails and then males should pursue anything that remotely resembles a conspecific female (e.g. possesses an ovipositor or a wide abdomen). That should also be the case when the density of females is so low that learning to recognize morphs is constrained by the limits of a male's memory. Above the upper boundary of the learning rule, sexual dimorphism is expected when high  $U_{\text{mdis}}$  favours males that diverge from female coloration (see also Sherratt & Forbes 2001). Then, any production costs of the polymorphism to females should favour monomorphism of female offspring (Fig. 2).

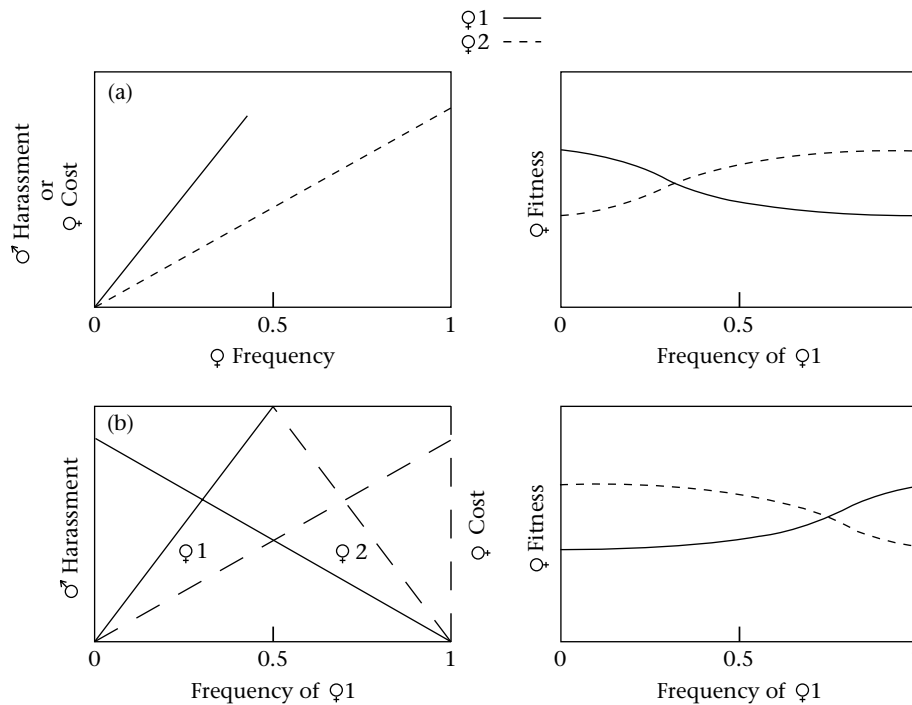
**Negative Frequency-dependent Selection as the Resolution of Sexual Conflict**

*Mate learning by males and assortment of harassed females to an ideal free distribution*

Within the bounds of the learning rule, males exert positive detection-dependent harassment towards female morphs (Table 2). Unconstrained by a need to frequent male-controlled resources, females are expected to sort to an ideal free distribution (Fretwell & Lucas 1970) such that the costs of harassment towards both morphs are equal. Thus, at equilibrium, the fitness but not necessarily the frequency of the two morphs is expected to be equal. In the simplest case of no heterospecific distractors, male harassment towards a morph is a function of OSR, population density and morph frequency. Female costs of harassment are a function of male density ( $N$ ), cost per

harassment and morph frequency. Hence, the shape of male preference (see Ritchie 1996) should covary with female costs. Harassment is expected to increase positively with morph frequency, but should often do so asymmetrically with respect to morph types because of morph–environment interaction effects. These include morph differences in crypsis, in female behaviour that affects  $a_x$  independent of  $D_x$  (Fig. 5a) and in costs accrued per mating attempt or morph differences in optimal mating frequency (Fig. 5b). Then, equilibrium frequencies are expected to vary from those predicted by OSR, density and global morph frequency alone.

Across a range of density and OSR, the predicted morph frequencies are those at which morph harassment costs are equal. Consistently high harassment should deflect morph frequencies towards equality (Fig. 2), except when constrained by underlying genetics (e.g. incomplete dominance that results in a third morph type). For example, with no genetic drift, the difference between the observed morph frequency and the genetic equilibrium distribution for a given population may indicate differences in morph crypsis ( $s_A, s_H$ , A = andromorph, H = heteromorph), per capita encounter rates ( $a_A, a_H$ ) and/or per capita cost per mating attempt. Equilibrium requires that when  $s_A > s_H$  (all else being equal), the frequency of A > H, and when  $s_A < s_H$ , the frequency of A < H. More precise frequency predictions are possible by quantifying the relevant habitat-specific probability distributions. But the data sets that would provide sufficient power to test such predictions may often be prohibitively



**Figure 5.** Asymmetrical equilibrium frequencies of two female morphs caused by morph–environment interactions: (a) frequency-independent costs generated by asymmetrical vector distances, signal-to-noise ratios, and/or behavioural effects such as habitat segregation or activity level (equilibrium frequency = 0.3 for ♀1); (b) negative frequency-dependent costs generated by asymmetry of morph cost/harassment (equilibrium frequency = 0.7 for ♀1). Lines originate at 0 for ♀1, at 1 for ♀2. In this extreme case, costs are inversely proportional to harassment rates, and equilibrium frequencies are the reverse of those predicted from harassment rate alone.

large. Nevertheless, the above predictions suggest testable hypotheses to explain why andromorphs are usually the minority morph (Fincke et al., in press). For example, despite its relatively low and confusing  $d_{\text{male}}$ , a bright blue andromorph should be more conspicuous in a grassy field, compared to a dull green, tan, or even blue heteromorph whose signal-to-noise ratio there is relatively low. Other nonmutually exclusive possibilities are that the andromorph is more active or suffers higher cost per mating attempt, relative to the heteromorph.

Across a species' geographical range, ROC curves for female signals should be habitat specific. Variation in habitat characteristics that determine the degree of noise in the system affects  $p$ , whereas variation in OSR and the heterospecific distractor pool affects  $q$  (Fig. 1). Variation in population density and OSR changes the value of  $v_m$  relative to  $U_m$ , and equilibrium morph frequencies should differ among populations of the same species and they do (Table 2). Context-dependent genetic plasticity in gene expression is expected because any genetic response to selection only occurs between generations, too slow for tracking local changes in harassment levels. Variable harassment may result in changes in morph frequency over a season (e.g. Fincke 1994a; Sirot et al. 2003). With few exceptions (Fincke 1987; Sternberg 1996), morph colour of mature females is fixed in most polymorphic species (Corbet 1999), so density cues at the larval stage are a likely mechanism (Miller & Fincke 1999). Plasticity in colour expression is consistent with seasonal patterns of intermediate morphs (e.g. *Enallagma*, unpublished data) and may also explain the abundance of intermediates in other genera (e.g. *Aeshna*, Walker 1953; *Ceriagrion*, Andrés & Cordero 1999).

## PART 2: METHODS AND RESULTS

### Taxonomic Distribution of Female-specific Signal Variation in Odonates

#### Testing interspecific predictions of the LMR hypothesis

To explain the evolution of female-specific signal variation driven by sexual harassment, the LMR model assumes that male attention towards single females is sufficiently high to decrease female fitness but below the level at which the optimal male tactic is to cue to general features of conspecific females (Fig. 2). Between those bounds, polymorphic signalling should provide the greatest benefits when females that do not need sperm are often disturbed, as when pairings form in feeding areas (e.g. Fincke 1982) or when females lay eggs alone and unguarded while males are still active (e.g. Kaiser 1985; Paulson 1998). Even if per capita harassment is high, a polymorphic ruse may be constrained if female behaviour or location reveals her sexual identity and receptive state, or when the habitat or signal modality provides little noise. The benefits of female signal polymorphism should be relatively low for territorial or lekking species where receptive females seek out mates that remain localized in discrete areas (often oviposition sites).

I tested these predictions using a sample of 58 Anisoptera and 120 Zygoptera, which represented nearly

all female-specific colour polymorphic species and their female monomorphic congeners known to occur in Europe and North America (excluding Mexico). Data were gleaned from field guides (Walker 1953; Hammond 1983; d'Aguilar et al. 1986; Peters 1987; Askew 1988; Dunkle 1989, 1990, 2000; Westfall & May 1996; Needham et al. 2000; Sternberg & Buchwald 2000), species accounts (Bilek 1964; de Marchi 1990; Forbes 1994; Kotarac 1996; Jödicke 1997) and personal communication with S. W. Dunkle, R. Jödicke, M. L. May and D. R. Paulson. I excluded from the analysis two polymorphic species (*Lestes sponsa*, *Libellula jesseana*) because each represents less than 5% of otherwise monomorphic genera (see Fincke et al., in press). To control for phylogenetic effects (Felsenstein 1985), one should test whether per capita mating attempts towards single females differ between polymorphic and monomorphic sister species. In the absence of such detailed data, I tested for trends within genera using a dichotomous rank as a surrogate for harassment level. Given few comparable estimates of population density and OSR, I assumed that females of species described as 'rare' or 'restricted in range' experience less harassment than 'common', 'locally abundant' or 'wide ranging' species, whose density and OSR, and hence harassment rates, are probably higher. A species was scored as 'polymorphic' if colour variants of sexually mature females were known from at least one population, and was scored as 'common' if it was known to be so over at least part of its range. Unless stated otherwise,  $P$  values refer to two-tailed Fisher's exact tests.

Among European and North American Odonata, the polymorphism was not constrained phylogenetically, being as widespread in families of Zygoptera (2/8) as in families of Anisoptera (2/5,  $P = 1.0$ ). However, the polymorphism was three times as common in damselfly genera (10/33) as in dragonfly genera (7/69,  $P < 0.001$ ). As shown in Table 4, 67 (56%) of the damselfly species and 37 (64%) of the dragonfly species in my sample displayed the polymorphism. However, 62% of the latter occurred in a single genus, *Aeshna*. Among monomorphic *Enallagma*, more species had only andromorphic females than only heteromorphic ones ( $\chi^2_1 = 8.9$ ,  $P = 0.003$ ), as might be expected if the andromorphic state is the ancestral condition. No such tendency was significant in other genera. For monomorphic species within genera, there was no significant association between a species' rarity and the morph type that was fixed.

Within each of four genera (*Argia*, *Coenagrion*, *Enallagma* and *Aeshna*) that together comprised a majority of the polymorphic species in the sample, the polymorphism occurred more frequently in common species than in rare species. For *Ischnura*, the trend was in the expected direction ( $P = 0.13$ ), after excluding the six monogamous species (Robinson & Allgeyer 1996) where sexual harassment was expected to be minimal. Monogamous females remate only for sperm replenishment and males respect female refusal signals (Fincke 1987). Three of the six *Ischnura* are monomorphic and another two effectively so because andromorphs are rare (Dunkle 1990).

Of the 104 polymorphic species, males of only one species, *Calopteryx splendens*, remain localized at mating

**Table 4.** The distribution by suborder, family and genus of North American and European female polymorphic species and their monomorphic congeners (A: andromorphs; H: heteromorphs), and the type of mating strategy used by males

	Monomorphic species			Polymorphic species		Mating system
	A only	H only				
<b>Zygoptera</b>						
Calopterygidae:						
<i>Calopteryx</i>	2	6	(5/8)	1	(1/1)	Oviposition site territoriality
Coenagrionidae:						
<i>Argia</i>	6	9	(6/15)	15	(14/15)**	Nonlocalized mate searching
<i>Ceriagrion</i>	0	0		1	(1/1)	Nonlocalized mate searching
<i>Chromagrion</i>	0	0		1	(1/1)	Nonlocalized mate searching
<i>Coenagrion</i>	3	1	(0/4)	11	(8/11)*	Nonlocalized mate searching
<i>Enallagma</i>	15	3	(9/18)	17	(17/17)**	Nonlocalized mate searching
<i>Erythromma</i>	0	1	(1/1)	1	(1/1)	Nonlocalized mate searching
<i>Ischnura</i>	0	3	(2/3)	18	(17/18)	Nonlocalized mate searching
<i>Nehalennia</i>	3	1	(0/4)	1	(1/1)	Nonlocalized mate searching
<i>Pyrrhosoma</i>	0	0		1	(1/1)	Encounter site territoriality
<b>Anisoptera</b>						
Aeshnidae:						
<i>Aeshna</i>	2	6	(2/8)	20	(14/20)*	Encounter site territoriality and nonlocalized mate searching
<i>Anax</i>	3	1	(2/4)	3	(3/3)	Encounter site territoriality
<i>Basiaeschna</i>	0	0		1	(1/1)	Nonlocalized mate searching
<i>Oplonaeschna</i>	0	0		1	(1/1)	Encounter site territoriality
Libellulidae:						
<i>Erythrodiplax</i>	0	4	(3/4)	3	(3/3)	Encounter site territoriality
<i>Leucorrhinia</i>	2	5	(3/7)	5	(5/5)	Encounter site territoriality
<i>Crocothemis</i>	0	1	(1/1)	1	(1/1)	Encounter site territoriality

Values in parentheses are the proportions of species described as common, as opposed to rare, that were used to test the assumption that the polymorphism is a response to sexual harassment. \* $P < 0.05$ ; \*\* $P < 0.01$ .

and oviposition sites ( $P < 0.01$ ). This species supports the trend because its polymorphic females are harassed by congeneric males on adjacent territories (de Marchi 1990). Males of the other species either search widely for mates or use encounter site territoriality, defending a perch from which they patrol patches of shoreline for incoming females (see Gribbin & Thompson 1991).

## DISCUSSION

Describing the LMR hypothesis in the language of signal detection illustrates its generality as a dynamic, co-evolutionary model. Within habitats, male receivers that learn and female signal emitters that are behaviourally plastic should opportunistically alter ROC curves (Fig. 1). Habitat structure, population density and OSR should independently affect per capita harassment rates. Thus, morph–environment interactions are expected to vary across habitats, and male preferences for morphs should covary with female costs of harassment. Despite doubts that a single model can adequately explain the maintenance of these polymorphisms (e.g. Andrés et al. 2000, 2002; Sirot & Brockman 2001; Van Gossum et al. 2001b), the data to date are generally consistent with the LMR hypothesis (Table 2). Because the visual modality is a particularly noisy one relative to other sensory channels (Greenfield 2002), females of other diurnal taxa that use visual cues for sex recognition may be pre-adapted to respond to harassment with similar signal variation.

Sexual harassment is known to occur in polymorphic butterflies whose males search for and court females (Cook et al. 1994), making them good candidates for learned mate recognition by both sexes. Direct evidence that negative frequency-dependent selection exerted by a learning receiver is sufficient to maintain multiple signal variants was recently found in blue jays, *Cyanocitta cristata*, responding to virtual prey (Bond & Kamil 2002).

My findings that female-specific signal polymorphisms occur more frequently in common than in rare species, and infrequently when males remain localized for mating (Table 4), tentatively support the assumption that the polymorphism evolved in response to sexual harassment by mate-searching males. The preponderance of the polymorphism in *Aeshna*, among Anisoptera, and its rarity in other mate-searching families such as gomphids and lestids suggest that behaviour, habitat structure and scale, in concert with density and OSR, also affect per capita mating attempts. For example, because *Aeshna* lay eggs endophytically, lone females may be at greater risk of harassment compared to gomphids whose females lack ovipositors and release eggs quickly over the water surface (D. R. Paulson, personal communication) with an obvious motion that also belies a female's receptive state. Relative to damselflies, the large size of many dragonflies, coupled with their tendency to fly over rather than amongst vegetation, decreases signal noise and effectively increases the number of individuals with which they can interact. The fast flight of many species may make females

recognizable via a male's motion detector neurons (Olberg & Worthington 2000) at speeds and distances greater than those over which colours can be detected (see Greenfield 2002). Studies that quantify per capita mating attempts in polymorphic and monomorphic populations, and learning experiments, particularly with polymorphic Anisoptera, should offer rigorous tests of the LMR hypothesis.

Even though harassment has been viewed consistently as the selective pressure driving female signal divergence in odonates, the alternatives to the LMR hypothesis (Table 1) all effectively presume a pre-existing male sensory bias for heteromorphs (Fig. 1). Thus, it is not surprising that Sherratt's (2001) signal detection model of male mimicry predicts that males learn to recognize andromorphs but not heteromorphs. That model, however, is internally inconsistent with respect to its frequency-dependent component, a point revealed by the author's a posteriori prediction that although andromorphs might be equally preferred, they should never be more preferred than heteromorphs. Additionally, Sherratt's mimicry model includes no cost of a miss, an opportunity cost that should favour male learning. Staddon & Gendron's (1983) model of a predator searching for cryptic prey, upon which Sherratt's model was based, included the cost of a missed opportunity. Those authors predicted a frequency-dependent switch in receiver preference, a result not inconsistent with the LMR model.

Females are not considered to mimic congeneric females, presumably because phylogeny offers a parsimonious explanation for those signal similarities. However, for species sympatric over evolutionary time, the lack of divergence from female congeners is consistent with a net distractor benefit for females. It remains unclear whether andromorphs represent the derived state as might be expected of a 'male mimic' that has diverged from a conspicuously 'female type'. This may not be the case for *Enallagma*, where the andromorphic state is the most common one among monomorphic species (Table 4). Molecular phylogenies (Chippendale et al. 1999; Brown et al. 2000) have yet to resolve the issue. In any case, given that andromorphs are the sole female type in many species, any pre-existing male template for 'conspecific female' is unlikely biased towards a morph-specific character. Thus, substituting 'gynomorph' for 'heteromorph' (e.g. Paulson 1999; Van Gossum et al. 2001b) may reveal a bias in human cognition but offers little heuristic value, as it simply makes more explicit the misleading assumption that some morphs are innately more likely to be perceived as 'female' by potential mates.

I suggest that polymorphic females, which have diverged morphologically and in some cases behaviourally from each other, exploit a more general pre-existing bias for conspecific female characters in the male's sensory system. In response to the challenge posed by this signal variation, males increase their detection efficiency by learning details of female morphology and behaviour. A male's temporary preference for a morph type that results from his experience is best interpreted as a temporary bias in a male's neurophysiology, rather than mate choice (e.g. Van Gossum et al. 2001a). The preference per se carries no fitness consequences for either the male receiver or the

female emitter (see also Smith 1984). However, these sensory preferences of males offer insights on female biases for certain sensory modalities that are vulnerable to manipulation by conspecifics (West-Eberhard 1984). Although described as 'pre-existing', such biases in female neurophysiology vary between and within individuals (Ritchie 1996; Brooks & Endler 2001). Furthermore, although they have been interpreted as sensory exploitation by males (Ryan et al. 1990), that need not always be the case. In my example of receiver exploitation, under conditions of low density, a male's sensory bias is mutually beneficial to both sexes (Fig. 2). Mutual benefit is also likely when the presumed 'sensory exploitation' occurs after a female selects a mate on the basis of visual cues (e.g. Córdoba-Aguilar 1999).

Indeed, a mutually beneficial outcome resolves the presumed paradox of *Ischnura gemina*, a species under low sexual selection but which is nevertheless sexually dimorphic in body coloration (Haferník & Garrison 1986). As a rare species, *I. gemina* females should often benefit from the increased detectability provided by a single female signal (Fig. 2). This prediction is consistent with the species' low variation in lifetime mates per male relative to that of other coenagrionids (reviewed by Fincke et al. 1997), the absence of the andromorph in the study population, and its rarity more generally (Garrison & Haferník 1981). In contrast, Sherratt & Forbes (2001) cite the sexual dimorphism of *I. gemina* as supporting an 'aposomatic' benefit that males gain by diverging from the female signal. The LMR model predicts such an antiharassment benefit for conspicuous males, but only in species where male mating attempts (and sexual selection) are relatively higher. When male mating attempts are low, harassment towards both sexes should be low. Importantly, to the extent that sexual harassment, without requiring coercive copulations, selects for male divergence in colour pattern, the same should hold for females.

The speciose families of coenagrionids and aeshnids, which include most of the female polymorphic species, support a role for sexual conflict (Arnqvist et al. 2000) and for polymorphisms (West-Eberhard 1989) in the evolution of biodiversity. However, the LMR hypothesis suggests a process of speciation driven solely by the dynamics of learning sexual signals, akin to 'sensory drive' (Endler & McLellan 1988), independent of sexual selection or ecological niche partitioning. Across a species' range, morph-environment interactions unpredictably influence the shape of male preference and its concomitant female costs. The extent of temporal partitioning of the adult flight season should reflect the relative costs and benefits of heterospecific detractors. When the only resource to be partitioned is the temporal and spatial signalling niche and the only requirement for reproductive isolation is slight modification of an initially plastic receiver bias, divergence in the absence of reinforcement should proceed rapidly. Such a scenario is supported by evidence for recent radiation within the *Enallagma*, a genus of wide-ranging ecological generalists (McPeck 1996; McPeck & Brown 2000), whose mating system makes it vulnerable to genetic drift (Fincke 1982) and favours learned mate recognition (Miller & Fincke 1999).

The general LMR hypothesis is applicable to any taxon for which sexual attention (towards either sex) carries a significant net cost (e.g. Holland & Rice 1999; Moore et al. 2001; Schlupp et al. 2001) or benefit (i.e. sire-seeking species, reviewed by Andersson 1994), and variable signalling has evolved biologically or culturally (see Gowaty 1997) in response to it. Quantifying effects of social systems on the context and content of learning by the receiver sex should be particularly fruitful.

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