

REVIEW

Endocrine disruption of male mating signals: ecological and evolutionary implications

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Summary

1. Endocrine disrupting chemicals (EDCs) are chemicals that interfere with proper hormonal functioning in exposed animals. They enter the natural environment through multiple sources, and many non-target wildlife species are exposed to them via several modes. Exposure causes altered hormone levels, importantly gonadal hormones, resulting in changed reproductive characteristics.
2. Vertebrate male mating signals convey important mate quality information to females. These signals are dependent on androgens for their production and maintenance. Female responses to signals depend on oestrogens. Disrupting these pathways jeopardizes signal production and reception, which has implications for mating system ecology.
3. Besides affecting various aspects of the vertebrate physiology, EDCs can impair hormonal functioning by binding to or blocking hormone receptors, or by altering production and function of hormones or hormone receptors.
4. We consider the ecological implications of multi-generational signal disruption by EDCs. Altered signals can influence population dynamics and sex ratios; local extinctions are possible. Community-level dynamics may be affected via interspecific dependence on signals or population fluctuations.
5. We then address the evolutionary effects of EDC-altered male mating signals in vertebrates and discuss how females may respond to altered signals over evolutionary time. Trans-generational reduction in signal reliability can lead to reduced preference and eventual loss of the signal trait and to the evolution of new traits as signals of mate quality. Genetic divergence between endocrine disrupted and undisrupted populations may result, perhaps giving rise to speciation.
6. Finally, we recommend areas of research to further explore some of the issues addressed in this review. We suggest field surveys to document existing alterations in mating systems and genetic divergence in endocrine disrupted populations. Long-term mesocosm studies and mathematical models would be useful to predict the fate of mating signals and female responses as a result of prolonged endocrine disruption. EDCs have been the focus of ecotoxicology for some time now, and we feel that this analysis should now enter the realm of evolutionary biology to determine the subtle, yet far-reaching effects on exposed non-target wildlife.

Key-words: altered signals, androgens, oestrogenic and anti-androgenic compounds, demasculinization, female response, feminization, sexual selection, signal reliability

Introduction

Endocrine disruption, the interference with proper hormonal functioning by exogenous compounds, has explicitly been a focus of ecological research for almost two decades now (since Colborn 1991). Some of the most important effects of these endocrine disrupting chemicals (EDCs) are the sub-lethal effects on populations caused by reproductive

malfuctions. The most important of these are effects on reproductive traits, and these can have long-term ecological as well as evolutionary significance, as we will emphasize. Endocrine disruptors can alter reproductive success by affecting all aspects of the reproductive system, including gonadal formation, production of hormones and gametes, sex determination (Basrur 2006), formation of egg shells (Porter & Wiemeyer 1969) and production (Kelce & Wilson 1997; Basrur 2006) and maintenance of mating signals and behaviours (Palanza & vom Saal 2002; Milnes *et al.* 2006).

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Several reviews have addressed endocrine disruption from ecological (Colborn, vom Saal & Soto 1993; Colborn 1995; Jones & Reynolds 1997; Crews, Willingham & Skipper 2000; Guillette *et al.* 2000; Wingfield 2008), physiological (Basrur 2006; Milnes *et al.* 2006; Patisaul & Adewale 2009) and clinical (Toppari *et al.* 1996; Kelce & Wilson 1997) perspectives.

Endocrine disruptors can have lasting effects in local populations. Many of these chemicals are persistent in soil and animal tissue at low concentrations and can bioaccumulate (Smolen & Colborn 1997); their effects are observable even at supposedly safe levels. The effects can be multi-generational either by exposure to soils containing persistent endocrine disruptors or via maternal effects (Clotfelter, Bell & Levering 2004). Multi-generational changes in mating signals and behaviours in a local population can be of ecological significance if reproductive success is altered and of evolutionary significance if populations evolve genetic responses to these alterations. Evolutionary effects may include altered mating systems or development of resistance to endocrine disruptors. If these changes are hereditary, intraspecific differences across populations may lead to genetic divergence.

In this review, we address the effects of endocrine disruptors on mating signals and behaviours in male vertebrates and show how these changes can have ecological and evolutionary significance in wild populations. We focus primarily on the oestrogenic and anti-androgenic effects of endocrine disruptors in vertebrate systems, as these are the most common effects of EDCs (Guillette 2006); androgenic contaminants are found mainly in livestock feedlot wastes (Soto *et al.* 2004; Kolok *et al.* 2007; Khan *et al.* 2008) and a few pesticides (Barbaglio *et al.* 2006). First, we outline concepts surrounding signalling theory and address altered signals and responses with the goal of understanding the implications of EDC-altered signals. Next, we review the control of these mating signals by androgens, and then elucidate the mechanisms by which EDCs can disrupt the production and maintenance of these signals. We then explore the ecological and evolutionary implications of altered mating signals and female responses as a result of prolonged EDC-exposure. Finally, we recommend areas of research that could further explore some issues addressed in this article. We focus mainly on EDCs disrupting male signals, their potential for altering female responses, and the resulting implications for mating systems. Alteration of female signals or other reproductive characteristics, like number of eggs or size of eggs, is a separate and complex topic in itself and will not be considered in this review.

Male mating signals and female receivers – definitions

For present purposes, we define *mating signals* as male morphological and behavioural traits that may be capable of conveying information about the transmitter's quality and of influencing his reproductive success via female choice. Male *quality* expresses benefits that the male provides to the female, which directly or indirectly increase her fitness. *Displays* are behaviours aimed at attracting the attention of females and

consequently showing off specific morphologies. Zahavi (1975) suggested that signals are costly to produce and maintain, 'confer[ring] a handicap on survival'. These costs may include metabolic costs of production and maintenance, and predation and parasitization risks due to the conspicuous nature of the signal or the added burden of a large ornament. In some systems where there are neither metabolic nor predatory costs on signal production and maintenance, social rules enforce signal honesty (Harris sparrows, *Zonotrichia querula*: Rohwer & Rohwer 1978; house sparrows, *Passer domesticus*: Moller 1987). Signals thereby allow for assessment of quality, as implied by studies showing positive correlations between signal strength and male quality. For example, acquired resistance, a measure of quality in guppies (*Poecilia reticulata*), correlates with sigmoidal displays and orange colour spots (Lopez 1998); foraging ability, another heritable trait that measures quality in guppies, is associated with coloration (Karino, Utagawa & Shinjo 2005); bill colour of male blackbirds (*Turdus merula*) correlates with parental abilities (Preault *et al.* 2005); and redness of northern cardinals (*Cardinalis cardinalis*) is strongly associated with quality of territory the male defended (ability to defend a good territory was the measure of quality; Wolfenbarger 1999). A signal is a reliable indicator of quality if there is a strong correlation between trait values expressed by the males and their quality, as defined according to the species (Maynard Smith & Harper 2003).

signal has to be detectable, discriminable and assessable. We define detectability as the probability that the signal stands out from noise and is thus recognizable as a signal; discriminability as the probability that the receiver can accurately discern the level of the signal compared with the range of signal values produced by other individuals in the population; and assessability as the probability that the female can accurately associate the signal value with the appropriate quality level. Females receive these signals and respond more strongly to males expressing higher trait values (Grafen 1990). We refer to the measure of the females' response to a given quality as responsiveness. A female's response to a signal (i.e. how much she invests – time, energy, eggs – in that particular mating event) may be hereditary (Pomiankowski 1987), and a response has a cost to the female, either metabolic or through predation risk, or as lost mating opportunities (Pomiankowski 1987). Females should have distinct thresholds in true trait value below which they do not respond and above which they respond maximally. But trait values are perceived with error (Hoelzer 1989) and females differ in their threshold magnitude, resulting in responsiveness that can be expected to increase in a sigmoid fashion with male trait value. For each quality value, there is a 'best' response that maximizes female fitness (Grafen 1990).

To describe discriminability, we refer to Fig. 1: here the *x*-axis represents the value of the trait (for example, wavelength being reflected, reflectance of a particular wavelength, frequency of sound waves, etc.), while the *y*-axis represents frequency density. Two representative curves are shown, each representing a particular mean trait value corresponding to a quality value. For explanatory purposes in this review, the

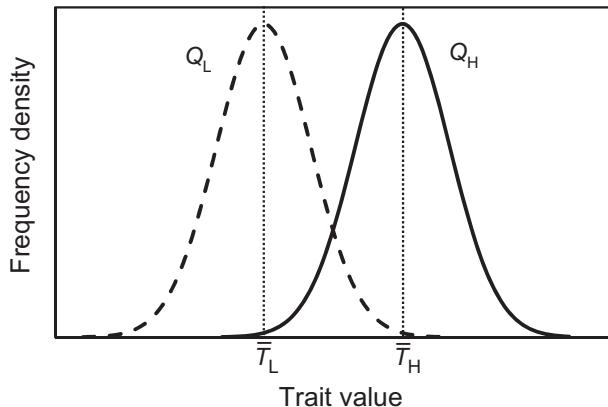


Fig. 1. Discriminability between signal trait values represented by individuals of two differing quality values. The solid curve represents the trait value (T_H) produced by the high quality male (Q_H) while the broken curve represents the trait value (T_L) produced by the low quality male (Q_L). The means are represented by \bar{T}_H and \bar{T}_L respectively. Discriminability is a function of the difference between high and low-quality trait means, divided by their common standard deviation (effect size: Cohen 1969). The higher the discriminability, the greater is the probability that the high trait stands out distinctly from the low trait. The overlapping areas allow for incorrectly identifying the low trait as being produced by the high quality male or *vice versa*.

curves represent a mean high trait value (\bar{T}_H) produced by a high quality male (expressing quality Q_H), and a mean low trait value (\bar{T}_L) produced by a low quality male (expressing quality Q_L). The y -axis then represents frequency of trait values expressed by males of quality Q_H and Q_L . The closer these curves are to each other, the less discriminable is the high trait value from the low trait value. Discriminability is thus a function of the difference between high- and low-quality trait means, divided by their common standard deviation (cf. effect size of Cohen 1969). In reality, quality values will occur along a continuum, and corresponding trait values will also occur continuously. Discriminability would then refer to the probability that a trait value from a Q_H distribution is greater than a trait value from a Q_L distribution, for any pair of trait values selected randomly from the two distributions. Discriminability could be reduced either by smaller difference between the means, or by increased variance.

Altered signals and responses

Here we address altered signals and their implications, with a view to discussing implications of EDC-altered signals further in the article. *Altered signals* are traits used for signalling quality whose means have shifted substantially in a short span of time. After the change, these traits may or may not continue to signal the true quality of the signaller. Signals may be altered due to novel selection pressures like habitat changes (e.g. see the case study of great tits, *Parus major*, reviewed by Slabbekoorn & Ripmeester 2008). It is possible that the altered signal may continue to be discriminable as well as reliable, remaining a dependable indicator of quality, even if it is altered. Females may undergo an assessability lag, during which the sigmoid response curve is displaced along the axis

of male quality because of decline in trait values (Fig. 2a). Eventually under selection, by shifts in behaviour or by evolutionary change, this curve may shift back to its former position along the quality axis. Consequently, if the trait values remain constant, the female response curve shifts along the axis of male trait values so that the new trait values generate responses similar to those previously associated with high and low male qualities (Fig. 2b). Further, if endocrine disruption were to induce oestrogenicity, females could become more responsive to male displays (as seen in ovariectomized African clawed frogs, *Xenopus laevis* treated with a combination of oestradiol and progesterone: Kelley 1982; tungara frogs, *Physalaemus pustulosus* during periods of high circulating oestradiol: Lynch *et al.* 2005), thus shifting the female response curve to the left and leading to less discrimination between high and low signal values (Fig. 3a). In other words, females could become less choosy. An alternate possibility is that females become more choosy (as seen in zebra finches, *Taeniopygia guttata* treated with oestradiol: Vyas *et al.* 2008, 2009) by responding even lower to low signals and higher to high signals (Fig. 3b). In this case, the sigmoid response curve has a steeper slope about the same inflection point. A similar change in the curve, but with a shallower slope, could also produce less choosy responses. The exact theoretical mechanism by which oestradiol produces choicer or less choosy female responses is not clear, but regardless there is evidence for both cases.

Some alterations lower the discriminability of the signal. In Fig. 4, suppose after exposure to endocrine disruptors the high trait curve moves closer to the low trait curve (Fig. 4b), or varied responses to the endocrine disruptor within the population lead to increased variances (Fig. 4c); then the signal will be less discriminable or less reliable, respectively. Lowered discriminability implies a smaller range of trait values within the population, and does not necessarily imply unreliability of the signal. However, increased variance can reduce the correlation between trait value and quality, thereby reducing reliability (Fig. 4c). Females may then be unable to rely on these traits to assess male quality. Not all altered signals are rendered unreliable, but they may be less reliable.

We assume that the exogenous compound responsible for signal alteration does not generally affect quality itself. However, this may not be the case in all situations. For example, if the compound is an anti-androgenic or oestrogenic compound, the same vector might enhance immunocompetence by reducing androgen levels (Folstad & Karter 1992), or reduce immunocompetence via other pathways (Christin *et al.* 2003; Brodkin *et al.* 2007; Markman *et al.* 2008; reviewed in Ahmed 2000). In many animals, immunocompetence is a measure of quality (Hamilton & Zuk 1982; Lopez 1998). Such more complex cases are beyond the scope of this review.

In a system where a trait has evolved to be a reliable signal, and alterations render it either less reliable or unreliable, it becomes costly for females to depend on that signal as an indicator of quality. In such situations, one might expect females to stop responding to the signal, or respond more weakly. As illustrated in Fig. 5, the loss or weakening of the signal-quality

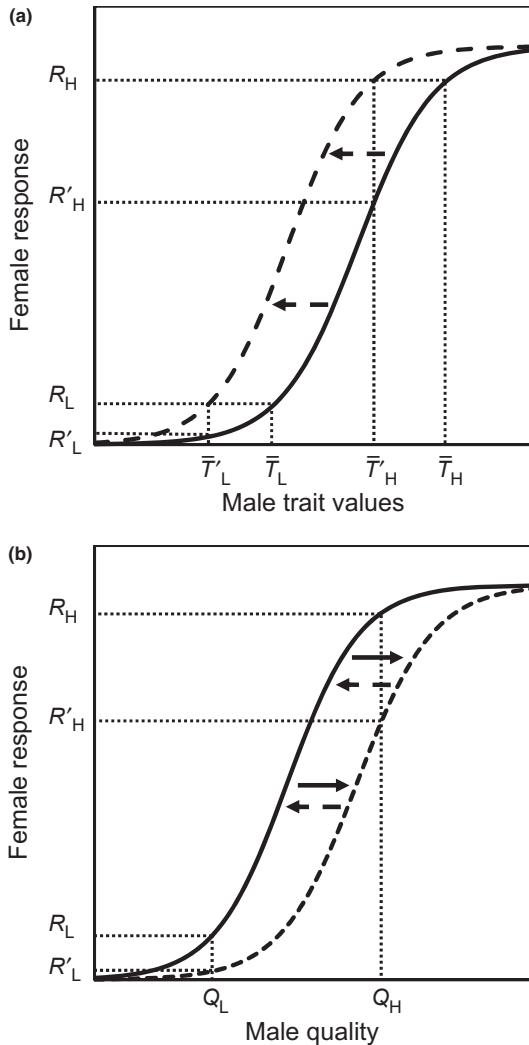


Fig. 2. Female responses to the altered male signals. The solid line represents original female responsiveness to unaltered signals. (a) After endocrine disruption, females respond R'_H and R'_L respectively to the altered mean trait values \bar{T}'_H and \bar{T}'_L , which is a lower than R_H (response to \bar{T}_H) and R_L (response to \bar{T}_L). This reduced response increases fitness costs to both males and females, imposing selection pressures on females to alter their responses. Hence, across generations, female responses should adjust to the altered signals such that a strong response (R_H) should now match the altered mean high trait value \bar{T}'_H and the weak response (R_L) should match \bar{T}'_L . The time taken for this shift is the assessability lag. (b) After endocrine disruption, both high quality and low quality males signal lower than their original means. Females will associate these lowered trait values with lower quality and respond more weakly leading to a shallower response curve (broken line). Hence there is a shift in female responses to male quality, which follows the shift (solid arrow) in female responses to trait values. Eventually, females adapt to the altered trait values and their responses to quality shift back to the original (broken arrows).

correlation can lead to a cyclic pattern of reduced female responsiveness to the signal and to the consequent further weakening of the signal-quality correlation. Reduced female choosiness (as in Fig. 3a) relaxes selection pressures on the signal to be discriminable and through a similar cyclical pattern leads to the signal becoming a less reliable indicator of mate

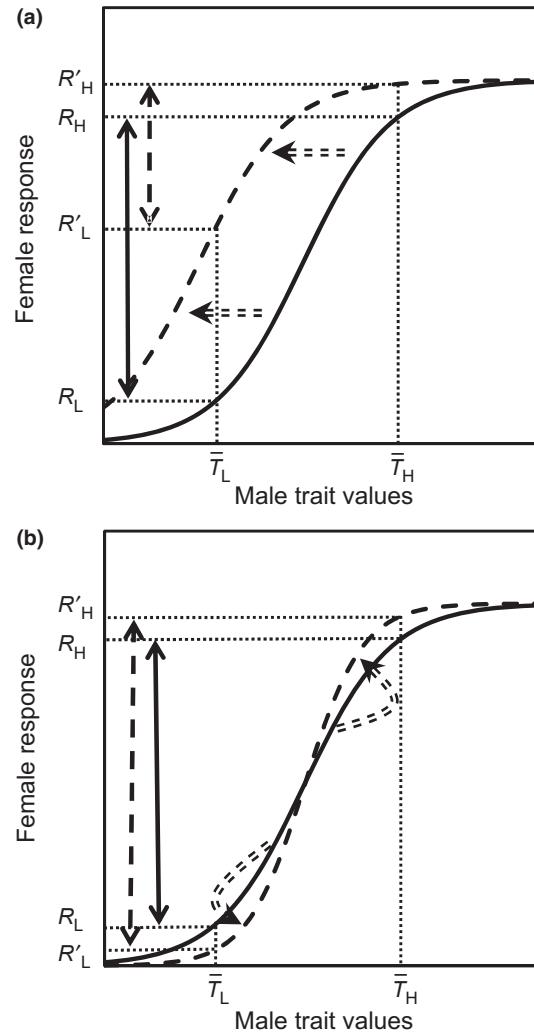


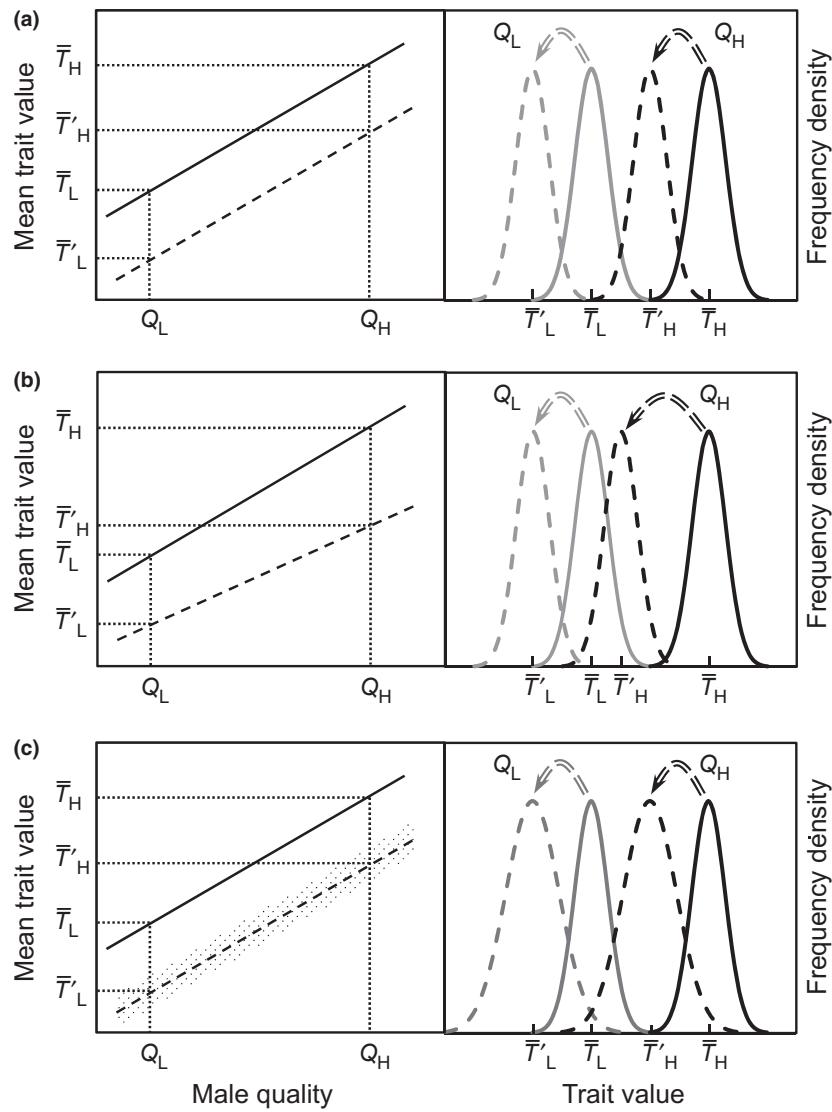
Fig. 3. Altered female responses to male traits as a result of endocrine disruption. (a) Exogenous oestrogens increase female responses to displaying males, which moves the female response curve to the left (dashed line). Hence for the same male trait value, females respond more strongly. This also reduces the difference in response to a high trait value versus a low trait value, thereby reducing female discrimination between two trait values. Female choosiness (i.e. discrimination between high and low trait values) is depicted by the solid and dashed double ended arrows between the high and low responses, before and after EDC exposure, respectively. Note that this reduced discrimination is particularly clear when the two male traits are somewhat symmetrical on either side of the inflection point. (b) Exogenous oestrogens could alter the response curve by shifting it about the inflection point with a steeper slope. This would produce choicer responses to the same male traits.

quality. A combination of effects of EDCs on both male signals and female responses can hasten the process of rendering the signal unreliable (Fig. 5). Conversely, increased female choosiness (as in Fig. 3b) raises selection pressures to make signals more discriminable. If males are able to respond to these pressures, the signal can become a more reliable indicator of mate quality; but if males are unable to make their signals more discriminable, choicer females face high costs of unreliable signals and are likely to stop using the trait as a quality indicator. Other traits may evolve to become primary

Fig. 4. Characteristics of altered male signals after exposure to EDCs. High quality males (Q_H) produce a mean trait value \bar{T}_H before disruption and \bar{T}'_H after disruption. Low quality males (Q_L) produce a mean trait value \bar{T}_L before disruption and \bar{T}'_L after disruption. Panels on the left associate male trait value with male quality. Regressions will generally have variation around the lines, but this has not been shown (except in panel c) for clarity's sake. Panels on the right are frequency density plots of male trait values in the population expressed by high quality and low quality males. Solid lines represent trait values before endocrine disruption and broken lines after endocrine disruption. In the frequency density plots, black curves represent high trait values, and grey curves represent low trait values. (a) The slope of the regression line after disruption may be the same as that of the regression line before disruption; in this case the signal will continue to be reliable (same slope) and discriminable (same d). (b) If exposure to EDC causes a proportional reduction in trait values, then the slope will become lower, reducing reliability as well as discriminability (by reducing the mean between \bar{T}'_H and \bar{T}'_L curves). (c) Response to the endocrine disruptor will not be similar by all individuals of a given quality in the population. This will increase the variance of the frequency density curves. The slope may or may not remain the same after disruption (for simplicity's sake, it has been depicted as unchanged in this figure). Increased variance will reduce discriminability, as well as the reliability (by a reduction in correlation between trait value and quality). If this is combined with a reduced slope, then the outcome will be an even less discriminable and reliable signal.

indicators of quality, while the earlier trait might disappear (Morris *et al.* 2005) or become secondary cues in female mate assessment (Scheffer, Uetz & Stratton 1996; Seehausen & van Alphen 1998; reviewed in Candolin 2003).

Signals evolve to be specifically received by conspecifics and often serve as mate-recognition factors (courtship songs of sympatric flies, *Drosophila ananassae* and *D. pallidosa*: Yamada, Matsuda & Oguma 2002; mating preferences of the swordtail fish, *Xiphophorus pygmaeus*: Hankison & Morris 2003; also reviewed in Ptacek 2000; Schlüter 2001). If received and responded to by heterospecifics, hybridization may occur. This can happen in closely related sympatric species with similar signals (bluegill sunfish, *Lepomis macrochirus* and pumpkinseed sunfish, *L. gibbosus*: Konkle & Philipp 1992). Changes between populations in sexual traits are quite often driven by sexual selection (reviewed in Panhuis *et al.* 2001). The co-evolution between signallers and receivers (males and females, respectively, in the case of this review) based on the trait strengthens the linkage between mate quality advertising and assessment. Altered signals could hence blur the distinction between closely related sympatric species, leading to



hybridization and possibly loss of species (Seehausen, van Alphen & Witte 1997; Seehausen & van Alphen 1998).

Hormonal regulation of mating signals and female responses

Testosterone, an important androgen, is believed to play a key role in the development and maintenance of ornaments and other signals in male vertebrates (Hillgarth & Wingfield 1997). Synthesis of 5 α -dihydrotestosterone (DHT) from testosterone is necessary for the development of external sexual organs (Neubert 2002). Aromatization of testosterone into oestrogen in the brain is essential for the development and execution of appropriate male behaviours (Ball & Balthazart 2004).

For the purpose of this review, male traits will be subdivided into male-specific anatomies, male-specific morphologies and male-specific behaviours, all relating to reproductive function. ‘Anatomy’ will refer to internal organs, such as the larynx, vomeronasal organ and brain, responsible for the production or perception of signals, while ‘morphology’ will refer to external features such as colour patterns, plumage and

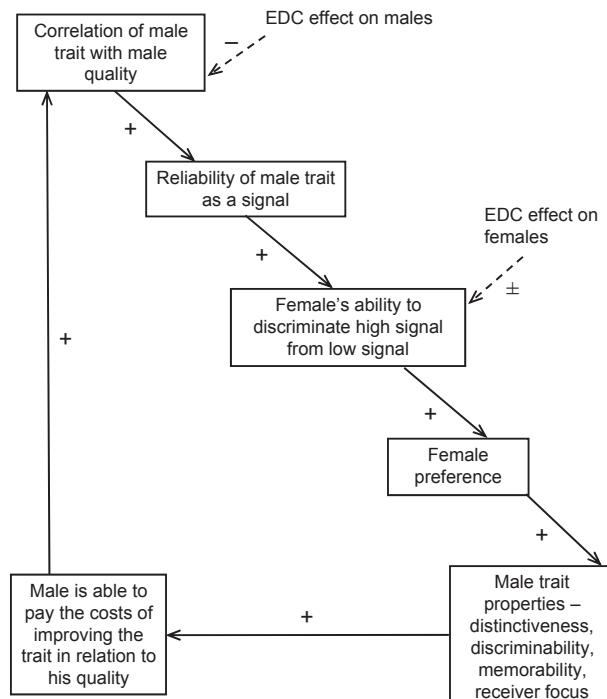


Fig. 5. Mechanism by which a trait might evolve into a signal or be lost. If there is a positive correlation between the male trait and male quality within the population, the trait has a stronger probability of becoming reliable as a signal of true quality. The more reliable a trait is as a signal, the stronger the selection on females to discriminate between high and low signalers, thereby strengthening female preference. As female preference strengthens, there is selection on the male trait to become more distinctive, discriminable, and increase specificity to be received by desired receivers only. There are generally costs associated with improving these traits, and high quality males are able to afford these costs better than low quality males (Grafen 1990; Moller & Lope 1994). This feeds back into further strengthening the correlation between variation in the trait and variation in male quality in the population. Conversely, if the correlation between trait and male quality is reduced (due to exposure to EDCs) as in Fig. 4, there will be subsequent negative impacts at all stages of the chain causing a weakening of the male trait properties and a further weakening of the correlation between trait and quality. Lowered female choosiness (due to EDC exposure) as in Fig. 3a can also lead to the same result. This process is expedited when both males and females are affected by EDCs. Increased choosiness increases costs to females if males, due to endocrine disruption, are unable to make their signals more discriminable; hence this too leads to a similar outcome.

other ornaments. ‘Behaviour’ will refer only to sex-specific reproductive behaviours. We will explore the role of androgens in the development and expression of these phenotypes.

Androgens are crucial for the proper development of sexually dimorphic anatomies. The example of the development of the larynx in anurans, illustrated below, provides a well-studied example. Males of most anuran species vocalize as a mating signal. Females of most species do not vocalize, while those that do have a different vocalization pattern from males. It is the difference in larynx structures that permits this difference between males and females.

Male vocalization requires certain specific muscle types that develop only in the presence of androgens. Male and female *X. laevis* produce distinctly different calls (Tobias, Marin &

Kelley 1991). Production of male calls requires certain muscle types (fast twitch) that do not develop in females (Sassoon, Gray & Kelley 1987; Marin, Tobias & Kelley 1990; Tobias, Marin & Kelley 1991). A larynx specific myosin heavy chain gene (LM) isolated from laryngeal muscles of *X. laevis* is responsible for conversion of laryngeal muscle type from slow twitch to fast twitch after metamorphosis (Catz *et al.* 1992). Expression of LM is regulated by endogenous androgens, especially DHT (Catz, Fischer & Kelley 1995); the maintenance of fast twitch muscle fibres also requires androgens (Potter, Bose & Yamaguchi 2005). Similarly, the syrinx in songbirds is an androgen-sensitive organ (Gong *et al.* 1999; reviewed in Wade 2001): female zebra finches with increased testosterone increase the size of their syrinxes (Gong *et al.* 1999; Wade & Buhlman 2000), while castrated males have reduced syrinxes, which can be reversed with testosterone or androsterone treatment (Harding, Sheridan & Walters 1983). This has mainly been explored in zebra finches.

Males of many vertebrate species have conspicuous morphologies like bright plumage, large tails and characteristic colour patterns that signal the individual’s quality to conspecific females. Development and maintenance of these sexually dimorphic morphologies are believed to be regulated by androgens and have been well studied in various taxa (red jungle fowl, *Gallus gallus* combs: Zuk, Johnsen & Maclarty 1995; superb fairy-wren, *Malurus cyaneus* plumage: Peters, Astheimer & Cockburn 2001; house sparrow badges: Gonzalez *et al.* 2001; Strasser & Schwabl 2004; guppy coloration: Jayasooriya *et al.* 2002; zebra finch beaks: McGraw, Correa & Adkins-Regan 2006; cirri lengths of Shermani salamanders, *Plethodon shermani*, used in uptake of pheromones: Schubert *et al.* 2006; cichlid *Pundamilia nyererei* nuptial coloration: Dijkstra *et al.* 2007).

The role of androgens in mating behaviours of vertebrates has been studied quite extensively in different taxa. Male reproductive behaviours may be defined as actions performed by males that increase mating success, reproductive success and offspring survival. These include territoriality, courting females, vocalization, mounting females, building nests and parental care. Studies from different taxa have shown the dependence of these behaviours on androgens. 11-Ketotestosterone (KT), a potent teleost androgen was found to be required for parental care in bluebanded goby (*Lythrypnus dalli*) (Rodgers, Earley & Grober 2006), courtship behaviour in mosquitofish (*Gambusia holbrooki*) (Toft & Guillette 2005) and guppies (Baatrup & Junge 2001; Bayley, Junge & Baatrup 2002) and female recognition and courtship in goldfish (*Carassius auratus*) (Thompson *et al.* 2004b).

Studies on brain regions responsible for sexual behaviour in birds and mammals have shown that the preoptic area (POA) and medial preoptic nucleus (POM) in the brain control these behaviours (reviewed in Ball & Balthazart 2004). These regions are sexually dimorphic and larger in males than in females. They are rich in androgen receptors. Castration causes these regions of the brain to shrink and corresponds to a reduction in sexual behaviour, while implanting testosterone in the POA or POM can restore sexual behaviour to pre-castration levels. Electrolytic lesions of the POM also disrupt sexual behaviours.

It is believed that aromatization of testosterone into oestrogen and DHT in these regions of the brain are responsible for male sexual behaviours (Ball & Balthazart 2004).

Empirical studies have correlated testosterone levels with mating behaviours in several bird species (singing, pursuing females, aggression towards males, territoriality in red grouse, *Lagopus lagopus scoticus*: Watson & Parr 1981; altered mating systems from monogamy to polygyny in white-crowned sparrows, *Zonotrichia leucophrys pugetensis*, and song sparrows, *Melospiza melodia*: Wingfield 1984; crowing and mounting attempts in Japanese quail, *Coturnix coturnix japonica*: Balthazart, Foidart & Hendrick 1990; bower features in satin bowerbirds, *Ptilonorhynchus violaceus*: Borgia & Wingfield 1991; extra pair copulations and time spent with paired female in mallard ducks, *Anas platyrhynchos*: Davis 2002). Similar patterns are also seen in amphibians (vocalization pattern in *X. laevis*: Kelley 1978; calling rates in tungara frogs: Marler & Ryan 1996; clasping behaviour in *X. laevis*: Potter, Bose & Yamaguchi 2005; activity levels associated with recognizing female pheromones in Shermani salamanders: Schubert *et al.* 2006; also reviewed in Moore, Boyd & Kelley 2005).

Oestradiol has been implicated in several taxa as the primary driver for female responses to male mating signals. In female tungara frogs, oestradiol treatment increases receptivity, a positive response to a conspecific male call (Lynch *et al.* 2006; Chakraborty & Burmeister 2009), and permissiveness, a positive response to any male call, including unattractive calls (Lynch *et al.* 2006). Similarly, female tungara frogs were more receptive to male calls, and less choosy between attractive and unattractive calls during amplexus, the stage associated with increased levels of circulating oestradiol when females are ready to oviposit (Lynch *et al.* 2005). In another study, oestradiol treatment made the frogs *more* choosy (Lynch *et al.* 2006); but here the females chose between an attractive conspecific call and a hybrid artificial call, which may simply resemble a heterospecific call rather than an unattractive conspecific call.

Female *X. laevis* treated with a combination of oestradiol and progesterone increase receptivity to males (Kelley 1982). Similar oestrogenic control of female responses to male mating behaviours has been seen in zebra finches (Vyas *et al.* 2008, 2009), where oestrogen treated females were more receptive to male songs, but also more discriminating between complex and simple male songs. Female white throated sparrows (*Zonotrichia albicollis*) implanted with oestradiol responded to male songs with 'copulation solicitation displays', which corresponded to an increased expression of *zenk* (also known as *egr-I*) expression in the auditory forebrain (Maney, Cho & Goode 2006). *Zenk* expression is associated with positive responses to male songs. Another study on the same species showed that *zenk* expression increased in nine brain regions thought to be part of the 'social behaviour network' in response to male songs only in oestradiol treated females (Maney *et al.* 2008). Similarly, female tungara frogs treated with human chorionic gonadotropin (which stimulates the production of gonadal hormones) showed higher expression of *egr-I* in the auditory midbrain in response to

male choruses (Lynch & Wilczynski 2008). This mechanism is dependent on catecholamines, which allow the brain to respond selectively to important stimuli (Le Blanc *et al.* 2007). Oestrogen treatment of female white throated sparrows increased density of catecholaminergic innervation in the auditory forebrain and the number of catecholaminergic cells in brain regions involved in song learning and production (Le Blanc *et al.* 2007).

Endocrine disruption of mating signals

The term endocrine disruption refers to the interference with proper functioning of the endocrine system due to exposure to exogenous compounds. Common types of EDCs include organochlorides, organophosphates, polychlorinated biphenyls (PCBs), phthalates, synthetic hormones and hormone-blockers and phytoestrogens. These enter the natural environment via such sources as pesticides, industrial effluents, pulp mill effluents, plastics and sewage. Significant routes of exposure include direct exposures from living in contaminated soil or water, as well as indirect exposures through eating contaminated prey (Markman *et al.* 2007, 2008; Park *et al.* 2009; Walters *et al.* 2010). It is important to note that EDCs are often irregularly distributed along a landscape, exposing individuals differentially within a population.

Many ecological stressors that are not endocrine disruptors by definition also alter mating signals (heavy metals: Gorissen *et al.* 2005; Hallinger *et al.* 2010; acidification: Lorenz & Taylor 1992; Ortiz-Santiestra *et al.* 2009; hypoxia: Abrahams, Robb & Hare 2005; Kuperberg, Brown & Clotfelter 2009). Exploring these mechanisms is beyond the scope of this review. Here we restrict our discussion to EDCs, but note some effects of non-EDC contaminants and stressors (along with EDCs) on mating signals in Table 1.

Goksoyr *et al.* (2003) list the mechanisms by which EDCs can alter the natural functioning of hormones: (i) agonistically, by binding to hormone receptors and mimicking natural hormones; (ii) antagonistically, by blocking or altering the binding of natural hormones to hormone receptors; (iii) altering production and breakdown of natural hormones; and (iv) altering production and function of hormone receptors.

Oestrogenic EDCs are agonistic and compete with oestradiol to bind to oestrogen receptors (ER- α or - β) (Kuiper *et al.* 1998), or increase endogenous oestrogens by inducing aromatization (Fan *et al.* 2007). Exposure to oestrogenic EDCs is associated with decreased circulating testosterone levels in male vertebrates (e.g. 4-tert-octylphenol (OP): Blake & Boockfor 1997; Kim *et al.* 2007; bisphenol-A: Takao *et al.* 1999; Nakamura *et al.* 2010; endosulfan: Saiyed *et al.* 2003; atrazine: Hayes *et al.* 2010; Victor-Costa *et al.* 2010; o,p'-DDT: Mills *et al.* 2001), thereby altering androgen-regulated mating signals. The mechanism by which oestrogenic EDCs decrease testosterone production in testes appears to be via the reduced expression of steroidogenic enzymes (estadiol and diethylstilbestrol: Bartke, Williams & Dalterio 1977; di(n-butyl) phthalate: Thompson, Ross & Gaido 2004a; OP: Kim *et al.* 2007; PCB: Murugesan *et al.* 2008) and altered

cholesterol metabolism and transport (di(*n*-butyl) phthalate: Thompson, Ross & Gaido 2004a; OP: Kim *et al.* 2007) in Leydig cells.

Endocrine disrupting chemicals that have anti-androgenic effects in vertebrates prevent the binding of androgen with the androgen receptor (AR), thereby inhibiting transcription of AR-dependent genes. Binding of androgen to AR causes a conformational change in AR that is required for stabilization against proteolytic degradation, and for the AR dimerization necessary for transcriptional activation (Quigley *et al.* 1995; Zhou *et al.* 1995). Mechanisms by which anti-androgens inhibit the functioning of AR-dependent gene transcription are by preventing AR binding to DNA or by preventing initiation of transcription (Truss, Bartsch & Beato 1994); most of the studied environmental anti-androgens function by the former mechanism (Kelce & Wilson 1997). This disruption of AR-dependent gene transcription can interfere with sex differentiation, development of sexually dimorphic anatomies, morphologies and behaviours, production of sperm and maintenance of sexually dimorphic morphologies and behaviours (as illustrated in Table 1), ultimately affecting the individual's reproductive success.

Evidence of contaminant induced alteration of male mating signals is seen in various taxa exposed to a range of chemicals. Table 1 lists examples of altered expression of male mating signals by exposure to various EDCs as well as non-endocrine contaminants. In most cases, exposure to the contaminant reduced the expression of the signal compared with the controls. Edwards & Guillette (2007) suggest that the increased gonopodial length of nitrate-exposed mosquitofish could be due to the inhibition of steroid synthesis because of the deactivation of P450 enzymes by nitrates. Of special interest is the paradoxical positive effect of EDCs on song characteristics accompanied by increased HVC volume, the brain region involved in singing, in the case of European starlings (*Sturnus vulgaris*), which increased their attractiveness to female starlings (Markman *et al.* 2008). These results are supported by evidence for the role of oestrogens in the development of male-specific song nuclei in the brain of songbirds (Schlinger 1997; Holloway & Clayton 2001). However, the increased song complexity was accompanied by reduced immunocompetence, which has implications for fitness (Markman *et al.* 2008). It is not clear whether the increased song complexity was proportional to mate quality in this study. But if immunocompetence can be considered a measure of mate quality, then the increased song complexity and decreased immune responses as a result of EDC-exposure only blurs the correlation between signal and quality, leading to females being attracted to individuals of perhaps lower quality than expected. However, these results are not consistent with other studies; Iwaniuk *et al.* (2006) showed a decreased volume of brain regions involved in singing and sexual activities in American robins (*Turdus migratorius*) that came from nests with eggs containing high DDT levels. Heavy metals also appear to negatively affect song characteristics (see Table 1 for details). Hence the effects of EDCs on birdsong appear to depend on the particular pollutant, and

the exact mechanisms of action are not clear. The effects of various pollutants on reproductive behaviours of fish including courtship behaviours, parental care and aggression have been reviewed in Jones & Reynolds (1997).

Ecological implications of altered male mating signals

Signal disruption due to feminization of males exposed to EDCs can have significant ecological effects, if the contaminant affects a large section of the population. Altered mating signals can include size of ornaments, intensity of coloured signals, pheromonal production and courtship behaviours such as displays, nest building and competitiveness (reviewed in Clotfelter, Bell & Levering 2004). Females discriminate against males with EDC-altered mating signals (e.g. Arellano-Aguilar & Garcia 2008; Secondi *et al.* 2009), thus directly affecting the males' fitness. Altered demographics, and local extinctions in extreme cases, are possible if females do not adapt or otherwise adjust to the altered signals soon enough. If the altered signal is not reliable, both males and females incur higher costs that reduce reproductive success. Costs to males include reduced mating opportunities; costs to females include possible reductions in offspring number and quality. Similar costs also arise for females if endocrine disruption renders them less choosy; in this case it is also unduly costly for males to have discriminable signals. If, however, females are rendered choosier, they incur heavier costs by depending on unreliable signals. Increased choosiness can increase the frequency of extra-pair copulations (EPCs) in species where this occurs (Kempenaers, Verheyen & Dhondt 1997). Increased mating frequency increases fitness costs such as predation risks, energy costs, the risk of pathogen transfer and so forth (Keller & Reeve 1995). Increased EPCs can further alter demographics by decreasing effective population sizes. Fitness costs to females and propagation of lower quality individuals as a result of signal mis-communication have consequences for population persistence (Kokko & Brooks 2003). The effects on individuals have obvious links to population level effects via reduced reproductive success resulting from signal mis-communication and supernormal clutch sizes (with reduced success) from female–female pairs as a result of reduced availability of male partners (Hunt & Hunt 1977; Ryder & Somppi 1979; Fox 1992).

The effects of mate choice on population dynamics have been reviewed by Quader (2005), and the implications are relevant to altered mating signals. It has been suggested by several authors that environmental changes are more threatening to species with higher degrees of sexual selection (Kokko & Brooks 2003; Morrow & Pitcher 2003); altered mating signals in such species could affect population viability. The resulting low fitness of individuals in these contaminated habitats can produce ecological sinks (Matson *et al.* 2006). Sex ratios can be skewed due to decreased predatory risks for males as a result of less obvious ornaments. This can also have community and ecosystem level effects if population sizes fluctuate uncharacteristically (e.g. Whiles *et al.*

Table 1. Empirical studies showing altered reproductive traits in male vertebrates after contaminant-exposure

Species	Trait disrupted	EDC	Reference	
Guppy (<i>Poecilia reticulata</i>)	Sigmoid display rate Time spent in mating behaviours Area of orange colour spots Gonopodium length Nest building behaviour, courtship behaviour Courtship behaviour Olfactory response to female pheromones Courtship behaviour Median fins Courtship behaviours Courtship Leading female to nest Completion for nesting sites Gonopodium length	→ → → → → → → → → → → → → ↑	Flutamide, DDE, Viclozolin Flutamide, DDE, Viclozolin Viclozolin, Flutamide 4-tert-Octylphenol Viclozolin Fenitrothion Perchlorate Atrazine Atrazine, simazine Tributyltin, mixture of tributyltin + PCBs Methyl parathion Methyl parathion 17α -ethynodiol oestradiol 17α -ethynodiol oestradiol 17β -ethynodiol oestradiol Nitrate	(Baatrup & Junge 2001) (Baatrup & Junge 2001) (Baatrup & Junge 2001) (Toft & Baatrup 2001) (Bayley, Junge & Baatrup 2002) (Sebire <i>et al.</i> 2009) (Bernhardt & Hippel 2008) (Moore & Waring 1998) (Moore & Lower 2001) (Nakayama <i>et al.</i> 2004) (Arellano-Aguilar & Garcia 2008) (Arellano-Aguilar & Garcia 2008) (Saaristo <i>et al.</i> 2009) (Saaristo <i>et al.</i> 2009) (Saaristo <i>et al.</i> 2009) (Edwards & Guillette 2007)
Three-spined stickleback (<i>Gasterosteus aculeatus</i>)		→	Hypoxia	(Abrahams, Robb & Hare 2005; Kuperberg, Brown & Clotfelter 2009)
Atlantic salmon (<i>Salmo salar</i>)		→	Nitrate	(Secondi <i>et al.</i> 2009)
Medaka (<i>Oryzias latipes</i>)		→	Nitrate	(Secondi <i>et al.</i> 2009)
Amarillo fish (<i>Girardinichthys multiradiatus</i>)		→	Acidification	(Ortiz-Santaliestra <i>et al.</i> 2009)
Sand goby (<i>Pomatoschistus minutus</i>)		→	Acidification	(Ortiz-Santaliestra <i>et al.</i> 2009)
Mosquitofish (<i>Gambusia holbrookii</i>)		→	Acidification	(Ortiz-Santaliestra <i>et al.</i> 2009)
Fighting fish (<i>Betta splendens</i>)	Opercular display	→	Acidification	(Hayes <i>et al.</i> 2002)
	Secondary sexual traits (combination of filament length, tail height, hind foot web area)	→	Acidification	(Hayes <i>et al.</i> 2010)
	Olfactory cues	→	Acidification	(Hayes <i>et al.</i> 2010)
	Total courtship time	→	Acidification	(Hayes <i>et al.</i> 2010)
	Persuasion index	→	Acidification	(Hayes <i>et al.</i> 2010)
	Time to begin courtship	→	Atrazine	(Guillette <i>et al.</i> 1996, 1999)
	Larynx size	→	Atrazine	(Adkins-Regan & Garcia 1986)
	Size of nuptial pads	→	Atrazine	(Halldin 2005)
	Size of breeding glands	→	Mixture of oestradiol + diethylphthalate + bisphenolA + dibutylphthalate	(Markman <i>et al.</i> 2008)
	Larynx structure resembled female larynges	↑	Mixture of oestradiol + diethylphthalate + bisphenolA + dibutylphthalate	(Markman <i>et al.</i> 2008)
	Penis size	→	DDT	(Iwaniuk <i>et al.</i> 2006)
	Strutting and copulatory behaviour	→	Mercury	(Hallinger <i>et al.</i> 2010)
	Reproductive behaviours	→	Mercury	(Hallinger <i>et al.</i> 2010)
	Song characteristics (time spent singing, number of song bouts, song bout duration, repertoire size)	→	Mercury	(Hallinger <i>et al.</i> 2010)
	HVC (brain area controlling song)	↑	Mercury	(Gorissen <i>et al.</i> 2005)
	Brain regions involved in singing and sexual behaviour	→		
	Song characteristics (tonal frequency, note types per song, average strophe length, peak frequency of most repeated element)	→		
	Song characteristics (tonal frequency, peak frequency and bandwidth of buzz notes, number of note types per song)	→		
	Amount of song, repertoire size	↓	Lead	
American robin (<i>Turdus migratorius</i>)				
Carolina Wren (<i>Troglodytes aedon</i>)				
House Wren (<i>Troglodytes aedon</i>)				
Song sparrow (<i>Melospiza melodia</i>)				
Great tit (<i>Parus major</i>)				

Notes: The arrows indicate the direction of change compared to controls. See Jones & Reynolds (1997) for a review of the effects of pollutants on reproductive behaviours in various fish species.

¹These studies were conducted on alligators inhabiting contaminated lakes. The contaminant is suspected to be pp-DDE, but it is possible that other contaminants might have induced the change in the measured trait.

2006; Brown & Lawson 2010). Altered mating signals can affect parasite–host relationships where parasites detect hosts by their mating signals (Zuk & Kolluru 1998).

Gomulkiewicz & Holt (1995) developed a population growth model to predict when populations would avoid extinctions in novel environments that reduce fitness. They defined a species-specific critical threshold level of population size, N_c , below which the population is at risk of extinction due to demographic stochasticity. Reduced reliability of signals under severely altered environmental conditions could trigger a decline below N_c . In this case, natural selection will drive altered female preferences to the extent that these are genetic; sexual selection on males may produce greater investment in signalling to increase signal expression despite endocrine disruption, potentially causing population size to increase above N_c . In the model, the degree of initial maladaptation to the novel environment β_0 depends directly on the difference between the initial mean trait value and the optimal trait value for the altered environment. Initial maladaptation also depends inversely on the variance in the trait value about the mean. Assume the trait is female responsiveness, the ability to correctly assess male quality and respond accordingly. Altered signals might require females to alter their responses (as in Fig. 2). Hence their original responsiveness will be a maladaptation. The farther this is from the responsiveness required to maximize fitness in the face of altered male signals, and the lower the original variation in this trait was, the higher the degree of maladaptation. If β_0 is very high as a result of strong co-evolution between the trait and female responsiveness over the years, then there is a higher chance of local extinctions. The assessability lag (during which females shift their response curve to adapt to the new trait values) will be a crucial factor in determining whether the population will be able to rise above N_c before stochasticity eliminates it.

Exposure to EDCs can have physiological implications that might be important for carotenoid-based signal expression. The carotenoid allocation trade-off between mating signal and immunocompetence plays an important role in the evolution of many mating systems (Hill 1991; Folstad & Karter 1992; Zuk 1992; Lozano 1994); disruption of this relationship can have ecological and evolutionary implications. Elevated androgen levels retard an individual's immune response (Folstad & Karter 1992), leading to the honesty of androgen-regulated signals (Immunocompetence Handicap Hypothesis: Folstad & Karter 1992). Carotenoids can function as immunoenhancers (McGraw & Ardia 2003; Grether *et al.* 2004; but see also Kolluru *et al.* 2006). Also androgens are thought to have a positive effect on bioavailability of plasma carotenoids because of increased dietary intake due to elevated androgens, increased mobilization of carotenoids from body stores, or increased absorption efficiency of ingested carotenoids as a result of elevated androgen levels (Blas *et al.* 2006). Most carotenoid-based signals are believed to be truthful signals because a high quality individual (defined by his immunocompetence) can allocate more carotenoids to the signal and less to his immune system (Faivre *et al.* 2003; Alonso-Alvarez *et al.* 2004). Besides affecting

androgen levels, EDCs can directly or indirectly impact immunocompetence (Ndebele, Tchounwou & McMurray 2003; Hayes *et al.* 2006; Brodkin *et al.* 2007; Filby *et al.* 2007; reviewed in Ahmed 2000; Inadera 2006), circulating plasma carotenoid levels, and consequently the allocation of carotenoids to the different functions. Altered immune responses are crucial to population dynamics especially in environments with high pathogen and parasite densities. Thus understanding how EDCs might affect immune responses and allocation of carotenoids can be of ecological importance.

Evolutionary implications of altered male mating signals

Evolved resistance to pollutants in target and non-target species has been documented; a large body of literature exists on this topic (here we cite a few examples: Hemingway & Ranson 2000; Twigg, Martin & Lowe 2002; Bard 2000; Brammell *et al.* 2004; Lopes *et al.* 2008; Brausch & Smith 2009; Arzuaga & Elskus 2010; reviews: Dover & Croft 1986; Roush & Mckenzie 1987; Croft & van de Baan 1988; Leibee & Capinera 1995). If individuals develop resistance to EDCs, their mating signals may not alter. However, there are bound to be differential levels of resistance within a population with some individuals being better able to resist the pollutant than others; hence the degree of signal alteration will differ accordingly. Whether this will correlate with quality cannot be predicted. If resistance correlates with quality, then the altered signal may also correlate with quality, maintaining signal reliability; otherwise, signals may become less reliable. Further, some populations may evolve resistance, while others may not. This is an important topic that cannot be addressed within the scope of this article. We restrict our discussion to situations where signals are subject to being altered by EDCs.

Altered signals in local populations due to persistent multi-generational exposure to EDCs can have significant evolutionary implications. Genetic divergence in the form of resistance to EDCs has been detected (Elskus *et al.* 1999; Crews, Willingham & Skipper 2000). Divergence as a result of sexual selection in altered habitats has been documented (Seehausen, van Alphen & Witte 1997; Craig & Foote 2001). However, divergence due to selection on altered signals resulting from EDCs has not been examined. Vertebrate and invertebrate traits can evolve rapidly across a few generations (Thompson 1998; Lande, Seehausen & van Alphen 2001), notably including reproductive proteins (Clark, Aagaard & Swanson 2006). Labonne & Hendry (2010) showed with a simulation model that phenotypic divergence in response to natural and sexual selection can occur within 20 generations; the simultaneous evolution of female preference is somewhat slower, taking up to 200 generations or longer. It is worth examining whether these anthropogenic factors can lead to varied responses of females to male signals, disappearance of signals in some populations or evolution of novel signals in others.

Many ecological and behavioural factors can cause or facilitate disruptive selection and ultimately speciation. The most common of these factors are female preference for male

phenotypes (Seehausen, Mayhew & van Alphen 1999; Ptacek 2000) and environmental changes (passerine birds: Barracough, Harvey & Nee 1995; cichlid fishes: Seehausen, van Alphen & Witte 1997; mouse subspecies, *Mus musculus domesticus* and *M. m. musculus*: Laukaitis, Critser & Karn 1997; Anurans: Ptacek 2000; Little Greenbul, *Andropadus virens*: Slabbekoorn & Smith 2002). Craig & Foote (2001) discovered a polymorphism in sockeye salmon (*Oncorhynchus nerka*) as a response to altered environment. Anadromous sockeye landlocked in freshwater lakes are non-anadromous and are called kokanee. Both sexes of sockeye and kokanee turn bright red at maturation. However, fresh water systems are poor in nutritional resources and should provide relatively low levels of carotenoids. Sockeye bred in fresh water remain green due to a lack of carotenoids. Apparently because of a sexual preference for the colour red, kokanee evolved more efficient mechanisms of carotenoid utilization, thus diverging genetically from the ancestral sockeye (Craig & Foote 2001). This is a clear example of genetic divergence driven by selection on a signal altered due to habitat modification.

Male signal production and female response to the received signal have co-evolved (Arnqvist & Rowe 2005) such that females can adjust their response to varying levels of signal quality. In recent decades, rapid environmental changes have lead to drastic alterations of habitats of many animals, with important implications for mating interactions. For example, turbidity reduces perceptivity of visual signals in aquatic species (Seehausen, van Alphen & Witte 1997), structural modifications of habitats alter perception of auditory signals (Telford, Dyson & Passmore 1989; Gerhardt 1992), and noisy environments cause animals to vocalize less (Lengagne 2008). If novel environmental changes prevent the signal perceived by the female from reliably reflecting quality, will female responses shift accordingly? A different disruption of these signalling systems can occur when environmental changes affect the male trait, causing him to alter the transmitted signal. In this case, females perceive signals as they are produced, but it is the production that is disrupted. But female perception of signals can also be altered by EDC-exposure, as discussed above. In any case, environmental changes are causing a discrepancy between male traits and female assessment of male quality.

Female responses to male signals can be a strong driving force for genetic divergence. In a population where sufficient numbers of individuals are exposed to endocrine disruptors, the exposed males may no longer be able to produce signals that correspond to their quality. There may be reduced discriminability as well as reliability (Fig. 2). Such ideas have been suggested by other authors (Secondi *et al.* 2009) but remain to be tested. Females should rapidly lose the preference across generations if the trait no longer signals true quality. This process should be hastened by altered female choosiness (Figs 3 and 5).

Males of several swordtail fish species of the genus *Xiphophorus* have tails with long swords apparently to indicate larger body size to females (Basolo 1998a,b; Rosenthal & Evans 1998). Females of the descendant species *X. nigrensis* have lost their preference for the sword, yet the males have not lost

their swordtails. Basolo (1998a) and Rosenthal, Wagner & Ryan (2002) postulate that increased predation risks of associating with sword-bearing males, or scarcity of heterospecifics reducing the need for strong species recognition, may have undermined preference for the ornament. If production and maintenance of the sword were expensive, there would be natural selection pressures on males to lose the sword. Though the sword is a relatively inexpensive ornament with regard to metabolism (Rosenthal, Wagner & Ryan 2002), predation risks associated with a conspicuous ornament are high, and the persistence of the trait is perplexing (Rosenthal, Wagner & Ryan 2002). It is possible that the sword has other purposes, such as determining dominance in intraspecific competition (Rosenthal, Wagner & Ryan 2002).

But sexually selected male traits can be lost (reviewed in Wiens 2001). Swordtail fish species show a range of morphological and behavioural signals. Males of the species *X. continens* do not have any of the reproductive characteristics that other swordtail males exhibit as mating signals (Morris *et al.* 2005). These males are small and lack swords and colour patterns (vertical bars). A lack of female preference for large males and low male–male-competition may account for the loss of large body size in these males, but the loss of vertical bars and swords remain unexplained (Morris *et al.* 2005).

How do females then assess mate quality? A mutant female may use a different indicator to assess male quality that may not require androgens for maintenance. The cichlid fishes of the eutrophic Lake Victoria use body size to assess mates, whereas they were using colour before the disruption of visual signals by increasing turbidity (Seehausen, van Alphen & Witte 1997). There is a higher rate of hybridization in these lakes, leading to the loss of species and possibly emergence of new ones if hybridized fishes persist. Such situations may lead to the evolution of a new signal of quality that females use for mate assessment by starting a whole new sequence of co-evolutionary signal production and response between males and females (as illustrated in Fig. 5). Conversely, decreased female choosiness might lead to a scramble-competition mating system where females bias male mating success through resistance and cryptic choice (Dunn *et al.* 1999; Blanckenhorn *et al.* 2001; Nahrung & Allen 2004), with sexual selection acting more on male traits enabling better access to females (Dunn *et al.* 1999; Bertin & Cézilly 2003; Alcock & Kemp 2005; Bertin & Cézilly 2005; Greene & Funk 2009; Lu *et al.* 2010).

If the effects of EDCs span many generations, there is the possibility of a mutation in female preference that can be heritable. Female preferences for certain male traits are believed to be heritable (Lande 1981; Kirkpatrick 1982; Pomiakowski 1988; Haesler & Seehausen 2005). Labonne & Hendry's (2010) simulation of guppy evolution suggested 200 generations or more for detectable changes in female preference; for guppies, this can translate to about 70 years. Certain chemicals are extremely persistent in the environment. DDT, one of the most persistent organic pollutants, has a half-life in soil of up to 15 years, depending on the type of soil (Hazardous Substances Data Bank). This means that a 100 years

later c. 1% of the current amount of DDT will still be present in the soil. This may be significant in areas of intense use of the chemical. Further, some chemicals may continue to be used by humans for many years. Can this time frame be enough to produce genetic divergence? Also, would genetic changes persist in an environment free of endocrine disruptors?

With this in mind, we expect a population of animals exposed to endocrine disruptors to alter their mating systems relative to unexposed populations. Evolution of resistance should not affect this prediction due to differential degrees of resistance within a population. Females may be less choosy with less discriminable mating signals, or females may rely on different indicators of male quality. It is also possible that females could evolve more astute sensory systems. In extreme cases where signals become totally unreliable, a new system of mate quality assessment may evolve – a system different from that of conspecifics not exposed to endocrine disruptors. If the original male trait was based on pre-existing sensory biases, the female preference may re-establish in the population, leading to the reemergence of that trait as a signal. Otherwise, in rare cases, this genetic divergence might lead to speciation if the new male trait used for quality assessment becomes elaborated under selection associated with refocused female preference. To our knowledge, speciation as a result of EDC-exposure has not been documented, but genetic divergence in the form of resistance has been observed (Elskus *et al.* 1999; Crews, Willingham & Skipper 2000). EDCs often do not affect entire populations due to their irregular distribution in the environment; further there is usually gene flow between exposed and unexposed groups. However, when large amounts of persistent EDCs cover an extensive area (e.g. Lake Apopka: Woodward *et al.* 1993), animal populations inhabiting these places might diverge from their unexposed relatives after multiple generations of exposure and relative isolation.

Future directions

Field studies on altered male reproductive characteristics have been conducted in EDC contaminated habitats (reviewed in Rattner 2009). Of further interest would be to study whether endocrine disruption alters female responses to EDC-exposed and unexposed males, and to quantify fitness costs of these altered responses. To understand the evolutionary implications of endocrine disruption, we need data on whether the relationship between a male mating signal and the measure of quality for that species is comparable in contaminated versus uncontaminated habitats. Quantifying the allocation of dietary pigments like carotenoids, as well as those synthesized *de novo* like melanin and pterins, to various physiological and reproductive functions, would provide insights into the effects of endocrine disruption on the value of these pigments as mediators of honest signals. Mathematical models could be developed to project the fate of a signal in disrupted environments. Long-term mesocosm experiments using species with short generation times might provide better insights into these questions. Larger variances in measured

traits as a response to EDCs might imply variance within the population in resistance to the contaminant, raising questions about the mechanics of differential development of resistance to EDCs among individuals.

Genetic divergence and perhaps speciation could be extreme results of persistent exposure of local populations to endocrine disruptors; however, there is no direct empirical evidence of such phenomena. When responses occur on evolutionary time scales, experiments to test these hypotheses might be unrealistic in many systems. Comparative genomic studies of species in contaminated and un-contaminated areas could provide us with information on genetic divergence between endocrine disrupted and non-disrupted populations. Mathematical models could project the fate of populations with disrupted signalling systems. While ecological and physiological implications of EDCs have received scientific focus, it is now necessary to divert these efforts to the understanding of rapid evolutionary changes in local populations exposed to EDCs over several generations.

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