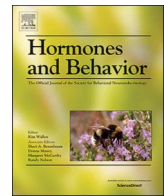




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Review article

## Mate choice, sexual selection, and endocrine-disrupting chemicals

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## ABSTRACT

Humans have disproportionately affected the habitat and survival of species through environmental contamination. Important among these anthropogenic influences is the proliferation of organic chemicals, some of which perturb hormone systems, the latter referred to as endocrine-disrupting chemicals (EDCs). EDCs are widespread in the environment and affect all levels of reproduction, including development of reproductive organs, hormone release and regulation through the life cycle, the development of secondary sexual characteristics, and the maturation and maintenance of adult physiology and behavior. However, what is not well-known is how the confluence of EDC actions on the manifestation of morphological and behavioral sexual traits influences mate choice, a process that requires the reciprocal evaluation of and/or acceptance of a sexual partner. Moreover, the outcomes of EDC-induced perturbations are likely to influence sexual selection; yet this has rarely been directly tested. Here, we provide background on the development and manifestation of sexual traits, reproductive competence, and the neurobiology of sexual behavior, and evidence for their perturbation by EDCs. Selection acts on individuals, with the consequences manifest in populations, and we discuss the implications for EDC contamination of these processes, and the future of species.

## 1. Introduction

As a species, humans have had a disproportionate influence on the quality of our environment. This accelerated during the Industrial Revolution, when heavy metals and coal contaminated the air, soil, and water. By the mid-1800s the burning of coal in England polluted the air, particularly in the midlands north of Birmingham, the heart of industrialization in that country. This resulted in a shift in the peppered moth morphological phenotype. The normal light color of this species was conspicuous against the accumulated soot on trees and other surfaces, making it easy prey. The less common dark (melanic) phenotype became more prevalent (Kettlewell, 1955). Recent evidence indicates this color shift is attributable to a small suite of genes involving a specific mutation that appeared in 1819 (Van't Hof et al., 2016; van't Hof et al., 2011). As air quality has improved, “the dark-colored peppered moths are vanishing as quickly as they emerged” (Editorial Board, Nature, 2016). This is an early example of an adaptive change in a species in response to anthropogenic contamination, and the potential for humans to influence evolutionary change.

The consequences of the more recent Chemical Revolution, beginning in the mid-twentieth century, have been accumulating over the past 75 years. A subset of these chemicals or their breakdown products

can mimic the action of naturally occurring hormones. These are designated as endocrine-disrupting chemicals (EDCs), defined by an Endocrine Society expert group as “chemicals or mixtures of chemicals that mimic, block, or interfere with hormones in the body's endocrine system” (Zoeller et al., 2012). EDCs have been best studied for their actions on the body's endocrine functions, particularly reproduction, thyroid, metabolism (including diabetes and obesity), and hormone-sensitive cancers such as those of the prostate, breast, and endometrium (Gore et al., 2015).

Of these endocrine systems, the influence of EDCs on reproduction has the deepest history, beginning in the 1960s with Rachel Carson's *Silent Spring* (Carson, 1962). This book called attention to the devastating consequences of widespread pesticide use on wildlife, and brought this issue to the forefront of public awareness for the first time. Since then, hundreds if not thousands of papers have documented adverse reproductive outcomes of a broad spectrum of chemicals, not just pesticides but also industrial chemicals, plastics and plasticizers (Fudvoye et al., 2014; Wang et al., 2016). Of particular importance are studies demonstrating the particular vulnerability of the developing organism. It is not surprising that fetal, infant, and adolescent developmental stages are highly sensitive to EDCs; these are phases of life when endogenous hormones undergo dynamic changes that are

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responsible for growth, maturation, and sexual development (Pinson et al., 2016; Walker and Gore, 2017). In the case of reproductive systems, this includes the progressive and sequential development of the reproductive tract, accessory sex structures and secondary sexual characteristics in response to gonadal hormones. The brain's neuroendocrine systems controlling hypothalamic-pituitary-gonadal function also play key roles, as a hypothalamic neural network must develop properly to result in appropriate male- and female-specific reproductive physiology and behavior (Pinson et al., 2016; Walker and Gore, 2017).

Despite the wealth of information on EDCs on reproduction, there is relatively little consideration of how EDCs might alter sexual selection, influence reproductive success, and ultimately, drive evolutionary change (Crews et al., 2007; Jasarevic et al., 2012; Rosenfeld and Trainor, 2014; Skinner, 2015). The vast majority of experimental studies have relied on pairing animals in the laboratory and determining whether offspring were produced. This is a crude measure of reproductive success that does not take into consideration the complexities of mate choice. Thus, the evidence for effects of EDCs on the more subtle yet realistic aspects of mate choice is largely lacking. In this article, we will provide background on sexual selection and discuss areas of research that are needed to connect EDC exposures to this process.

## 2. Sexual selection: the importance of mutual mate choice

Although the observation of change in form through time, or evolution, had been commented on, Darwin provided the first plausible mechanism through which evolution could be achieved, namely natural selection. Natural selection was believed to work via certain individuals having a functional advantage for breeding and survivorship (Darwin, 1888). As genetics became an established science and was incorporated into evolutionary theory, NeoDarwinians focused on the Biological Species Concept, which asserted that sexual behavior evolved to identify and separate species; change in form and function was due to accumulation of advantageous mutations. This enabled individuals carrying these mutations to be more likely to successfully reproduce and pass on the genetic underpinnings of these functional advantages.

Sexual selection is a mode of natural selection, operating through two processes: *intrasexual* competition, by which members of the same sex compete for access to mates; and *intersexual* selection, with members of one sex choosing mates of the opposite sex. Sexual selection per se comprises two components (Gowaty, 2015). First, the mechanisms involve behavioral, physiological, and opposite-sex mate choice. Second, reproductive success is operationally defined as individuals whose young themselves produce young (i.e., grandchildren). Since evolution depends upon reproductive success, the individual will try to choose the best mate of those available (Carson, 2003). This was a fundamental change in perspective; that is, from viewing behavior as a barrier to hybridization of species to an emphasis on traits that best reflect the overall fitness of the individual. The premise is that certain individuals will be more successful at reproducing due to higher fitness, such as being a more attractive mate or expressing traits that give them an advantage as competitors (Darwin, 1888).

Here we focus on reciprocal mate choice, as this is what occurs in nature (Fig. 1). Although not specifically stated by Darwin, it was assumed that the individual chosen must also accept the courting individual as a mate (Carson, 1987). This wisdom has been practiced in animal husbandry since before biblical times. The experimental work on mate choice is relatively recent, dating to F.H.A. Marshall (Marshall, 1936). Lehrman's (1965) pioneering studies on the ring dove, in retrospect, have not been followed. One of the few, and first, studies is that of Huck et al. (Huck et al., 1985) in which female hamsters selected from three potential mates in a large seminatural enclosure. Indeed, in most instances, actual apparatus used have been highly artificial, usually limiting choice to one of two individuals under rather spartan conditions. In behavioral ecological research the reproductive state of the

stimulus animals often are not known, while in experimental laboratory work the hormonal states of the stimulus animal are controlled. Finally, it is assumed that the stimulus animals are typical of the species. This last stipulation becomes problematic when we consider the effects of EDCs on individuals.

While we emphasize the importance of mutual mate choice, the choice is typically the female's domain due to her greater investment in producing young. Despite this, the chosen males still have to accept the females as partners. The basis for female choice includes characteristics such as colorful plumage and elaborate song in birds, colorful patterns in scales in reptiles and fish, and courtship dances in many classes; these are some of the traits employed by males to display themselves as attractive mates for female choosers, who evaluate these cues prior to mating (Ryan, 1990). In other mating systems where males are the rare (limiting) sex, e.g., pipefish and phalaropes, the male is courted by females and it is he who chooses the mate.

Individual differences in both the presentation of sexual traits as well as how others perceive these traits matters profoundly. Mate choice experiments in the laboratory, while useful, do not mimic how, in nature, dyadic interactions allow for mutual agreement. Frank Beach early on advocated a 'holistic' approach that included the male and the female as an interacting unit and the importance of individual differences (Beach, 1947; Beach, 1983). This concept was further developed by Daniel S. Lehrman in his studies of the reproductive cycle of the ring dove (Lehrman, 1965). How individual differences are negotiated to form long-lasting bonds was a long-standing research effort with beagles by Beach. For example Beach and LeBoeuf (1967) found that receptive bitches displayed a preference for particular males and would go so far as to attack other males whose advances they did not want. Another remarkable example of how forced, versus free, choice is important is illustrated by the work of Brennan and colleagues (Brennan et al., 2010). In ducks, males will occasionally flock together and forcefully mate with a female. The oviduct of female ducks has evolved in both form and function; there are receptacles that can redirect the penis, and hence impair sperm delivery. This modification is employed during such forced copulations, thereby avoiding insemination. Thus, the performance failure by a partner (unsuccessful fertilization) leads to new mates being sought.

This individual variation is the substance of evolutionary change, and making the correct choice of a mate can dictate a female's reproductive success. This is seen particularly in long-lived species where it has been possible to monitor an individual's lifetime reproductive success. For example, in a now 24-year study in the monogamous blue-footed booby, Drummond and colleagues found that bonded couples that stayed together over several breeding season hatched more eggs, produced more fledglings, and established their clutches earlier than newly coupled birds (Sanchez-Macouzet et al., 2014). In this species, the basis for female choice is the coloration of the males' feet, with bright blue-footed males chosen over darker-footed males. The bright blue pigmentation comes from carotenoid found in fish and, hence, the pigmentation in the feet reflects the foraging ability of the male. The degree of pigmentation is also an indication of the male's immune condition. As males age the quality of the webbing degrades and is indicative of sperm quality (Cronin, 1993; Velando et al., 2006). If females are forced to mate with dark blue-footed males, egg survival is decreased. If the bright-blue feet are masked with dark blue mascara, females will avoid these males (Velando et al., 2006). A similar situation was found in Coulson's 35-year study of kittiwake gulls in Northumberland, England, a species that often pairs for life. Not only do successful kittiwake pairs fledge more young; they also produce eggs faster, indicating that females in these pairs reach breeding condition earlier (Coulson, 2011). Some pairs of kittiwakes, however, were found to have a different mate the next breeding season. About half of these pairs did not re-form, possibly due to death of one partner. In the other half, pairs of kittiwakes "divorced." The cause of divorce could be traced to the failure of the pair to fledge at least one egg the preceding

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