



An endocrine-disrupting agricultural contaminant impacts sequential female mate choice in fish[☆]

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ARTICLE INFO

Article history:

Received 20 November 2017

Received in revised form

15 February 2018

Accepted 15 February 2018

Keywords:

Agricultural pollution

Endocrine-disrupting chemical

Poecilia reticulata

Sequential mate choice

Trenbolone

ABSTRACT

The environmental impact of endocrine-disrupting chemicals (EDCs)—compounds that interfere with endocrine system function at minute concentrations—is now well established. In recent years, concern has been mounting over a group of endocrine disruptors known as hormonal growth promotants (HGP), which are natural and synthetic chemicals used to promote growth in livestock by targeting the endocrine system. One of the most potent compounds to enter the environment as a result of HGP use is 17 β -trenbolone, which has repeatedly been detected in aquatic habitats. Although recent research has revealed that 17 β -trenbolone can interfere with mechanisms of sexual selection, its potential to impact sequential female mate choice remains unknown, as is true for all EDCs. To address this, we exposed female guppies (*Poecilia reticulata*) to 17 β -trenbolone at an environmentally relevant level (average measured concentration: 2 ng/L) for 21 days using a flow-through system. We then compared the response of unexposed and exposed females to sequentially presented stimulus (i.e., unexposed) males that varied in their relative body area of orange pigmentation, as female guppies have a known preference for orange colouration in males. We found that, regardless of male orange pigmentation, both unexposed and exposed females associated with males indiscriminately during their first male encounter. However, during the second male presentation, unexposed females significantly reduced the amount of time they spent associating with low-orange males if they had previously encountered a high-orange male. Conversely, 17 β -trenbolone-exposed females associated with males indiscriminately (i.e., regardless of orange colouration) during both their first and second male encounter, and, overall, associated with males significantly less than did unexposed females during both presentations. This is the first study to demonstrate altered sequential female mate choice resulting from exposure to an endocrine disruptor, highlighting the need for a greater understanding of how EDCs may impact complex mechanisms of sexual selection.

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1. Introduction

Chemical pollutants are accumulating in environments worldwide at an alarming pace and scale (Kolpin et al., 2002; WHO-UNEP, 2012; Arnold et al., 2014). Of great concern are endocrine-disrupting chemicals (EDCs)—compounds that can alter the endocrine function of organisms at minute concentrations (in the

low ng/L range) by interfering with hormonal communication (Kavlock and Ankley, 1996; Lintelmann et al., 2003; Buchanan and Partecke, 2012; Brander, 2013). Endocrine-disrupting chemicals encompass a broad range of both artificial compounds, which include pharmaceuticals, metals, plastics and pesticides (Diamanti-Kandarakis et al., 2009), and natural hormones, such as xenoestrogens (Gore et al., 2015). They can infiltrate ecosystems during their production, use, and/or disposal (WHO-UNEP, 2012), with common sources including wastewater from industry and households, agricultural and suburban run-off, and solid waste (Diamanti-Kandarakis et al., 2009). Once in the environment, many EDCs have a tendency to bioaccumulate (Crews et al., 2007; Walker

[☆] This paper has been recommended for acceptance by Maria Cristina Fossi.

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and Gore, 2011), and have therefore continually been detected at elevated concentrations in wildlife tissues, even in the most remote regions on Earth (e.g., polar bears in the Arctic, Letcher et al., 2010; amphipods in the Mariana Trench, Jamieson et al., 2017).

One group of EDCs with the potential to impact wildlife is hormonal growth promotants (HGPs), which are natural and synthetic chemicals used to promote growth in livestock (Hunter, 2010; Sellin Jeffries et al., 2011; Kolodziej et al., 2013; Johnson, 2015). HGPs are used globally, and their use is particularly widespread in several of the world's leading beef-producing nations. For example, in the USA, which is the world's leading beef producer, it is estimated that 20 million cattle (i.e., approximately two thirds of the total livestock in the country) currently receive HGP implants (Johnson, 2015). Although HGPs generally include mixtures of natural and synthetic hormones (Lange et al., 2001; Hunter, 2010), the most commonly administered androgen in HGP implants is trenbolone acetate (Hunter, 2010), which is a highly efficient and potent synthetic steroid (Neumann, 1976). Trenbolone acetate is hydrolysed within implanted cattle to produce the biologically active steroid hormone 17 β -trenbolone, which enters the environment via run-off of urine and faeces. Once present in the aquatic environment, 17 β -trenbolone has a tendency to accumulate as a result of its long half-life (~260 days measured in animal waste; Schiffer et al., 2001) and has been detected at concentrations ranging from 1 to 20 ng/L in waterways upstream and downstream of cattle farm outflow points (Durhan et al., 2006) to 162 ng/L in tile-drained agroecosystems (Gall et al., 2011).

A growing number of studies have demonstrated that exposure to 17 β -trenbolone can have alarming impacts on wildlife, particularly in aquatic environments. Exposure has been linked with severe morphological and physiological abnormalities in fish, including abnormal gonadal development (Örn et al., 2006), reduced reproductive output (Ankley et al., 2003), irreversible masculinisation (Baumann et al., 2014), and even complete and functional sex reversal (Larsen and Baatrup, 2010; Morthorst et al., 2010). We now know that 17 β -trenbolone can also induce behavioural abnormalities, with recent research revealing that environmentally realistic exposure concentrations can affect risk-taking behaviour in guppies (*Poecilia reticulata*; Heintz et al., 2015), as well as reproductive behaviour and sexual selection processes in both guppies (Bertram et al., 2015; Tomkins et al., 2016, 2017) and eastern mosquitofish (*Gambusia holbrooki*; Saaristo et al., 2013). However, the potential impacts of 17 β -trenbolone on more complex mechanisms of sexual selection remain poorly understood, as is also true for EDCs generally.

Sexual selection, by directly influencing mating outcomes, has important consequences for reproductive success, population dynamics and broader evolutionary processes (Candolin and Wong, 2012). Because sex hormones regulate the expression of a range of behaviours under sexual selection (Beyer et al., 1976; Munakata and Kobayashi, 2010), exposure to endocrine disruptors is likely to influence sexual selection processes. Indeed, recent research has revealed that, in simultaneous mate choice experiments (i.e., when females are presented with two or more males at the same time), exposure to environmentally relevant concentrations of endocrine-disrupting chemicals can impair female mate choice in sand gobies (*Pomatoschistus minutus*; Saaristo et al., 2009) and guppies (Tomkins et al., 2016). However, in nature, opportunities for females to make direct comparisons between suitors are often limited (Jennions and Petrie, 1997). In many species, it is more common for females to encounter mates sequentially (Bradbury and Andersson, 1987), making investigating the effects of EDCs on sequential female mate choice more ecologically relevant.

Guppies are a small, freshwater fish that occur in contaminated environments around the world (e.g., López-Rojas and Bonilla-

Rivero, 2000; Widianarko et al., 2000). They are an ideal species for investigating the impacts of endocrine disruptors on the mechanisms of sexual selection as their mating system is driven primarily by female choice. Males compete for the attention of females, achieving copulations via two contrasting mating strategies. Briefly, males either mate consensually with females following successful courtship displays (termed 'sigmoid displays'), or gain copulations by sneaking up behind females and attempting to mate with them coercively (termed 'sneak' attempts) (Houde, 1997). Previous research investigating female mate choice in guppies has demonstrated that females show a strong preference for males with relatively large areas of orange pigmentation on their bodies (e.g., Houde, 1987; Kodric-Brown, 1989; Long and Houde, 1989; Endler, 1995; Grether, 2000; Kodric-Brown and Nicoletto, 2001). Orange colouration is an honest indicator of male quality in guppies, correlating positively with swimming performance (Nicoletto, 1993), foraging ability (Endler, 1980; Karino and Shinjo, 2007; Karino et al., 2007), sperm quality (Locatello et al., 2006; Pitcher et al., 2007) and sperm load size (Pitcher and Evans, 2001; Pitcher et al., 2007), as well as parasite resistance (Houde and Torio, 1992). However, these studies have relied almost exclusively on experimental set-ups in which females are able to make direct comparisons between males. This is true, despite the fact that, in the wild, female guppies will often have to make reproductive decisions based on sequential encounters with potential suitors (Houde, 1997; Pitcher et al., 2003). Guppies, therefore, provide an excellent opportunity to further our understanding of the impacts of EDCs on sexual selection by investigating the hitherto unknown impact of EDCs on sequential female mate choice.

Here, we test the hypothesis that short-term exposure to an environmentally realistic concentration of 17 β -trenbolone will impact sequential female mate choice in guppies. Given that 17 β -trenbolone has been shown to affect reproductive behaviour in guppies and other Poeciliids, we expected exposure to also disrupt female mate choice processes when males are encountered sequentially, which is often the more environmentally realistic scenario.

2. Methods

2.1. Fish collection and housing

Guppies were collected from Alligator Creek in Queensland, Australia (19° 26' 17" S, 146° 57' 01" E), where a wild population has established itself as a result of deliberate and/or accidental introductions from the pet trade. The sampling site is located inside the Bowling Green Bay National Park, and is thus thought to be a pristine location. Indeed, we have taken water samples from this site over consecutive years and found no presence of 17 β -trenbolone (ALS Group, unpublished data). Fish were actively collected using dip nets and brought back to Monash University in aerated containers, where they were acclimated to laboratory conditions (25–27 °C, 12:12 h light:dark regime) in sex-specific tanks for three months prior to exposure to ensure sexual receptivity during behavioural trials. Fish were fed *ad libitum* once daily with a commercial fish pellet (Otohime Hiramé larval diet, 580–910 μ m).

2.2. Chemical exposure and water testing

Female guppies were exposed to 17 β -trenbolone for 21 days via a flow-through system adapted from previous studies (Saaristo et al., 2013; Bertram et al., 2015; Tomkins et al., 2016, 2017). The system was comprised of six 54 L aquaria, consisting of three unexposed tanks and three 17 β -trenbolone-exposed tanks. A total of 120 females were randomly distributed between these six tanks

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