

1 **Habituation of mating preferences: A response to Chiandetti and Turatto**

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7 Our recent investigation of guppy female mating preference for novel sexual signals in males

8 revealed that this preference fulfils the criteria for both short-and long-term habituation [1].

9 Based on these results, we postulated that habituation, and a resulting preference for novel sexual

10 traits, plays an underappreciated role in the evolution of mating behaviour and the maintenance

11 of genetic variation. In their comment, Chiandetti & Turatto [2] review areas of the psychology

12 literature related to the results of our study. Because our study links two related fields—

13 evolutionary biology and psychology—we believe this exchange is beneficial for clarifying the

14 parallels and distinctions between our results and those of previous studies of habituation for the

15 benefit of researchers from these different disciplines.

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17 Chiandetti & Turatto remark that habituation of mating interest has been well studied and point

18 to the literature suggesting that the ‘Coolidge effect’— loss of interest in prior sexual partners—

19 can be accounted for by habituation (e.g. [3,4]). This is correct, but it is important to clarify a

20 fundamental difference between our results and this literature. Chiandetti & Turato describe

21 Daniel et al. [1] as reporting ‘habituation to the same male partner’ [2, p. 2]; however, this is not

22 correct. Rather than examining habituation to the same partner, as in studies of the Coolidge

23 effect, our study evaluated a different phenomenon: change of interest in a phenotype shared by

24 multiple males. The goal of our study was to test whether habituation can account for the mating
25 preference for rare/novel phenotypes that have been well documented in the literature (e.g.
26 [5,6]), but for which no proximate or evolutionary explanations have been forthcoming. This
27 distinction between preference for novel phenotypes and other preferences for novelty is
28 important because these different preferences have distinct evolutionary consequences. For
29 example, preference for novel phenotypes can generate negative frequency-dependent selection
30 on sexual signals and thus maintain genetic variation within populations [5]. Our results,
31 combined with the literature highlighted by Chiandetti & Turatto, suggests that habituation can
32 result in sexual preferences for novelty at multiple levels of biological organization. This raises
33 an intriguing question: what determines whether habituation leads to preference for novel
34 phenotypes and/or individuals? Possible explanations include differences in individual
35 distinctiveness of phenotypes or differences in receiver psychology (e.g. whether sexual signals
36 are cognitively represented as independent phenotypes or integrated into representations of
37 individuals). Addressing this question would be a fruitful avenue of future study.

38

39 Chiandetti & Turatto state that another area of the literature relevant to understanding our results
40 pertains to habituation of reinforcer effectiveness (HRE). Studies on HRE have documented that
41 reinforcers (e.g. rewards used in operant conditioning such as food or water) progressively wane
42 in effectiveness, which is partly attributable to habituation to the reinforcer [7]. This literature
43 provides examples of habituation affecting responsiveness to biologically meaningful stimuli,
44 even when consumption of the reinforcer is prevented [8], as was observed in our study.
45 However, we disagree with Chiandetti & Turatto's suggestion that our results are probably an
46 example of HRE. Exposure to males was not used as a reinforcer in our study, and studies

47 outside of the HRE literature (in which stimuli were also not used as reinforcers) have also
48 demonstrated that habituation to biologically meaningful stimuli can occur without consumption
49 (e.g. [9–12]). Therefore, it is not appropriate to describe our results as an example of HRE. Our
50 results, combined with other literature, suggest that waning interest in a biologically relevant, but
51 non-consumed, stimulus is a common feature of habituation, and not specific to HRE.

52

53 Chiandetti & Turatto remark that it is incorrect for us to conclude that ‘habituation causes a
54 preference for novel sexual signals’ [1, p. 1] because habituation is the reduced preference for
55 the common sexual signal. This statement appears to stem from semantic confusion about two
56 aspects of the wording we used to argue that habituation helps explain preference for novel
57 phenotypes, which we endeavour to clarify. First, while Chiandetti & Turatto are correct that
58 habituation is the reduced interest in the common phenotype, habituation is not equivalent to a
59 preference for novel phenotypes. Rather, a mating preference for novel phenotypes refers to
60 relatively more interest in rare phenotypes than common phenotypes. Preference for novelty can,
61 but does not necessarily, result from a decline in interest in common phenotypes. Consider a
62 scenario in which a common and a rare phenotype are sufficiently similar for exposure to either
63 phenotype to cause a decline in interest in both phenotypes (though stimulus specificity might
64 still be observed with respect to other, more dissimilar stimuli). In this case, habituation occurs
65 without a preference for the rare phenotype. Alternatively, consider a scenario in which the
66 common phenotype is more attractive for reasons unrelated to the phenotype’s frequency (e.g.
67 the common phenotype has larger colour spots, which females find more attractive). Habituation
68 to the common phenotype will only result in a preference for the rare type if the reduction in
69 interest in the common phenotype exceeds the advantage it had prior to habituation. As these

70 examples illustrate, whether habituation to sexual signals results in a preference for rare/novel
71 phenotypes is an empirical question—one addressed by Daniel et al. [1].

72

73 Second, while Chiandetti & Turatto correctly define habituation as a change in behaviour, this
74 change in behaviour can itself be a mechanism explaining other phenomena (e.g. preference for
75 novel phenotypes). Numerous studies explicitly refer to habituation as a mechanism causing
76 various clinical [13], behavioural [14], ecological [15] or evolutionary [16] phenomena. Note
77 that like Daniel et al. [1], these studies use the term mechanism in a broad sense, meaning the
78 process by which something comes about, but not necessarily the specific molecular or neural
79 machinery underpinning a behaviour. This broader usage of the term mechanism is common
80 within evolutionary ecology (e.g. [17,18]) and also occurs frequently within the psychology
81 literature (e.g. [13,19]). We therefore suggest that Chiandetti & Turatto's critique of our wording
82 stems not from a misusage of terms, but rather the multiplicity of meanings attached to those
83 terms.

84

85 Demonstrating that habituation causes preference for novel phenotypes does help to explain this
86 preference. Habituation and its neural underpinnings are ancestral and subject to selection in
87 non-mating contexts [20]. Thus, our findings lend plausibility to the sensory bias hypothesis as a
88 potential explanation for the evolutionary origins of mating preference for novel phenotypes.
89 Additionally, models have been proposed that offer insights into the neural and molecular
90 substrates responsible for habituation, some of which we cited in our study [20–22], and others
91 which Chiandetti & Turatto highlight [23–25]. Thus, by linking habituation and preference for

92 novel phenotypes, our findings have implications for understanding how and why this mating
93 preference exists.

94

95 To conclude, the literature reviewed by Chiandetti & Turatto has some parallels with, and
96 distinctions from, our study. We do not believe that this literature alters the interpretation of the
97 results in Daniel et al. [1], but hope that this exchange has clarified some of the terminology used
98 therein and helped readers to place our study in the context of broader habituation research.

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100 Data accessibility. The data supporting the original study are available from the Dryad Digital
101 Repository: [https://doi.org/10.5061/dryad. fp030jg](https://doi.org/10.5061/dryad.fp030jg) [26].

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103 Competing interests. We declare we have no competing interests.

104

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