

## RESEARCH ARTICLE

# Long-term persistence of exaggerated ornaments under Fisherian runaway despite costly mate search

 Anna Waffender  | Jonathan M. Henshaw 

Institute of Biology I, University of Freiburg, Freiburg, Germany

## Correspondence

Jonathan M. Henshaw, Institute of Biology I, University of Freiburg, Freiburg, Germany.

 Email: [jonathan.henshaw@biologie.uni-freiburg.de](mailto:jonathan.henshaw@biologie.uni-freiburg.de)

## Funding information

Bundesministerium für Bildung und Forschung

## Abstract

Exaggerated ornaments often evolve due to the mating preferences of the opposite sex. Genetic correlations between preferences and ornaments can lead both traits to elaborate dramatically in tandem, in a process known as 'Fisherian runaway'. However, in most previous models of Fisherian runaway, elaborate ornaments are not expected to persist when preferences are consistently costly to the choosing sex. In contrast, we show here that exaggerated male ornaments can be maintained long term even when females must pay a cost to choose their mates. Preferences per se are not costly in our model, but females can only act on their preferences by investing resources in mate search. We predict that mate search effort should decrease with the cost of sampling additional mates and increase with the number of possible ornaments that females can choose from. The potential for multiple exaggerated ornaments to coexist depends on subtleties of their cost structure: strict trade-offs (additive costs) favour sequential ornament evolution, whereas looser trade-offs (multiplicative costs) allow for coexistence. Lastly, we show that pleiotropy affecting both ornaments and preferences makes it difficult for Fisherian runaway to initiate, increasing the evolutionary time until ornamentation. Our model highlights the important but neglected role of mate search effort in sexual selection.

## KEYWORDS

Fisherian runaway, mate choice, mate search, ornaments, preferences, sexual selection, sexy sons

## 1 | INTRODUCTION

Much of the striking beauty of the animal world—from the oft-cited peacock's tail (Darwin, 1860) to the artistic sculptures of a bowerbird (Borgia, 1995; Uy et al., 2001)—evolved in response to sexual selection (Andersson & Iwasa, 1996; Andersson & Simmons, 2006; Shuker & Kvarnemo, 2021). A bewildering variety of ornaments cater to the aesthetic preferences of potential mating partners (Andersson, 1994; Prum, 2017; Rosenthal, 2017) despite the often considerable costs these ornaments impose on their bearers

(Andersson, 1982; Basolo & Alcaraz, 2003; Siefferman & Hill, 2005; Verhulst et al., 1999). Female long-tailed widowbirds (*Euplectes progne*), for example, prefer mates with long tail feathers, which has led to the evolution of unwieldy exaggerated tails in males (Andersson, 1982; Andersson & Andersson, 1994). Explaining the evolution of such exaggerated traits is nontrivial. Multiple existing models, such as Fisherian runaway (also known as 'sexy sons'), 'good genes' and 'sensory exploitation' (reviewed in Kuijper et al., 2012) provide apparently plausible explanations for exaggerated ornaments. These mechanisms are not mutually exclusive (Kokko

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2022 The Authors. *Journal of Evolutionary Biology* published by John Wiley & Sons Ltd on behalf of European Society for Evolutionary Biology.

et al., 2002, 2006), however, and their relative importance in the coevolution of preferences and ornaments remains highly contentious (Fisher, 1930; Henshaw et al., 2022; Jones & Ratterman, 2009; Prum, 2017; Radwan, 2008; Rosenthal, 2017).

### 1.1 | Fisherian runaway

One of the first attempts to explain how costly ornaments evolve was given by Ronald A. Fisher in his book *The Genetical Theory of Natural Selection*, where he outlined the process now known as 'Fisherian runaway' (Fisher, 1930; see also Henshaw & Jones, 2020). Fisherian runaway is a self-reinforcing process, driven by the genetic association between a preference for a certain trait in a sexual partner and the trait itself. The preference generates positive selection on the trait, which due to the genetic association, in turn generates positive selection on the preference. This can result in a positive feedback loop with ever-increasing traits and preferences over evolutionary time (Henshaw & Jones, 2020; Lande, 1981; Lehtonen & Kokko, 2012). Early models demonstrated that Fisherian runaway can result in the persistence of elaborate ornaments, at least under idealized assumptions (Kirkpatrick, 1982; Lande, 1981).

### 1.2 | Nothing comes for free: the costs of ornaments and preferences

Despite long-standing debates about the mechanisms of sexual selection, it is widely accepted that exaggerated ornaments are costly. Demonstrating such costs empirically is often tricky (Kotiaho, 2001), but costs of ornamentation have nonetheless been shown, for example in widowbirds, domestic fowl, bluebirds and guppies (Andersson, 1982; Basolo & Alcaraz, 2003; Garcia et al., 1994; Siefferman & Hill, 2005; Verhulst et al., 1999).

In contrast, the costs of maintaining and expressing preferences for such ornaments are both conceptually less straightforward (Edward, 2015; Wagner, 1998) and empirically often small and hence difficult to measure. Two different kinds of costs can be distinguished here—preference costs and choice costs—which can both exert selection on mate choice behaviour (Cotton et al., 2006; Jennions & Petrie, 2000; Judge et al., 2014). Preference costs relate to the ability to perceive and evaluate the traits of potential mates. For instance, females might pay fixed costs for investing in sensory or cognitive abilities. On the other hand, choice costs result from the execution of such preferences (i.e. realized mate choice; Cotton et al., 2006; Edward, 2015; Heisler et al., 1987). For instance, females might only pay costs when they reject potential mates, in which case choosier females and those who prefer rarer male phenotypes are expected to pay higher costs (Andersson, 1994; Kokko et al., 2015). Similarly, females might differ in the effort they invest in seeking out mating partners ('mate search effort'). Empirically, the precise circumstances under which females incur preference or choice costs are often difficult to pinpoint.

Despite empirical uncertainty, preference costs and mate search effort play a key role in the theoretical literature (Houle & Kondrashov, 2002; Kirkpatrick et al., 2006; Kokko et al., 2015; Pomiankowski, 1987). In many Fisherian models, stable equilibria collapse under the weight of even miniscule preference costs (Kokko et al., 2015; Kuijper et al., 2012). In contrast, Pomiankowski et al. (1991) showed that costly female preferences could be maintained indefinitely if mutation pressure is biased towards smaller ornaments. More recently, Kokko et al. (2015) modelled preference evolution in the case where preference costs depend on the abundance of the preferred male type (i.e. preferences for rarer male types are more costly). Under this assumption, the cost of preferring a particular male type vanishes as that type goes to fixation in a population, allowing initially costly preferences to persist long-term.

### 1.3 | Pleiotropy effect

As well as considering distinct causal mechanisms of sexual selection, the theoretical literature makes use of a wide range of genetic architectures and assumptions (Eshel et al., 2002; Fisher, 1930; Henshaw, 2018; Kirkpatrick, 1982; Kokko et al., 2002, 2015; Kuijper et al., 2012; Lande, 1981; Pomiankowski et al., 1991). Particularly interesting in this context is the potential for pleiotropy—i.e. genes that affect both preferences and ornaments (Shaw et al., 2011; Singh & Shaw, 2012). Such pleiotropy is best-studied in the context of 'magic traits' in the speciation literature (Servedio et al., 2011). If ornaments and preferences are determined in part by common genes, then changes in such genes can potentially lead to rapid reproductive isolation of previously intermating populations or even to sympatric speciation (Servedio & Bürger, 2018). However, the implications of pleiotropy for the within-population coevolution of ornaments and preferences are less well-understood.

The bowerbird family (Ptilonorhynchidae) provides an intuitive example of the potential for pleiotropy. The mating success of male bowerbirds depends on females' evaluations of their bower. Since the bower is an external structure, however, not only the female but also the male himself can evaluate the bower and alter it according to his own preferences. A similar taste in bower construction is crucial for a successful mating (Borgia, 1995; Endler, 2012; Uy et al., 2001). Such tastes may be determined at least partially by common underlying mechanisms in both sexes, including sensory and cognitive processes. As a result, we might expect some degree of pleiotropy, in which common genes affect both bower construction in males and bower preferences in females. The stalk-eyed fly (*Cyrtodiopsis dalmanni*) provides another interesting example. Female stalk-eyed flies prefer males with wider eye span and females with wider eye span show stronger preferences, potentially because they are better able to distinguish differences in male eye span (Hingle et al., 2001). This would indicate a pleiotropic association between the female preference and the morphological ornament. Although pleiotropy is potentially widespread, its impact on Fisherian runaway remains unknown.

Here, we develop an individual-based simulation model of Fisherian sexual selection that differs from previous models in several key assumptions. First, we assume that female preferences per se are not costly, but that females must invest resources to sample additional mates. Second, we investigate two different cost structures for exaggerated male ornaments (additive and multiplicative), representing a stricter or looser trade-off between investments in multiple ornaments. Third, we consider the possibility that ornaments and preferences can be determined pleiotropically. Fourth, we analyse the effects of variation in the number of potential ornaments on ornament-preference coevolution. Our aim was to explore how ornaments and preferences coevolve under Fisherian runaway, with a particular focus on the evolution and consequences of female mate search.

## 2 | METHODS

We simulated a population of  $N$  individuals with an even sex ratio. We assumed discrete, non-overlapping generations, each consisting of a single breeding season. We simulated the evolution of the following traits:

$t$  distinct male ornaments  $\mathbf{O} = (O_1, \dots, O_t)$

Female preferences  $\mathbf{P} = (P_1, \dots, P_t)$  for each of these ornaments

Female mate search effort  $M$

We first summarize the structure of this model, before considering each component in more detail. Breeding females choose their mates from among a set of 'suitors', whereby a female's number of suitors increases with her individual mate search effort. The expected number of times a female breeds is proportional to her fecundity, which is a decreasing function of mate search effort. This means that females must pay a cost in order to choose from multiple males. Suitors are chosen from the male population in proportion to each male's viability, which decreases with his ornament expression. We considered two different models for how the viability costs of multiple ornaments combine (additive and multiplicative). Among a set of suitors, male mating success is determined by female choice, which in turn depends on male ornament expression and the strength and direction of female preferences for each ornament. Each breeding event produces one offspring. Note that in contrast to many existing models of Fisherian sexual selection (Kokko et al., 2015; Pomiankowski, 1987; Pomiankowski et al., 1991), female preferences are not costly per se in our model. However, females can only exercise their preferences if they sample more than one suitor, which is costly. Male ornaments are not correlated with any other aspect of fitness or quality in our model, aside from their effects on viability and (potentially) male attractiveness (cf. Fromhage & Henshaw, 2022; Garcia et al., 1994; Iwasa et al., 1991; Zahavi, 1975).

In addition to this base model of multi-ornament Fisherian sexual selection, we considered the possibility that ornaments and preferences are determined pleiotropically (Fitzpatrick, 2004;

Shaw et al., 2011). The degree of pleiotropy ( $x$ ) controls the extent to which ornaments and preferences are determined by common genes. When  $x > 0$ , the genes determining ornaments and preferences overlap, such that the degree of overlap increases with  $x$ . In contrast, when  $x = 0$ , ornaments and preferences are determined by disjoint sets of genes.

### 2.1 | Genetics and pleiotropy

For simplicity, we assume a haploid genetic system with fair meiosis and perfect recombination. All individuals carry genes for all traits, even when expression is sex-limited.

The genetic system consists of  $2t + 1$  loci, with a continuum of possible alleles at each locus. We write individuals' allelic values as  $(g_1, g_2, \dots, g_{2t+1})$ , where each  $g_i$  is a real number. The alleles  $g_1$  through  $g_{2t}$  determine ornament and preference expression under varying degrees of pleiotropy ( $x$ ). The allele  $g_{2t+1}$  determines female mate search effort. The size of a male's  $i$ th ornament is given by:

$$O_i = \left(1 - \frac{x}{2}\right)g_i + \frac{x}{2}g_{i+t}. \quad (1)$$

Negative values of  $O_i$  are rounded up to zero. Similarly, the size of a female's  $i$ th preference is given by:

$$P_i = \frac{x}{2}g_i + \left(1 - \frac{x}{2}\right)g_{i+t}. \quad (2)$$

Note that  $P_i$  is not rounded and hence can potentially be negative. If  $x = 0$  then ornaments are determined entirely by the alleles  $(g_1, \dots, g_t)$  and preferences by the alleles  $(g_{t+1}, \dots, g_{2t})$ ; these gene sets do not overlap and hence there is no pleiotropy. At the other extreme, if  $x = 1$ , then all of the alleles  $(g_1, \dots, g_{2t})$  affect ornaments and preferences equally. Intermediate values of  $x$  represent partial pleiotropy.

The strength of a female's preference for a particular male is determined by the size of his ornaments and the strength of her preferences (see below). Positive preference values  $P_i$  correspond to preferences for larger ornaments, whereas negative values indicate preferences for smaller ornaments. If  $P_i = 0$  then the female is indifferent to the value of the  $i$ th ornament.

### 2.2 | Mate choice

Each generation,  $N$  females are chosen with replacement to breed, such that the probability a female is chosen is proportion to her fecundity. Each of these  $N$  breeding events will result in a single offspring, so that population size remains constant across generations. Each female chooses her partner from among  $1 + M^*$  suitor males, where  $M^*$  is a Poisson distributed random variable with mean equal to her mate search effort,  $M$ :

$$M^* \sim \text{Pois}(M) \quad (3)$$

Note that all females seek at least one mate, regardless of their mate search effort (i.e. there is no 'wallflower effect' in this model; De Jong & Sabelis, 1991; Kokko & Mappes, 2005). The suitors are selected randomly from the pool of males, weighted according to their viability.

A female's choice of mate from among her suitors is determined by her preferences  $P$  (see above). Writing  $O$  for the ornament vector of a male and  $P$  for the preference vector of a female, the female's overall 'rating'  $R$  for a male is given by:

$$R = s \mathbf{O} \cdot \mathbf{P}, \quad (4)$$

where  $\cdot$  is the dot product. A female chooses her partner from the  $1 + M^*$  suitors with probabilities proportional to her overall 'rating'  $R$ . The preference coefficient  $s$  can vary between  $s = 0$  (all males are preferred equally, regardless of  $P$ ) and  $s = \infty$  (females invariably choose the suitor with the highest rating).

The allelic values at the beginning of the simulation are drawn from a normal distribution with trait-specific initial means ( $\mu = 0$  for ornaments and preferences and  $\mu = 5$  for female mate search effort) and standard deviations of one, unless otherwise stated. Negative values for ornaments and mate search effort (but not preferences) are rounded up to zero.

### 2.3 | Costs of male ornaments and female mate search

In each generation, a male's viability ( $v$ ) is determined by his ornament expression and a fixed cost parameter ( $c$ ). The larger a male's ornaments, the higher his costs and the lower his viability. Males with  $v = 0$  are considered dead and do not mate. We consider two different models for the viability costs of ornaments—an additive and a multiplicative model. In the additive model, the marginal cost of enlarging an ornament depends only on the total size of all ornaments and not directly on the size of the ornament being enlarged. This means that, for a given male, the marginal cost of increasing ornament size is the same for all ornaments. In the multiplicative model, small ornaments are always cheap to enlarge, regardless of the size of the other ornaments, whereas the marginal cost of increasing large ornaments is high. These cost models are given respectively by:

$$v_{\text{additive}} = \max \left[ 0, 1 - c \left( \sum_{i=1}^t O_i \right)^2 \right] \quad (5a)$$

and

$$v_{\text{multiplicative}} = \prod_{i=1}^t \max [0, 1 - cO_i^2] \quad (5b)$$

Female preferences are not directly costly. Rather, choice costs arise because a female's mate search effort (i.e. searching for more suitors) decreases her fecundity. A female's fecundity is given by:

$$f = 1 - kM^2, \quad (6)$$

where  $k$  is a coefficient that influences the cost of mate search.

## 2.4 | Inheritance and mutations

At each locus, an offspring inherits the allele of either its mother or father with equal probability. Inheritance is independent at each locus (i.e. recombination is perfect). Random mutations may cause further changes in the offspring's genome. Mutations occur with trait-specific probabilities ( $\pi$ ) per allele per generation. Mutational effects have means of zero and trait-specific standard deviations ( $\sigma$ ). This results in six mutation parameters:  $\pi_O, \pi_P, \pi_M, \sigma_O, \sigma_P, \sigma_M$ . Mutational effects are added to the existing allelic values. The offspring then become the parents of the next generation. 50% of the offspring are assigned at random to be females and the other 50% are assigned as males.

In our model negative values for ornament size and mate search effort are possible only at the genetic level. At the phenotypic level, negative genetic values for these traits are rounded up to zero. Females with mate search effort of zero are assumed to mate with the first male they encounter, whereas an ornament of size zero is assumed not to exist. This is different from other models that assume a naturally selected optimum from which ornaments can increase or decrease (Tazzyman et al., 2014).

## 2.5 | Model output

Model outputs (e.g. the average values of each trait in a given generation) were saved every tenth generation for simulations run over  $10^5$  generations and every thousandth generation for simulations run over  $10^7$  generations. Average values of each trait were then calculated over the duration of each simulation run.

The following outputs of our model require some further explanation:

- 'Average total ornament size': the mean of the sum of all ornaments' sizes, taken over all individuals and all recorded generations of a simulation run.
- 'Average individual ornament size': the mean size of individual ornaments (i.e. the average total ornament size divided by the number of possible ornaments).

We refer to an ornament as 'exaggerated' if it exceeds a threshold of 0.2 in mean size during a simulation run. This threshold is largely arbitrary but was chosen to be sufficiently high to block out ornaments which are only fleetingly present (cf. Figures 1 and 4). We thus also present:

- 'Average number of exaggerated ornaments': for each generation, we calculated the number of ornaments that exceeded the size threshold. We then took the average of these numbers over all recorded generations in a simulation run.

- 'Average size of exaggerated ornaments': for every generation, we calculated the average size of those ornaments that exceeded the size threshold. We then took the average of these averages over all generations with at least one exaggerated ornament in a simulation run.

We analysed the model outputs visually (trait sizes plotted over the predetermined number of generations) and statistically (using generalized additive models and *t*-tests), based on 100 replicates for simulations run over  $10^5$  generations and 10 replicates for simulations run over  $10^7$  generations. All additive models were fitted using the 'gam' function in the R package mgcv with default parameter settings and assuming normally distributed errors (Wood, 2017).

The code for the model was written in Julia, Version 1.6.2 (2021-07-14; Bezanson et al., 2017; see [Supporting information](#)) and performed in Atom (Table 1).

### 3 | RESULTS

Our results show that Fisherian sexual selection can lead to the long-term persistence of exaggerated male traits, even when both male ornamentation and female mate search are costly.

#### 3.1 | Multiplicative cost structure supports the coexistence of multiple ornaments

We modelled two different cost structures associated with male investment in multiple ornaments. The long-term coexistence of

TABLE 1 Parameters and variables used in the model.

Parameters	
$N$	Population size
$t$	Number of ornaments
$x$	Degree of pleiotropy affecting ornaments and preferences
$s$	Preference strength coefficient
$k$	Mate search cost
$\pi_O, \pi_P, \pi_M$	Mutation probabilities per allele per generation for each trait
$\sigma_O, \sigma_P, \sigma_M$	Standard deviations of mutational effects
Variables	
$\mathbf{O} = (O_1, \dots, O_t)$	Male ornaments
$\mathbf{P} = (P_1, \dots, P_t)$	Female preferences
$M$	Female mate search effort
$v$	Male viability
$1 + M^*$	Female's number of suitors
$f$	Female fecundity
$g_1, g_2, \dots, g_{2t+1}$	Allelic values at each locus. Loci $1, \dots, 2t$ determine ornaments and preferences; locus $2t + 1$ determines mate search effort

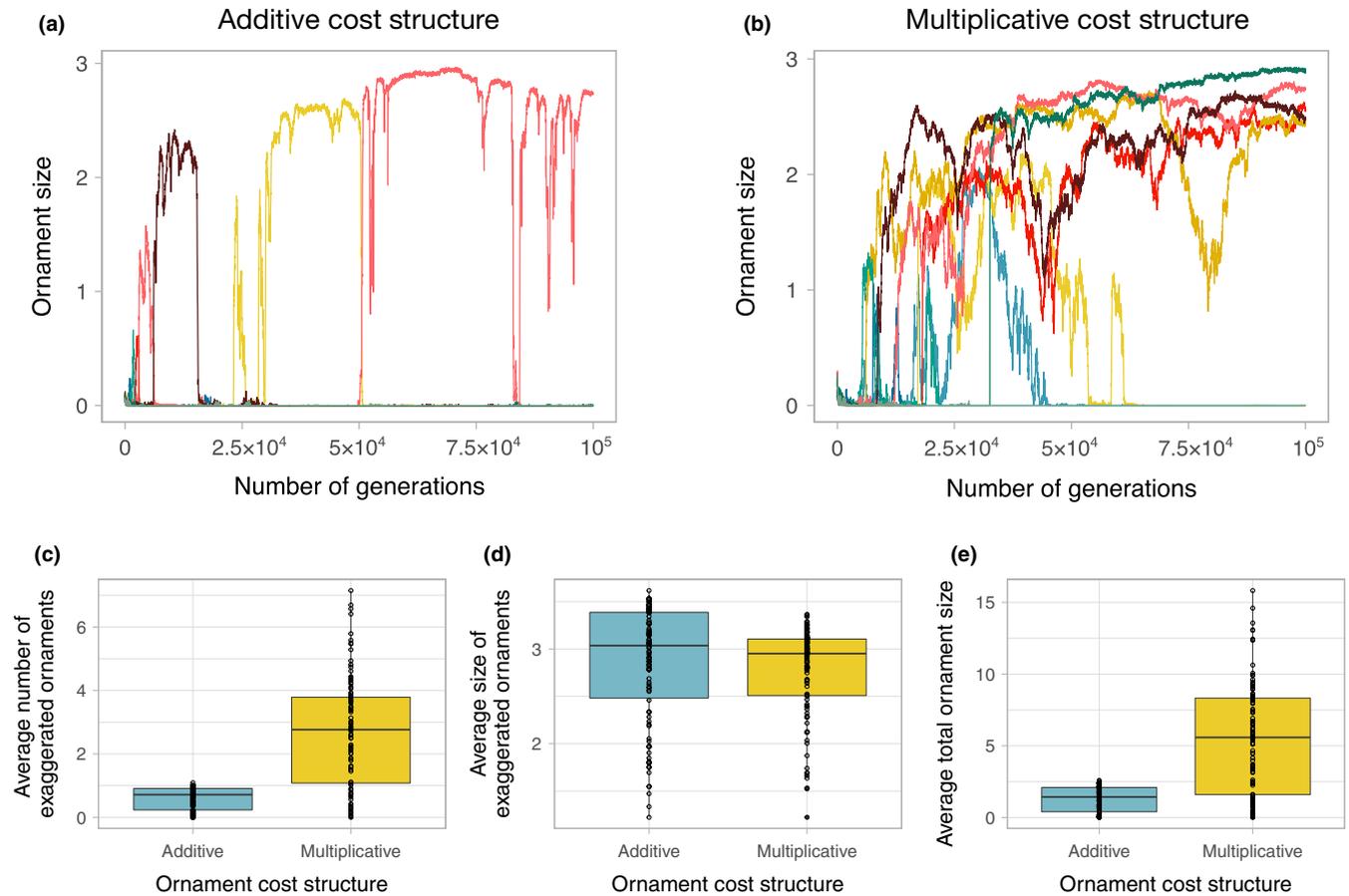
multiple exaggerated ornaments was common under the multiplicative cost structure but rare under the additive structure (Figure 1). In the additive model (equation 5a), the marginal cost of enlarging an ornament does not depend directly on that ornament's size, but rather on an individual's total investment in all ornaments. The marginal costs of increasing large and small ornaments are consequently equal. Given equal marginal costs, selection for exaggeration acts most strongly on the ornament with the highest marginal benefit (i.e. the ornament most strongly preferred by females). As a result, typically only one exaggerated ornament was expressed at any given point in time under the additive model, and ornaments replaced one another sequentially (Figure 1a,c). In contrast, under the multiplicative model (equation 5b), all ornaments were initially cheap to produce, regardless of a male's investments in other ornaments. This facilitated the evolution of multiple coexisting ornaments (Figure 1b,c). The average number of exaggerated ornaments was consequently significantly higher when ornament costs were multiplicative (Welch's *t*-test:  $T_{107.14} = -11.58, p < 10^{-15}$ ) (Figure 1c). On the other hand, the average sizes of individual exaggerated ornaments were indistinguishable between cost structures (Welch's *t*-test:  $T_{182.98} = 0.93, p = 0.36$ ) (Figure 1d). Since the multiplicative model led to a greater number of exaggerated ornaments but no difference in mean ornament size, the average total ornament size was significantly larger in the multiplicative model (Welch's *t*-test:  $T_{108.88} = -10.47, p < 10^{-15}$ ) (Figure 1e).

#### 3.2 | Higher mate search costs decrease female mate search effort and male ornament expression

A female's fecundity decreases with her individual mate search effort, with the costliness of such mate search controlled by the cost parameter  $k$  (equation 6). When mate search was highly costly, females reduced their investment in finding partners and consequently chose from a smaller pool of suitors (Figure 2a; additive model with log-transformed mate search costs,  $p < 10^{-15}$ ). Since the benefits of ornament exaggeration are smaller when males face fewer direct competitors, males responded to such reductions in mate search effort by producing smaller ornaments (Figure 2b). The average total ornament size consequently decreased significantly as the cost of mate search increased (additive model with log-transformed mate search costs,  $p < 10^{-15}$ ). It is nonetheless notable that exaggerated ornaments can persist in our model despite non-zero costs of mate search to females.

#### 3.3 | Mate search effort increased with the number of potential ornaments to choose from

As the number of potential ornaments ( $t$ ) increased, female mate search effort increased under both the additive and the multiplicative cost structures (for both cost structures: additive models,  $p < 10^{-15}$ ) (Figure 3a,d). This indicates that the benefit of being choosy



**FIGURE 1** Ornament evolution with additive and multiplicative cost structures. Exemplary model outputs when the viability costs of male ornaments were additive (a) and multiplicative (b), showing the evolution of ten ornaments over  $10^5$  generations. Each colour represents one positive ornament. The additive cost model resulted in ornaments evolving sequentially, whereas the coexistence of multiple exaggerated ornaments was possible in the multiplicative cost model. Under the multiplicative cost structure, the average number of exaggerated ornaments exceeded the ones of the additive model (c). The average size of exaggerated ornaments was similar for both models (d), whereas the average total ornament size was higher under the multiplicative cost structure (e). Parameter values for all panels:  $N = 1000$ ,  $t = 10$ ,  $x = 0$ ,  $s = 0.05$ ,  $k = 10^{-5}$ ,  $\pi_O = \pi_P = \pi_M = 0.01$ ,  $\sigma_O = \sigma_P = \sigma_M = 1$ . Panels c, d, e are based on 100 runs per cost structure

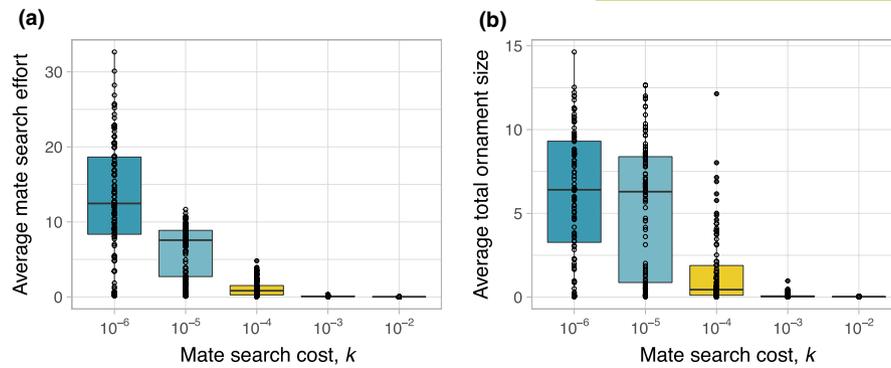
increases when there is wider variety of ornaments to choose from. As a consequence, the average total ornament size also increased significantly with the number of potential ornaments (for both cost structures: additive models,  $p < 10^{-12}$ ) (Figure 3b,e). Similarly, for fixed values of  $t$ , females invested more in mate search when the viability costs of ornaments were multiplicative (Figure 3a,d). This is because the tendency for multiple ornaments to coexist under multiplicative costs led to greater ornament diversity.

The coexistence of multiple ornaments under multiplicative costs resulted in a roughly linear increase in the total size of ornaments as the number of potential ornaments increased (Figure 3e). On the other hand, under the additive model, the average total ornament size increased only modestly with the number of ornaments (Figure 3b). As a consequence, average *individual* ornament size decreased significantly under the additive model but increased with the number of ornaments under the multiplicative model (additive models,  $p < 10^{-15}$ ) (Figure 3c,f). This is unsurprising, given that typically exactly one exaggerated ornament is present at any given time point in the additive model. As the number of potential ornaments

$t$  increases, the average size of individual ornaments must consequently decrease. We note that, since the initial total cost of ornaments scales linearly with their number in the additive model, it was necessary to reduce the initial standard deviation of ornament size for this model when  $t > 20$  (see Figure 3 legend), as otherwise males were not viable at the beginning of the simulations. Results generated with the different initial stand deviations with  $t = 20$  showed no significant differences in the average mate search effort, the average total ornament size or the average individual ornament size (Welch's  $t$ -tests: all  $p > 0.05$ ; results not shown).

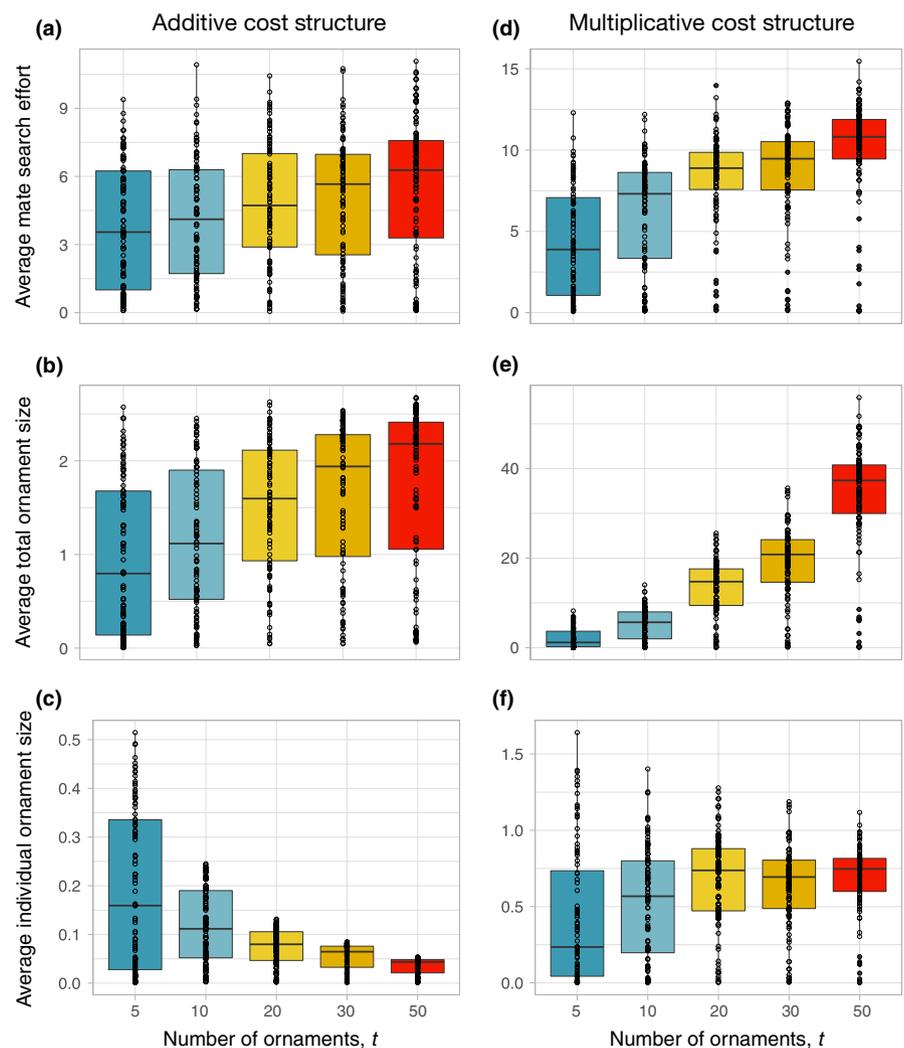
### 3.4 | The higher the degrees of pleiotropy, the longer it takes for ornaments to evolve

Exploratory runs of the model indicated that exaggerated ornaments emerge infrequently in the presence of pleiotropy. We consequently supplemented the original runs (over  $10^5$  generations) with additional runs over  $10^7$  generations (due to the computational



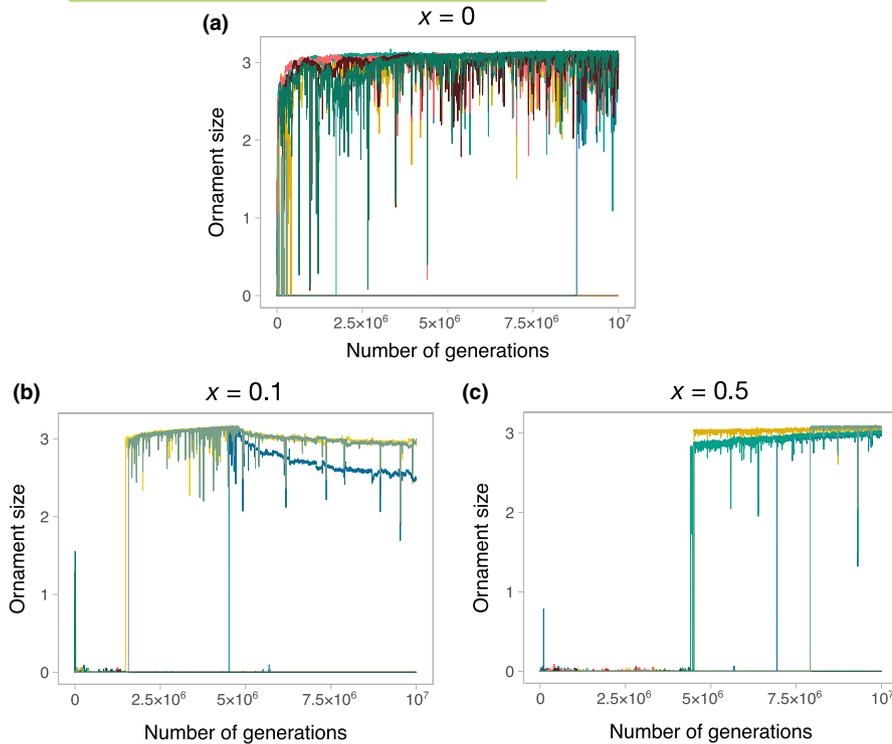
**FIGURE 2** Influence of mate search costs on female mate search effort and male ornamentation. Higher mate search costs ( $k$ ) led to lower mate search effort (a) and lower average total ornament size (b). For  $k > 10^{-4}$ , there was negligible mate search effort, meaning that females mated with the first male they encountered. Parameter values for both panels with the multiplicative cost structure and 100 runs each:  $N = 1000$ ,  $t = 10$ ,  $x = 0$ ,  $s = 0.05$ ,  $\pi_O = \pi_P = \pi_M = 0.01$ ,  $\sigma_O = \sigma_P = \sigma_M = 1$ .

**FIGURE 3** Influence of the number of ornaments on male ornamentation and female mate search effort. Average mate search effort increased with the number of potential ornaments ( $t$ ) under both the additive (a) and multiplicative (d) cost structure. Average total ornament size increased accordingly (b, e). Average individual ornament size increased under the multiplicative cost structure (f) but decreased under the additive cost structure (c). Parameter values for all panels with 100 runs each:  $N = 1000$ ,  $x = 0$ ,  $s = 0.05$ ,  $k = 10^{-5}$ ,  $\pi_O = \pi_P = \pi_M = 0.01$ ,  $\sigma_O = \sigma_P = \sigma_M = 1$ . The ornaments' initial standard deviation for  $t > 20$  was reduced to 0.25 to ensure that males were viable at the beginning of the simulation.



requirements, we replicated the latter simulations only 10 times per parameter choice). Exemplary model outputs over  $10^7$  generations show that the higher the degree of pleiotropy ( $x$ ), the longer it takes for exaggerated ornaments to initially evolve (Figure 4a–c). For  $x = 0$  (Figure 4a) exaggerated ornaments typically evolved within the first few hundred generations, whereas for  $x = 0.5$  the initial emergence

of exaggerated ornaments often took millions of generations (Figure 4c). Average total ornament size consequently decreased significantly with increasing degree of pleiotropy over both  $10^5$  and  $10^7$  generations (additive models,  $p < 10^{-15}$ ) (Figure 5a; Figure S1a). Similarly, mate search effort decreased significantly with increasing pleiotropy over both simulation lengths (additive models,  $p < 10^{-15}$ )



**FIGURE 4** Emergence of ornamentation under different degrees of pleiotropy. Exemplary model outputs with increasing degree of pleiotropy ( $x$ ) from  $x = 0$  (a),  $x = 0.1$  (b) to  $x = 0.5$  (c), showing the evolution of 10 ornaments over  $10^7$  generations. Each colour represents one positive ornament. The higher the degree of pleiotropy, the longer it takes for positive ornaments to evolve. Parameter values for all panels with the multiplicative cost structure:  $N = 1000$ ,  $t = 10$ ,  $s = 0.05$ ,  $k = 10^{-5}$ ,  $\pi_O = \pi_P = \pi_M = 0.01$ ,  $\sigma_O = \sigma_P = \sigma_M = 1$ .

(Figure 5c; Figure S1c). In contrast, the average size of exaggerated ornaments declined only modestly with increasing pleiotropy, especially in the longer simulation runs (Figure 5b; Figure S1b). Overall, these results suggest that pleiotropy makes it more difficult for exaggerated ornaments to emerge, without substantially influencing the size of exaggerated ornaments once they evolve.

## 4 | DISCUSSION

Our model shows that Fisherian sexual selection can lead to the long-term persistence of exaggerated male traits, even when mate search is costly to females. Our results also highlight the importance of choice costs, in particular mate search costs, as a key determinant of exaggerated ornamentation.

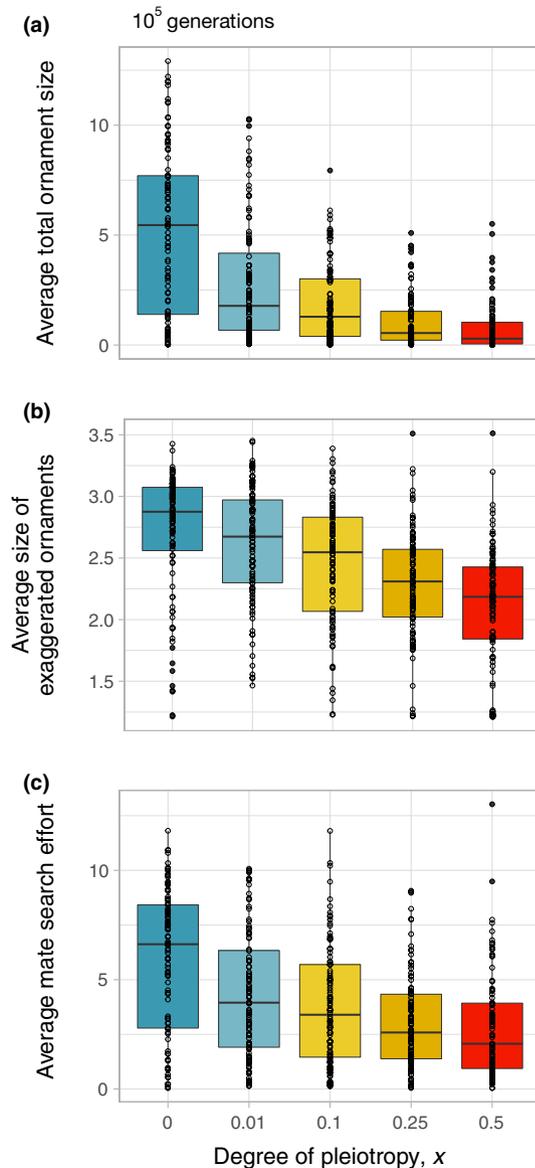
### 4.1 | Female costs in sexual selection models: Pay to play?

Although preferences per se are not costly in our model, females can only act on their preferences if they invest in mate search, which carries a fecundity cost. Our predictions contrast markedly with those of classical models, in which preferences themselves are assumed costly (Pomiankowski, 1987; Pomiankowski et al., 1991). Such models predict that ornament exaggeration is unstable in the presence of any preference cost, except when mutations on the ornament are negatively biased. On the other hand, the model of Kokko et al. (2015), with frequency-dependent costs of choice, predicts the long-term persistence of exaggerated ornaments. In the latter

model, the costs of choice are negligible once a favoured ornament has gone to fixation. In contrast, females in our model continue to pay for mate search even after an ornament has stabilized.

Mate search costs nonetheless had a strongly inhibitory effect on male ornamentation in our model. Even relatively modest mate search costs (e.g.,  $k = 10^{-3}$ , corresponding to a 0.1% reduction in fecundity to seek one additional mate) sufficed to completely suppress female mate search and thereby male ornamentation (Figure 2). Thus, as soon as mate search costs exceeded the indirect benefits of mate choice, females minimized their mate search effort, which eliminated selection pressure on males to evolve exaggerated ornaments. Our Fisherian model consequently only predicts exaggerated ornaments when mate search is cheap and therefore does not explain such ornaments in systems with higher costs to females. Our model might therefore be most applicable to species that form leks.

The costs of mate search are assumed to depend only on a female's mate search trait in our model and not on the strengths of her preferences. Thus, we might imagine females expending a certain fixed amount of time or energy on mate search, before returning to the most preferred male. This is similar to a 'best-of- $n$ ' strategy, whereby a choosing female samples  $n$  males before choosing her most preferred mate from among them (Dombrovsky & Perrin, 1994; Janetos, 1980). Since such strategies require the ability to remember and then relocate previously encountered males (Janetos, 1980), they might be most applicable to species with leks or fixed territories, in which males can be reencountered reliably. Alternatively, females may mate with multiple males and subsequently use cryptic choice to determine the sire of their offspring. For instance, some insects can allocate sperm from different males to separate sperm storage organs, allowing mate choice to be temporally separated from the



**FIGURE 5** Influence of the degree of pleiotropy on male ornamentation. Changes in average total ornament size (a), the average size of exaggerated ornaments (b) and average mate search effort (c) with increasing degree of pleiotropy ( $x$ ) for simulations over  $10^5$  generations. Parameter values for all panels with the multiplicative cost structure:  $N = 1000$ ,  $t = 10$ ,  $s = 0.05$ ,  $k = 10^{-5}$ ,  $\pi_O = \pi_P = \pi_M = 0.01$ ,  $\sigma_O = \sigma_P = \sigma_M = 1$ . The panels are based on 100 runs per degree of pleiotropy.

act of mating (Ala-Honkola & Manier, 2016; Eberhard, 1996; Firman et al., 2017). Our mate search model is less applicable to species in which females must accept or reject each potential mate they encounter and can never return to rejected males.

Mate search costs are difficult to quantify in empirical settings (Dougherty & Shuker, 2015; Wagner, 1998). Nonetheless, multiple studies have demonstrated their existence and showed that both preference costs and mate search effort fundamentally depend on a species' biology, environment and mate search strategy (Byers et al., 2005, 2006; Dougherty & Shuker, 2015;

Gibson & Bachman, 1992; Wickman & Jansson, 1997). In pronghorn (*Antilocapra americana*), most females actively sample mates (Byers et al., 2005, 2006). Byers et al. (2005) showed that although choosiness is usually favoured, it is abandoned when conditions are unfavourable, indicating that choosiness carries costs which can become untenable under rough conditions. A different mate search strategy is found in lekking species such as the small heath butterfly (*Coenonympha pamphilus*) and the greater sage-grouse (*Centrocercus urophasianus*). Here, studies suggest that costs of mate search, such as avoiding males on their way to a lek or increased predation, are most likely outweighed by the possibility of indirect benefits of mating with preferred males on leks (Gibson & Bachman, 1992; Wickman & Jansson, 1997). These empirical studies indicate that mate search effort and its associated costs play a non-negligible role in sexual selection. However, they also indicate that it is difficult to draw general conclusions without closely considering the species' mate search system.

Indirect benefits of mate choice are often classified as either 'Fisherian' (also known as 'sexy sons') or as 'good genes' (reviewed in Kuijper et al., 2012). Our results are based on a Fisherian model, meaning that the only possible benefit of mate choice to females is the potential to produce attractive sons (Fisher, 1930). In our model, male ornaments alone are not correlated with any other aspect of fitness (e.g. viability or survival). In contrast, a 'good genes' model might predict mate search even in the presence of higher costs, because the indirect benefits are potentially larger (Zahavi, 1975). Although the distinction between 'Fisherian runaway' and 'good genes' models has a long history (Baumgartner et al., 2011; Eshel et al., 2002; Iwasa et al., 1991; Kuijper et al., 2012; Pomiankowski & Iwasa, 1993), these models are perhaps better thought of as points along a continuum than mutually exclusive alternatives (Kokko et al., 2002).

## 4.2 | The coexistence of multiple ornaments

In this study, we use the term 'ornament' broadly to include all traits that mainly function as signals to potential mates during courtship. The bowerbird family provides many fine examples of multiple coexisting ornaments, which include plumage and other visual features, songs and the external structures comprising the bower (Borgia, 1995; Uy et al., 2001). The types of resources required to produce such ornaments are presumably very variable. It is conceivable that the expression of, for example a novel colour for which the dietary components have already been accumulated (García-de Blas et al., 2015) would be less costly than exaggerating an existing colour for which all readily available resources have been exhausted. If individual ornaments are initially cheap, then their costs might be approximately multiplicative, and our model predicts the coexistence of multiple ornaments in such cases. On the other hand, elaborate structures and other ornaments that consume substantial resources might be more consistent with an additive cost structure, restricting the coexistence of multiple ornaments. It would

be interesting to compare the numbers of coexisting structural and non-structural ornaments across multiple species to test whether such predictions are borne out empirically. The coexistence of multiple ornaments is also predicted by the model of Pomiankowski and Iwasa (1993), who similarly assumed multiplicative viability costs. They additionally predict that coexistence will collapse if the costs to females of preferring multiple ornaments become too extreme. In contrast to the additive cost structure, the multiplicative cost structure therefore relates to previous cost assumptions (e.g. Iwasa & Pomiankowski, 1994; Pomiankowski & Iwasa, 1993). However, in our model, these costs solely apply to evolution of ornaments, while preferences themselves are cost free, allowing for easier preference evolution.

### 4.3 | The evolutionary consequences of pleiotropy

By allowing for partial pleiotropy, we investigated how shared loci might influence the coevolution of ornaments and preferences. Our results show that the higher the degree of pleiotropy, the longer it takes for ornaments to evolve, without necessarily reducing the size of individual ornaments (Figures 4 and 5). To understand this result, it is helpful to consider the initiation of Fisherian runaway in more detail. In the absence of pleiotropy, female preferences initially evolve mainly by genetic drift. This can allow strong preferences to evolve even before a corresponding ornament emerges. For instance, the genus *Xiphophorus* consists of 'platyfish' and 'swordtails' (Basolo, 1995), with males of the latter species developing a sword-shaped ornament. Interestingly, preferences for the sword are present not only in swordtail females but also in females of the swordless platyfish species, whose males entirely lack this ornament (Basolo, 1995). This suggests that preferences may often emerge prior to corresponding ornaments (Rosenthal et al., 2001; Ryan et al., 2010) and sometimes reach the threshold needed for Fisherian runaway to take off once the preferred ornament eventually arises (Kirkpatrick, 1982; Lande, 1981).

Pleiotropy might inhibit this process by coupling the emergence of ornament and preference closely in time. When pleiotropy is strong, positive preferences may lead to the immediate expression of the corresponding ornament in males. However, such preferences may not yet be strong enough to kick-start Fisherian runaway. If the viability costs of the emerging ornament outweigh the initially weak sexual selection, the result is negative net selection on the ornament and, by extension, the preference. The tight genetic association between ornaments and preferences under pleiotropy can consequently suppress Fisherian runaway, impairing the evolution of ornaments, which, in turn, selects against female mate search effort due to a lack of ornament diversity. Weak pleiotropy is most likely the norm for male ornaments that do not involve the bearer's cognitive and sensory processes, such as colours or morphological structures. Pleiotropy could, however, be substantial for ornaments that are not only evaluated by a female but also actively altered by the male. However, the rapid coevolution of presumably pleiotropic

male ornaments and female choice—as seen for example in the spotted bowerbird (*Chlamydera maculata*) (Borgia, 1995)—cannot be explained by our model, which instead predicts that pleiotropy should hinder Fisherian runaway.

In our model, the potential for pleiotropy implicitly links the scales on which ornaments and preferences are expressed. For example, a one-unit change in an 'ornament gene' will lead to a change of  $x$  in the corresponding preference and vice versa, where  $x$  is the degree of pleiotropy. Future models could include an additional parameter allowing a difference in the scaling between ornaments and preferences. For example, a one-unit change in an 'ornament gene' could lead to a change of  $Ax$  in preference, whereas a one-unit change in a preference gene would lead to a change of  $\frac{1}{A}x$  in the ornament. For large values of  $A$ , this could allow preferences to drift to high values more easily, as the costs of pleiotropic ornament expression would be smaller. It is not clear what would determine the value of  $A$  empirically, however.

Our model assumes that ornaments are expressed only in males. However, since most of the genome is shared between males and females, most newly evolving ornaments are likely expressed—at least initially—in both sexes (Kraaijeveld, 2019). The club-winged manakin (*Machaeropterus deliciosus*) serves as an astonishing example (Prum, 2017). Males of this species attract females by stridulating their wings, which is made possible by their unique club-shaped wing bones. Unsurprisingly, this unusual morphology interferes with flight performance and presumably imposes significant costs. Since wing formation takes place during early embryonal development before major differentiation between the sexes, both males and females are born with club-shaped wings. Despite this, females apparently do not obtain any advantages from their unusual wings (Prum, 2017). It is conceivable that the emergence of novel ornaments is often inhibited by their expression in females, where they carry similar costs but presumably provide fewer benefits. Future models could explicitly account for the secondary evolution of sex-based differential expression in both Fisherian ornaments and corresponding preferences (Connallon et al., 2010).

## 5 | CONCLUDING REMARKS

Our model highlights the fundamental importance of mate search effort in the evolution of sexual ornamentation. Strong preferences can only be acted on if their bearers sample multiple potential mates. The extent of such sampling depends in turn on the costs of mate search. Mate search costs are likely more amenable to empirical estimation than the preference costs that underlie many previous models. For instance, one of the main predictions of our model—that males should be more highly ornamented when mate search is cheap—could be tested by comparing ornaments among related species that differ in the density of advertising males. Moreover, we see no reason to assume that the importance of mate search effort is restricted to Fisherian models. Much could be gained by incorporating mate search effort into 'good genes' and 'direct benefits' models of sexual selection.

## AUTHOR CONTRIBUTIONS

AW and JMHW designed the model and wrote the code. AW drafted the manuscript. Both authors revised the manuscript.

## ACKNOWLEDGEMENTS

We are grateful to Julius Rombach for logistical support. Andrew Pomiankowski provided feedback that greatly improved the manuscript. JMHW was supported by the German Federal Ministry of Education and Research (BMBF). Open Access funding enabled and organized by Projekt DEAL.

## CONFLICT OF INTEREST

The authors declare no competing interests.

## PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/jeb.14127>.

## DATA AVAILABILITY STATEMENT

The data for all figures are available on Dryad (doi: [10.5061/dryad.4tmgp4fdfs](https://doi.org/10.5061/dryad.4tmgp4fdfs)). See Supporting information for simulation code written for Julia v.1.6.2.

## ORCID

Anna Waffender  <https://orcid.org/0000-0003-4488-8278>

Jonathan M. Henshaw  <https://orcid.org/0000-0001-7306-170X>

## REFERENCES

- Ala-Honkola, O., & Manier, M. K. (2016). Multiple mechanisms of cryptic female choice act on intraspecific male variation in *Drosophila simulans*. *Behavioral Ecology and Sociobiology*, *70*, 519–532.
- Andersson, M. (1982). Female choice selects for extreme tail length in a widowbird. *Nature*, *299*, 818–820.
- Andersson, M. (1994). *Sexual selection*. Princeton University Press.
- Andersson, M., & Iwasa, Y. (1996). Sexual selection. *Trends in Ecology & Evolution*, *11*, 53–58.
- Andersson, M., & Simmons, L. W. (2006). Sexual selection and mate choice. *Trends in Ecology and Evolution*, *21*, 296–302.
- Andersson, S., & Andersson, M. (1994). Tail ornamentation, size dimorphism and wing length in the genus *Euplectes* (Ploceinae). *The Auk*, *111*, 80–86.
- Basolo, A. L. (1995). A further examination of a pre-existing bias favouring a sword in the genus *Xiphophorus*. *Animal Behaviour*, *50*, 365–375.
- Basolo, A. L., & Alcaraz, G. (2003). The turn of the sword: Length increases male swimming costs in swordtails. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *270*, 1631–1636.
- Baumgartner, A., Coleman, S., & Swanson, B. (2011). The cost of the sword: Escape performance in male swordtails. *PLoS One*, *6*, e15837.
- Bezanson, J., Edelman, A., Karpinski, S., & Shah, V. B. (2017). Julia: A fresh approach to numerical computing. *SIAM Review*, *59*, 65–98.
- Borgia, G. (1995). Complex male display and female choice in the spotted bowerbird: Specialized functions for different bower decorations. *Animal Behaviour*, *49*, 1291–1301.
- Byers, J. A., Byers, A. A., & Dunn, S. J. (2006). A dry summer diminishes mate search effort by pronghorn females: Evidence for a significant cost of mate search. *Ethology*, *112*, 74–80.
- Byers, J. A., Wiseman, P. A., Jones, L., & Roffe, T. J. (2005). A large cost of female mate sampling in pronghorn. *The American Naturalist*, *166*, 661–668.
- Connallon, T., Cox, R. M., & Calsbeek, R. (2010). Fitness consequences of sex-specific selection. *Evolution*, *64*, 1671–1682.
- Cotton, S., Small, J., & Pomiankowski, A. (2006). Sexual selection and condition-dependent mate preferences. *Current Biology*, *16*, R755–R765.
- Darwin, C. (1860). Letter to Asa Gray, 3 April 1860. Darwin Correspondance Project, "Letter no. 2743". <https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-2743.xml>
- De Jong, M. C. M., & Sabelis, M. W. (1991). Limits to runaway sexual selection: The wallflower paradox. *Journal of Evolutionary Biology*, *4*, 637–655.
- Dombrovsky, Y., & Perrin, N. (1994). On adaptive search and optimal stopping in sequential mate choice. *The American Naturalist*, *144*, 355–361.
- Dougherty, L. R., & Shuker, D. M. (2015). The effect of experimental design on the measurement of mate choice: A meta-analysis. *Behavioral Ecology*, *26*, 311–319.
- Eberhard, W. (1996). *Female control: Sexual selection by cryptic female choice*. Princeton University Press.
- Edward, D. A. (2015). The description of mate choice. *Behavioral Ecology*, *26*, 301–310.
- Endler, J. A. (2012). Bowerbirds, art and aesthetics: Are bowerbirds artists and do they have an aesthetic sense? *Communicative & Integrative Biology*, *5*, 281–283.
- Eshel, I., Sansone, E., & Jacobs, F. (2002). A long-term genetic model for the evolution of sexual preference: The theories of Fisher and Zahavi re-examined. *Journal of Mathematical Biology*, *45*, 1–21.
- Firman, R. C., Gasparini, C., Manier, M. K., & Pizzari, T. (2017). Postmating female control: 20 years of cryptic female choice. *Trends in Ecology & Evolution*, *32*, 368–382.
- Fisher, R. A. (1930). *The genetical theory of natural selection*. The Clarendon Press.
- Fitzpatrick, M. J. (2004). Pleiotropy and the genomic location of sexually selected genes. *The American Naturalist*, *163*, 800–808.
- Fromhage, L., & Henshaw, J. M. (2022). The balance model of honest sexual signalling. *Evolution*, *76*, 445–454.
- García, C. M., Jimenez, G., & Contreras, B. (1994). Correlational evidence of a sexually-selected handicap. *Behavioral Ecology and Sociobiology*, *35*, 253–259.
- García-de Blas, E., Mateo, R., & Alonso-Alvarez, C. (2015). Accumulation of dietary carotenoids, retinoids and tocopherol in the internal tissues of a bird: A hypothesis for the cost of producing colored ornaments. *Oecologia*, *177*, 259–271.
- Gibson, R. M., & Bachman, G. C. (1992). The costs of female choice in a lekking bird. *Behavioral Ecology*, *3*, 300–309.
- Heisler, L., Andersson, M., Arnold, S., Boake, C., Borgia, G., Hausfater, G., Kirkpatrick, M., Lande, R., Smith, J. M., & O'donald, P. (1987). The evolution of mating preferences and sexually selected traits. In J. W. Bradbury & M. B. Andersson (Eds.), *Sexual selection: Testing the alternatives* (pp. 96–118). Wiley.
- Henshaw, J. M. (2018). Finding the one: Optimal choosiness under sequential mate choice. *Journal of Evolutionary Biology*, *31*, 1193–1203.
- Henshaw, J. M., Fromhage, L., & Jones, A. G. (2022). The evolution of mating preferences for genetic attractiveness and quality in the presence of sensory bias. *Proceedings of the National Academy of Sciences of the United States of America*, *119*, 1–9.
- Henshaw, J. M., & Jones, A. G. (2020). Fisher's lost model of runaway sexual selection. *Evolution*, *74*, 487–494.
- Hingle, A., Fowler, K., & Pomiankowski, A. (2001). Size-dependent mate preference in the stalk-eyed fly *Cyrtodiopsis dalmanni*. *Animal Behaviour*, *61*, 589–595.

- Houle, D., & Kondrashov, A. S. (2002). Coevolution of costly mate choice and condition-dependent display of good genes. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 269, 97–104.
- Iwasa, Y., & Pomiankowski, A. (1994). The evolution of mate preferences for multiple sexual ornaments. *Evolution*, 48, 853–867.
- Iwasa, Y., Pomiankowski, A., & Nee, S. (1991). The evolution of costly mate preferences II. The “handicap” principle. *Evolution*, 45, 1421–1442.
- Janetos, A. C. (1980). Strategies of female mate choice: A theoretical analysis. *Behavioral Ecology and Sociobiology*, 7, 107–112.
- Jennions, M. D., & Petrie, M. (2000). Why do females mate multiply? A review of the genetic benefits. *Biological Reviews of the Cambridge Philosophical Society*, 75, 21–64.
- Jones, A. G., & Ratterman, N. L. (2009). Mate choice and sexual selection: What have we learned since Darwin? *Proceedings of the National Academy of Sciences of the United States of America*, 106, 10001–10008.
- Judge, K. A., Ting, J. J., & Gwynne, D. T. (2014). Condition dependence of female choosiness in a field cricket. *Journal of Evolutionary Biology*, 27, 2529–2540.
- Kirkpatrick, M. (1982). Sexual selection and the evolution of female choice. *Evolution*, 36, 1–12.
- Kirkpatrick, M., Rand, A. S., & Ryan, M. J. (2006). Mate choice rules in animals. *Animal Behaviour*, 71, 1215–1225.
- Kokko, H., Booksmythe, I., & Jennions, M. D. (2015). Mate-sampling costs and sexy sons. *Journal of Evolutionary Biology*, 28, 259–266.
- Kokko, H., Brooks, R., McNamara, J. M., & Houston, A. I. (2002). The sexual selection continuum. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 269, 1331–1340.
- Kokko, H., Jennions, M. D., & Brooks, R. (2006). Unifying and testing models of sexual selection. *Annual Review of Ecology, Evolution, and Systematics*, 37, 43–66.
- Kokko, H., & Mappes, J. (2005). Sexual selection when fertilization is not guaranteed. *Evolution*, 59, 1876–1885.
- Kotiaho, J. S. (2001). Costs of sexual traits: A mismatch between theoretical considerations and empirical evidence. *Biological Reviews of the Cambridge Philosophical Society*, 76, 365–376.
- Kraaijeveld, K. (2019). Genetic architecture of novel ornamental traits and the establishment of sexual dimorphism: Insights from domestic birds. *Journal of Ornithology*, 160, 861–868.
- Kuijper, B., Pen, I., & Weissing, F. J. (2012). A guide to sexual selection theory. *Annual Review of Ecology, Evolution, and Systematics*, 43, 287–311.
- Lande, R. (1981). Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Sciences of the United States of America*, 78, 3721–3725.
- Lehtonen, J., & Kokko, H. (2012). Positive feedback and alternative stable states in inbreeding, cooperation, sex roles and other evolutionary processes. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 367, 211–221.
- Pomiankowski, A. (1987). The costs of choice in sexual selection. *Journal of Theoretical Biology*, 128, 195–218.
- Pomiankowski, A., & Iwasa, Y. (1993). Evolution of multiple sexual preferences by Fisher's runaway process of sexual selection. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 253, 173–181.
- Pomiankowski, A., Iwasa, Y., & Nee, S. (1991). The evolution of costly mate preferences I. Fisher and biased mutation. *Evolution*, 45, 1422–1430.
- Prum, R. O. (2017). *The evolution of beauty: How Darwin's forgotten theory of mate choice shapes the animal world—And us*. Doubleday.
- Radwan, J. (2008). Maintenance of genetic variation in sexual ornaments: A review of the mechanisms. *Genetica*, 134, 113–127.
- Rosenthal, G. G. (2017). *Mate choice: The evolution of sexual decision making from microbes to humans*. Princeton University Press.
- Rosenthal, G. G., Flores Martinez, T. Y., García de León, F. J., & Ryan, M. J. (2001). Shared preferences by predators and females for male ornaments in swordtails. *The American Naturalist*, 158, 146–154.
- Ryan, M. J., Bernal, X. E., & Rand, A. S. (2010). Female mate choice and the potential for ornament evolution in túngara frogs *Physalaemus pustulosus*. *Current Zoology*, 56, 343–357.
- Servedio, M., & Bürger, R. (2018). The effects on parapatric divergence of linkage between preference and trait loci versus pleiotropy. *Genes*, 9, 217.
- Servedio, M. R., van Doorn, G. S., Kopp, M., Frame, A. M., & Nosil, P. (2011). Magic traits in speciation: ‘Magic’ but not rare? *Trends in Ecology & Evolution*, 26, 389–397.
- Shaw, K. L., Ellison, C. K., Oh, K. P., & Wiley, C. (2011). Pleiotropy, “sexy” traits, and speciation. *Behavioral Ecology*, 22, 1154–1155.
- Shuker, D. M., & Kvarnemo, C. (2021). The definition of sexual selection. *Behavioral Ecology*, 32, 781–794.
- Siefferman, L., & Hill, G. E. (2005). Male eastern bluebirds trade future ornamentation for current reproductive investment. *Biology Letters*, 1, 208–211.
- Singh, N. D., & Shaw, K. L. (2012). On the scent of pleiotropy. *Proceedings of the National Academy of Sciences*, 109, 5–6.
- Tazzyman, S. J., Iwasa, Y., & Pomiankowski, A. (2014). The handicap process favors exaggerated, rather than reduced, sexual ornaments. *Evolution*, 68, 2534–2549.
- Uy, J. A. C., Patricelli, G. L., & Borgia, G. (2001). Complex mate searching in the satin bowerbird *Ptilonorhynchus violaceus*. *The American Naturalist*, 158, 530–542.
- Verhulst, S., Dieleman, S. J., & Parmentier, H. K. (1999). A tradeoff between immunocompetence and sexual ornamentation in domestic fowl. *Proceedings of the National Academy of Sciences of the United States of America*, 96, 4478–4481.
- Wagner, W. E. (1998). Measuring female mating preferences. *Animal Behaviour*, 55, 1029–1042.
- Wickman, P.-O., & Jansson, P. (1997). An estimate of female mate searching costs in the lekking butterfly *Coenonympha pamphilus*. *Behavioral Ecology and Sociobiology*, 40, 321–328.
- Wood, S. N. (2017). *Generalized additive models: An introduction with R* (2nd ed.). Chapman and Hall/CRC.
- Zahavi, A. (1975). Mate selection—A selection for a handicap. *Journal of Theoretical Biology*, 53, 205–214.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Waffender, A., & Henshaw, J. M. (2023). Long-term persistence of exaggerated ornaments under Fisherian runaway despite costly mate search. *Journal of Evolutionary Biology*, 36, 45–56. <https://doi.org/10.1111/jeb.14127>