20 years of misunderstanding: Compensatory traits can explain U-shaped cost function of purely sexual traits

Running title: **Performance, ornaments, and compensatory traits**

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Number of table 1

Number of figures 2

Number of supplementary material 1

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The cost of ornamentation is often measured experimentally to study the relative importance of sexual and viability selection for ornamentation, but these experiments can lead to a misleading conclusion when compensatory trait is ignored. A famous, classic experiment on the outermost tail feathers in the barn swallow *Hirundo rustica*, explains that the U-shaped aerodynamic performance of the outermost tail feathers would be the evolutionary outcome mainly through viability selection for optimal tail length, but this conclusion depends on the assumption that compensatory traits do not cause reduced performance. Using a simple model experiment, I demonstrated that ornamentation evolved purely though sexual selection can produce a U-shaped cost function under the presence of compensatory traits. Therefore, U-shaped cost function (and the low performance of individuals with reduced ornaments) cannot be used to infer the evolutionary force favoring ornamentation, due to a previously overlooked concept, "overcompensation", which can increase, rather than decrease, the apparent cost of ornamentation.

Keywords: cost-reducing traits, cost of ornamentation, viability selection, sexual selection

Animals sometimes possess ornamentation that seem to have negative effects on survivorship, such as long tails and colorful plumage in birds (Andersson 1994). Many empirical studies have shown sexual selection for ornaments, explaining the evolution of seemingly costly ornaments (e.g., see Hill & McGraw 2006 for a review on birds). However, the mere presence of sexual selection does not necessarily mean that sexual selection has been the major selection force causing ornament elaboration, because focal traits can have mainly evolved via viability selection and sexual selection may have caused ornament elaboration only slightly beyond viability optimum (i.e., possible exaptation; Bergstrom & Dugatkin 2016). Then, it is not surprising to see that researchers have alternatively focused on the cost of ornamentation (e.g., Evans 1998; see below), because the ornaments' cost function would clarify the relative importance of sexual and viability selection on the focal traits.

A famous example is those testing aerodynamic performance of long outermost tail feathers in the barn swallows *Hirundo rustica* (Fig. 1; e.g., Evans 1998; Buchnan & Evans 2000; Bro-Jørgensen *et al.* 2007). Although long outermost tail feathers have been shown to be sexually selected (e.g., Møller 1988; reviewed in Møller 1994; Turner 2006; Romano *et al.* 2016), it remains unclear how and why long tails evolved due to the possible aerodynamic function of long tails (Norberg 1994). Evans and colleagues have experimentally shortened outermost tail feather length and measured aerodynamic performances of swallows (e.g., Evans 1998; Buchanan & Evans 2000; Rowe *et al.* 2001; also see Evans & Thomas 1997; Thomas & Rowe 1997 for the detailed descriptions of predictions). They predicted that, if long outermost tail feathers evolved purely through sexual selection, shortening the length should produce a decrease in aerodynamic cost (Fig. 1

upper left). Or, if it evolved purely through viability selection due to the aerodynamic function, shortening the length should increase the aerodynamic cost (Fig. 1 upper right). Lastly, if viability and sexual selection together favors the evolution of long tails, shortening the tail would decrease the aerodynamic cost first, and then increase the cost beyond the aerodynamic optimum (Fig. 1 upper middle). Their results were consistent with the last prediction with estimated peak values located around 10 mm shorter from the current tail length. Therefore, they concluded that tail feathers mainly evolved through viability selection and sexual selection would have elongated tails only around 10 mm (9–20%) beyond the aerodynamic optimum. However, this argument is problematic, because they do not consider compensatory traits, which have been reported to affect aerodynamic cost of long tails in many bird species including barn swallows (e.g., Balmford *et al.* 1994; Barbosa & Møller 1995; Møller *et al.* 1995; Møller 1996). In fact, several compensatory traits have been reported in barn swallows, including greater wingspans, wing area, aspect ratios, reduced wing loading, and so on (e.g., Møller *et al.* 1995; reviewed in Husak & Swallow 2011; also see Moreno & Møller 1996; Saino *et al.* 1997; Tubaro 2003 for other kinds of compensation). Animal performance could be affected by compensatory traits, which is thought to be the case in the peacock *Pavo cristatus*, another model species of sexual selection: peacocks with fully expressed trains, i.e., a costly trait, have a lower metabolic cost of locomotion than those with rudimentary trains possibly due to the presence of compensatory traits (Thavarajah *et al.* 2016). Similar but less striking results, such as no detectable performance cost of gorgeous ornaments, are repeatedly reported in ornamented animals (e.g., Baumgartner *et al.* 2011; Trappet *et al.* 2013; Kojima & Lin 2019).

The importance of compensatory traits has repeatedly been advocated (e.g., Møller 1996; Oufiero & Garland 2007; Husak *et al.* 2015). Using a hypothetical data set, Oufiero & Garland (2007) demonstrated that ignoring a compensatory trait led to an incorrect (and opposite) conclusion. Likewise, Husak & Swallows (2011) reviewed compensatory traits and proposed that a simple test of relationships between ornamentation and performance can lead to misleading conclusions (also see Husak *et al.* 2015 for an updated review). However, although these studies stress that manipulation experiments should consider compensatory traits carefully (e.g., Husak & Swallow 2011), it is still unclear whether and how compensatory traits affect cost function concerning ornament manipulation. Particularly, whether the low performance of individuals with reduced ornaments (and hence U-shaped cost function; see preceding paragraph) can be explained by compensatory traits is not known. As Oufiero & Garland (2007) used a hypothetical data set, a simple model experiment rather than complicated empirical data, would be helpful to demonstrate the potential influence of compensatory traits.

Here, I presented a simple model experiment to examine whether the U-shaped cost function (see Fig. 1) could be produced when the ornament has evolved purely through sexual selection for exaggerated ornamentation with the coevolution of compensatory traits. For this purpose, I used "chuonchuon" (Fig. 2 upper panel), a traditional balancing toy in Vietnam, as a model system. Chuonchuon is a suitable model, because its balance is determined by the whole phenotype, as in the locomotor performance of animals (e.g., see Husak & Swallow 2011). Clearly, this is NOT to test the function of particular traits (e.g., swallows' tails), but to test whether compensatory traits can cause reduced performance under an experimental reduction of

ornamental traits that has evolved purely through sexual selection. I first determined an evolutionary stable form of chuonchuon under the setting that long tails have been sexually selected (i.e., providing reproductive advantages) and its negative effects on balance (i.e., survival of chuonchuon) could be reduced by a compensatory trait, extended wings. Then, I tested the cost function of ornamentation by experimentally shortening tail length, as in the previous manipulation experiments in swallows listed above. I discussed the evolutionary implications of the observed pattern.

METHODS

Experimental setup

I used four commercially available "chuonchuon" for my experiment (ca. 7 cm length: Tirakita, Japan). I used unmanipulated chuonchuon as an ancestral state, in which neither sexually selected ornamentation nor compensatory traits have yet been evolved. Then, I used a plastic straw (0.4 g, 4 mm width and 160 mm length; Strix design, Japan) as an elongated tail. As a compensatory trait, I made extended wings using clay (0.8 g per wing, i.e., twice as heavy as a plastic straw to account for the lever principle; Fig. 2 middle panel).

I here simply set the situation with a set of dichotomous events, that is, only balanced chuonchuon can "survive," and only longer tailed chuonchuon in the population can "reproduce." Then, the ancestral form can survive anytime, but the tail-elongated form cannot survive when elongated tails make them unbalanced (I used a cut-off point as 30° deviation from the horizontal plane, here). Tail elongation made models unbalanced in the range of the current study (i.e., maximum length to −80 mm shortened tails;

see Fig. 1) and thus they cannot survive without compensatory traits, i.e., extended wings. Even when it survived, the ancestral form cannot have descendants when any derived forms with elongated tails (i.e., those with longer tails than ancestral form) exist. Because my interest here is not in the actual evolutionary trajectory but the cost function of the derived form, I obtained the evolutionary stable form by comparing the "fitness" of each form. For simplicity, I assumed continuous variation in tail length but assumed two discrete states of the extended wings (i.e., with and without extended wings). In this case, the evolutionary stable form is a chuonchuon with maximum elongated tails with extended wings. This is because chuonchuon with maximum elongated tails and extended wings can survive (i.e., balanced) and thus reproduce under any circumstances (i.e., they have the longest tails compared to all other forms). I did not subdivide compensatory traits (e.g., small/medium/large), because the purpose of the current study is not to quantify the exact peak performance or identify the best size of compensatory traits but to examine the effect of compensatory traits.

Measuring performance

As in manipulation experiments in the barn swallow (Buchanan & Evans 2000; Rowe *et al.* 2001), I shortened the extended tails of chuonchuon models (20 mm/40 mm/60 mm/80 mm, here) and took two pictures each time. From each of the two pictures, I measured the absolute angle of chuonchuon deviated from the horizontal plane as stability (or balance-ability: Fig. 2 middle panel) using ImageJ software. Then, I averaged the two measurements (repeatability = 0.99, $F_{19,20} = 270.24$, $P < 0.0001$; Lessells & Boag 1987) to have a representative estimate of stability for each treatment.

Statistics

To account for individual variation in performance, I used a Bayesian linear mixed-effects model with a normal error distribution to examine the stability of chuonchuon given tail shortening. Individual identity was used as a random effect. By calculating the Brooks-Gelman-Rubin statistic (Rhat), which must be <1.2 for all parameters (Kass *et al.* 1998), the reproducibility of the MCMC simulation was confirmed. Data analyses were conducted using the R statistical package (ver. 4.1.0; R Core Team 2021), using the function "MCMCglmm" (with its default setting) in the package "MCMCglmm" (Hadfield 2010).

RESULTS

I found a significant quadratic relationship between tail length manipulation and stability of the chuonchuon (Table 1; Fig. 2 lower panel): the stability of the chuonchuon, measured as an absolute angle deviated from the horizontal plane, increased with decreasing tail length until the peak value where chuonchuon had the maximum estimated stability and further tail shortening beyond the peak value decreased stability.

DISCUSSION

The main finding of the current study is that the apparent U-shaped cost function can evolve purely through sexual selection in the presence of compensatory traits (i.e., with no viability advantage of ornamentation). The importance of compensatory traits has repeatedly been advocated (reviewed in Møller 1996; Husak & Swallow 2010; Husak *et al.* 2015), but previous studies assume that compensatory traits still function as "cost-reducing"

traits regardless of the situation (e.g., see Husak *et al.* 2015, p. 18). Here, I showed that "overcompensation" could decrease performance, producing a U-shaped cost function. As an old Chinese proverb say, "too much is as bad as too little" at least in some cases. The assumption that the cost function can reveal the relative importance of sexual and viability selection (e.g., Buchanan & Evans 2000) is therefore unreliable. In other words, the prediction of sexual selection (i.e., Fig. 1C) is no longer valid, and can be replaced by U-shaped cost function as in Fig. 1B, indicating that the presence/absence of viability selection cannot be detected.

Of course, the current experiment using chuonchuon models does not mean that sexual selection always produces a U-shaped cost function (and does not mean that the same physical property, i.e., stability, determined the evolution of ornamentation, such as swallows' tail, and compensatory traits). Still, even without formal mathematical model, it seems likely that overcompensation will often reduce locomotor performance, particularly when locomotion requires co-opted, integrated phenotype (e.g., aerial locomotion). In fact, concerning the function of long tails in barn swallows, Norberg (1994) mentioned that "*any experimental shortening and lengthening of the outer tail feathers is likely to upset an original co-adapted character set…*" (p. 231). Also, macroevolutionary studies of swallows have supported sexual (rather than viability) selection explanation (e.g., Hasegawa *et al.* 2016; Hasegawa & Arai 2017, 2018, 2020a,b, 2021), demanding further experimental studies, possibly using a smaller amount of manipulation (so that overcompensation can be avoided) in many species with various ornamentation. An alternative approach, the manipulation of compensatory traits (sensu Møller 1996) would in theory be valuable to show the effect of overcompensation, but is impractical due to the

multi-dimensionality of compensatory traits (e.g., manipulations of wing size and shape are often difficult to conduct).

In addition, the current experiment provides useful insights. First, the cost of ornamentation can be transformed from one type to another. Extended wings enhanced the stability of chuonchuon with elongated tails, though they required additional investment (i.e., a production cost) instead (also see Møller 1996 for a similar argument). Furthermore, the production cost of compensatory traits can be much higher than the production cost of the ornament itself (see Methods). It is straightforward to conclude that a single measure of cost (e.g., aerodynamic cost) is inappropriate to approximate the total cost (and thus viability disadvantage) of ornamentation, even when the production cost of ornamentation itself seems negligible at first glance, as is the case for the outermost tail feathers in barn swallows (Fig. 1).

In summary, the current model experiment demonstrated that a U-shaped cost function, which is often thought to result from viability advantage of focal ornaments, can be observed when sexual selection has favored the evolution of the costly ornaments, due to the presence of compensatory traits. Future studies should consider that overcompensation can be detrimental and that more sophisticated experimental design is needed when inferring selection pressure on (and the evolutionary history of) ornamentation.

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Author Contribution MH performed data analysis and wrote the manuscript alone.

Conflict statement The authors declare no conflict of interest.

Permits This study does not include any treatments of animals, as all the information was gathered from model experiments.

Data availability Data attached as Table S1 will be deposited into osf.io once accepted.

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Table 1 Bayesian linear mixed-effects model of stability of chuonchuon in relation to experimental manipulation of elongated tails (N_{ID} = 4, $Ntotal$ = 20)

Variable	Coefficient [95% CI]	P_{MCMC}
Intercept	**22.37 [18.95, 25.97]**	**<0.0001**
Linear term of manipulation	**0.96 [0.71, 1.23]**	**<0.0001**
Quadratic term of manipulation	**8.36 [6.21, 10.51]**	**<0.0001**

The dependent variable is the absolute angle of chuonchuon deviated from the horizontal plane. I included chuonchuon ID as a random factor (variance = 0.20) in addition to units (variance = 15.39).

Significant test results (i.e. $P < 0.05$) are indicated in bold.

Figure legends

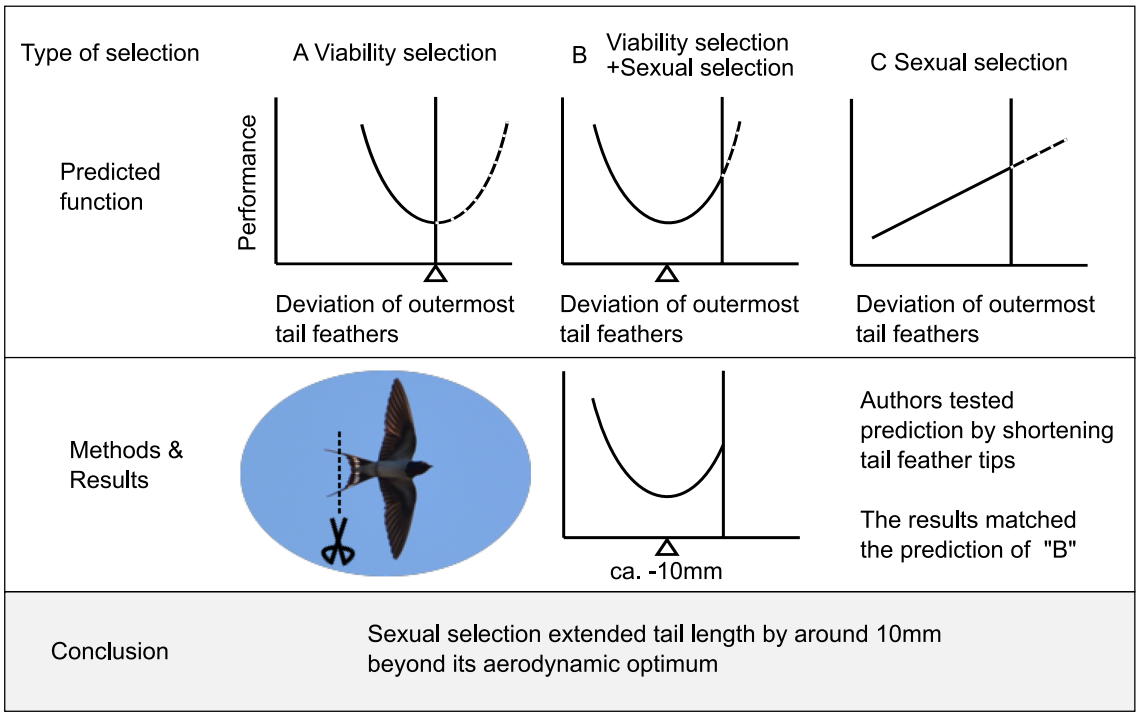

Fig. 1 Details of manipulation experiment of Evans and colleagues (see Evans 1998; Buchanan & Evans 2000; Rowe *et al.* 2001 for original figures; also see Evans & Thomas 1997; Thomas & Rowe 1997 for similar predictions). The vertical line in each plot indicates current ornament expression, and the triangle indicates ornament expression providing peak performance (note that lower values indicate higher performance here). Although they originally called deviation of outermost tail feathers (or possibly, narrowed part of outermost tail feather length) as a "streamer," I avoided this wording, because it implies some kinds of aerodynamic function of the ornaments, and because the formal definition of the streamer is unclear (and not to confound size and shape: Matyjasiak *et al.* 2009). Likewise, I used viability selection rather than natural selection to be precise.

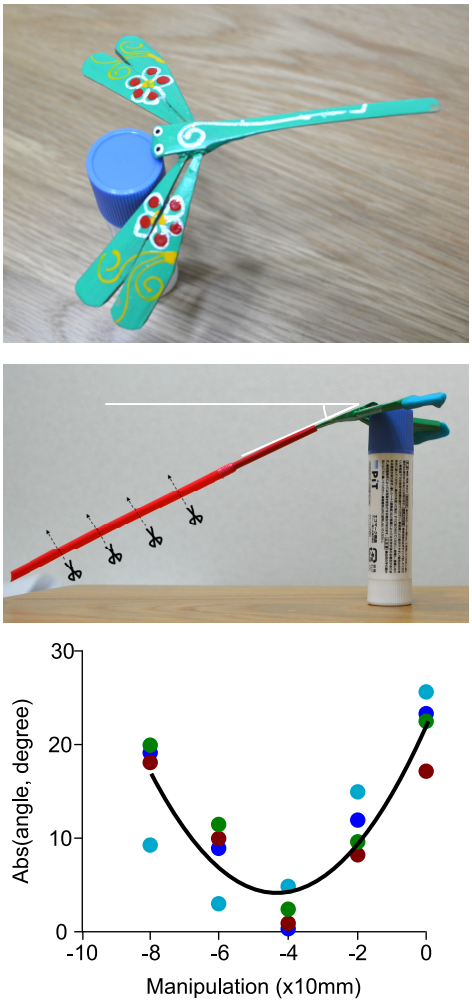

Fig. 2 Chuonchuon (upper panel), manipulated chuonchuon with elongated tails and extended wings (middle panel), and results of chuonchuon experiment (lower panel). A simple quadratic regression line is denoted (see Table 1 for a formal analysis). Individual identity was denoted by different coloration. Mean ± SE values of stability, measured by absolute angle deviated from horizontal plane, in ancestral state shown in upper panel was 4.87 ± 1.78 (range: 1.38–8.87). Note that tail elongation without extended wings made models unbalanced in the range of the current study (e.g., when elongated tails = 30 mm, which corresponds to the manipulation = −80 mm, mean stability ± SE = 36.60 ± 2.30, range = 32.69–42.93)