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

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

Masaru HASEGAWA[1]

[1] *Department of Environmental Science, Ishikawa Prefectural University, Nonoichi, Ishikawa 921-8836, Japan*

Number of table 1

Number of figures 2

Number of supplementary material 2

Author for corresponding

Dr Masaru Hasegawa

E-mail: perorobomusadiobe@gmail.com

Tel: (+81)- 46-858-1562

Acknowledgments

I thank Dr. Emi Arai, Dr. Shumpei Kitamura and his lab members at Ishikawa Prefectural University for their kindest advices and supports. I also thank Prof. Michael D. Jennions, reviewers, and English-proofing company (Enago) for their helpful comments. MH was supported by the KAKENHI grant of the Japan Society for the Promotion of Science (JSPS, 19K06850).

Data Availability Statement

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

Compliance with ethical standards

Conflict if interests The author declares no conflict of interest.

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

Author Contribution

I performed data analysis and wrote the manuscript alone.

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

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 (and thus many ornithological books follow their conclusions; e.g., Fjeldsa et al. 2020). 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

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

144 Here, using a simple "toy" model, I examined whether the U-shaped
145 cost function (see Fig. 1) could be produced when the ornament has evolved
146 purely through sexual selection for exaggerated ornamentation with the
147 coevolution of compensatory traits. Although I verbally explained potential
148 confounding effects of compensatory traits above, our simple model
149 experiment would directly demonstrate how compensatory traits affects the
150 performance of (virtual) animals with ornamentation. For this purpose, I used
151 "chuonchuon" (Fig. 2 upper panel), a traditional balancing toy in Vietnam, as
152 a model system. Chuonchuon is a suitable model, because its balance is
153 determined by the whole phenotype, as in the locomotor performance of
154 animals (e.g., see Husak & Swallow 2011). Different from purely verbal
155 models, simulations, or mathematical models, this kind of simple, physical

toy model would be intuitive (and thus suitable) for empirical researchers of animal performance to understand the importance of compensatory traits. Clearly, this toy model 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. Rather than testing the performance of models with arbitrary values of ornamental and compensatory traits, I first determined an evolutionary stable form of chuonchuon based on game theory 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

183 chuonchuon in the population can "reproduce." Then, the ancestral form can
184 survive anytime, but the tail-elongated form cannot survive when elongated
185 tails make them unbalanced (I used a cut-off point as 30° deviation from the
186 horizontal plane, here). Tail elongation made models unbalanced in the range
187 of the current study (i.e., maximum length to −80 mm shortened tails; see Fig.
188 1) and thus they cannot survive without compensatory traits, i.e., extended
189 wings. Even when it survived, the ancestral form cannot have descendants
190 when any derived forms with elongated tails (i.e., those with longer tails than
191 ancestral form) exist. Because my interest here is not in the actual
192 evolutionary trajectory but the cost function of the derived form, I obtained
193 the evolutionary stable form by comparing the "fitness" of each form. For
194 simplicity, I assumed continuous variation in tail length but assumed two
195 discrete states of the extended wings (i.e., with and without extended wings).
196 In this case, the evolutionary stable form is a chuonchuon with maximum
197 elongated tails with extended wings. This is because chuonchuon with
198 maximum elongated tails and extended wings can survive (i.e., balanced) and
199 thus reproduce under any circumstances (i.e., they have the longest tails
200 compared to all other forms). I did not subdivide compensatory traits (e.g.,
201 small/medium/large), because the purpose of the current study is not to
202 quantify the exact peak performance or identify the best size of compensatory
203 traits but to examine the effect of compensatory traits.
204
205 **Measuring performance**
206 As in manipulation experiments in the barn swallow (Buchanan & Evans
207 2000; Rowe *et al.* 2001), I shortened the extended tails of chuonchuon models
208 (20 mm/40 mm/60 mm/80 mm, here) and took two pictures each time. From
209 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 from the chuonchuon experiment 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 (see Fig. S1 for the corrected prediction).

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). When compensatory traits co-evolved with the sexually selected tail length to minimize the aerodynamic cost of tail length (Møller 1996), an experimental reduction in tail length alone cannot clarify

264 the aerodynamic cost of tail length, because the manipulation did not follow
265 the actual evolutionary pathway (see Fig. 3 for a schematic illustration; also
266 see Fig. S2 for an alternative scenario in which long tails have some
267 aerodynamic function). Also, all macroevolutionary studies of these aerial
268 insectivores so far have supported sexual (rather than viability) selection
269 explanation (e.g., Hasegawa *et al.* 2016; Hasegawa & Arai 2017, 2018,
270 2020a,b, 2021, 2022), demanding further experimental studies, possibly using
271 a smaller amount of manipulation (so that overcompensation can be avoided)
272 in many species with various ornamentation (i.e., phylogenetic comparative
273 "experiment"). An alternative approach, the manipulation of compensatory
274 traits (sensu Møller 1996; see also Fig. 3) would in theory be valuable to show
275 the effect of overcompensation, but is impractical due to the multi-
276 dimensionality of compensatory traits (e.g., manipulations of wing size and
277 shape are often difficult to conduct).

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

290 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. Given that compensatory traits coevolved with sexual traits (Møller 1996), the manipulation of sexual traits alone would not clarify the evolutionary force on sexual traits (see Figs. 3 & S2). 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.

Acknowledgment See Title page.

Author Contribution See Title page.

Conflict statement See Title page.

Permits See Title page

Data availability See Title page

REFERENCES

Andersson, M. 1994. *Sexual selection*. Princeton: Princeton Univ. Press.

Barbosa, A. & Møller, A.P. 1999. Aerodynamic costs of long tails in male barn swallows *Hirundo rustica* and the evolution of sexual size dimorphism. *Behav. Ecol.* **10**: 128–135. https://doi.org/10.1093/beheco/10.2.128

Balmford, A., Jones, I.L. & Thomas, A.L.R. 1994. How to compensate for costly sexually selected tails: the origin of sexually dimorphic wings in long-tailed birds. *Evolution* **48**: 1062–1070. https://doi.org/10.2307/2410366

Baumgartner, A., Coleman, S. & Swanson, B. 2011. The Cost of the Sword: Escape Performance in Male Swordtails. *PLoS ONE* **6**: e15837. https://doi.org/10.1371/journal.pone.0015837

Bergstrom, C.T. & Dugatkin, L.A. 2016. *Evolution*. New York: WW Norton & Co. Inc.

Bro-Jørgensen, J., Johnstone, R.A. & Evans, M.R. 2007. Uninformative exaggeration of male sexual ornaments in barn swallows. *Curr. Biol.* **17**: 850–855. https://doi.org/10.1016/j.cub.2007.03.042

Buchanan, K.L. & Evans, M.R. 2000. The effect of tail streamer length on aerodynamic performance in the barn swallow. *Behav. Ecol.* **11**: 228–238. https://doi.org/10.1093/beheco/11.2.228

Evans, M.R. 1998. Selection on swallow tail streamers. *Nature* **394**: 233–234. https://doi.org/10.1038/28297

Evans, M.R. & Thomas, A.L.R. 1997. Testing the functional significance of tail streamers. *Proc. R. Soc. Lond. B* **264**: 211–217. https://doi.org/10.1098/rspb.1997.0030

Fjeldsa, J., Christidis, L., Ericson, P.G.P. 2022. *The largest avian radiation: the evolution of perching birds, or the order Passeriformes*. Lynx edicions, Barcelona.

Hadfield, J.D. 2010. MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *J. Stat. Soft.* **33**: 1–22. https://doi.org/10.18637/ jss.v033.i02

Hasegawa, M., Arai, E. & Kutsukake, N. 2016. Evolution of tail fork depth in genus *Hirundo*. *Ecol. Evol.* **6**: 851–858. https://doi.org/10.1002/ece3.1949

Hasegawa, M. & Arai, E. 2017. Egg size decreases with increasing female tail fork depth in family Hirundinidae. *Evol. Ecol.* **31**: 559–569.

https://doi.org/10.1007/s1068 2-017-9895-2

Hasegawa, M. & Arai, E. 2018. Convergent evolution of the tradeoff between egg size and tail fork depth in swallows and swifts. *J. Avian Biol.* **49**: e01684. https://doi.org/10.1111/jav.01684

Hasegawa, M. & Arai, E. 2020a. Fork tails evolved differently in swallows and swifts. *J. Evol. Biol.* **33**: 911–919. https://doi.org/10.1111/jeb.13622

Hasegawa, M. & Arai, E. 2020b. Correlated evolution of biparental incubation and sexual tail monomorphism in swallows and martins (Aves: Hirundinidae). *Evol. Ecol.* **34**: 777–788. https://doi.org/10.1007/s10682-020-10066-w

Hasegawa, M. & Arai, E. 2021. Opposing population trends of fork-tailed swallows and reddish-coloured swallows in our changing world. *J. Evol. Biol.* **34**: 331–338. https://doi.org/10.1111/jeb.13736

Hasegawa, M. & Arai, E. 2022. Extrapair mating opportunity explains the evolutionary transition between the presence and absence of tail ornamentation in swallows. *Evol. Ecol.* 36: 899–913. doi: 10.1007/210682-022-10196-3

Hill, G.E. & McGraw, K.J. 2006. *Bird coloration II: function and evolution.* Cambridge: Harvard Univ. Press.

Husak, J.F. & Swallow, J.G. 2011. Compensatory traits and the evolution of male ornaments. *Behaviour* **148**: 1–29. https://doi.org/10.1163/000579510X541265

Husak, J.F., Henningsen, J.P., Vanhooydonck, B. & Irschick, D.J. 2015. A performance-based approach to studying costs of reliable signals. In: Irschick, D.J. Briffa, M. & Podos, J. (eds) *Animal signaling and function: an integrative approach.* Hoboken: Wiley Blackwell, pp. 47–74.

Kass, R.E., Carlin, B.P., Gelman, A. & Neal, R. 1998. Markov chain Monte

Carlo in practice: A round table discussion. *Amer. Stat.* **52**: 93–100. https://doi.org/10.2307/2685466

Kojima, W. & Lin, C.P. 2019. Sprint speed is not reduced by exaggerated male weapons in a flower beetle *Dicronocephalus wallichii*. *Ethology* **125**: 47–56. https://doi.org/10.1111/eth.12824

Lessells, C.M. & Boag, P.T. 1987. Unrepeatable repeatabilities: A common mistake. *Auk* **104**: 116–121. https://doi.org/10.2307/4087240

Matyjasiak, P., Marzal, A., Navarro, C., de Lope, F. & Møller, A.P. 2009. Fine morphology of experimental tail streamers and flight manoeuvrability in the house martin *Delichon urbica*. *Funct. Ecol.* **23**: 389–396. https://doi.org/10.1111/j.1365-2435.2008.01490.x

Moreno, E. & Møller, A.P. 1996. Morphological aspects of avian tail movements: a functional approach in hirundines. *Auk* **113**: 647–654. https://doi.org/10.2307/4088985

Møller, A.P. 1988. Female choice selects for male sexual tail ornaments in the monogamous swallow. *Nature* **332**: 640–642. https://doi.org/10.1038/332640a0

Møller, A.P. 1994. *Sexual selection and the barn swallow*. Oxford: Oxford Univ. Press.

Møller, A.P. 1996. The cost of secondary sexual characters and the evolution of cost-reducing traits. *Ibis* **138**: 112–119. https://doi.org/10.1111/j.1474-919X.1996.tb04317.x

Møller, A.P., de Lope, F. & Saino, N. 1995. Sexual selection in the barn swallow *Hirundo rustica*. VI. Aerodynamic adaptations. *J. Evol. Biol.* **8**: 671–687. https://doi.org/10.1046/j.1420-9101.1995.8060671.x

Norberg, R. 1994. Swallow tail streamer is a mechanical device for selfdeflection of tail leading edge enhancing aerodynamic efficiency and

flight manoeuvrability. *Proc. R. Soc. Lond. B* **257**: 227–233. https://doi.org/10.1098/rspb.1994.0119

Oufiero, C.E. & Garland, Jr T. 2007. Evaluating performance costs of sexually selected traits. *Funct. Ecol.* **21**: 676–689. https://doi.org/10.1111/j.1365-2435.2007.01259.x

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at http://www.R-project.org/ (accessed 11 September 2021)

Romano, A., Constanzo, A., Rubolini, D., Saino, N. & Møller, A.P. 2017. Geographical and seasonal variation in the intensity of sexual selection in the barn swallow *Hirundo rustica*: A metaanalysis. *Biol. Rev.* **92**: 1582–1600. https://doi.org/10.1111/brv.12297

Rowe, L.V., Evans, M.R. & Buchanan, K.L. 2001. The function and evolution of the tail streamer in hirundines. *Behav. Ecol.* **12**: 157–163. https://doi.org/10.1093/beheco/12.2.157

Saino, N., Cuervo, J.J., Ninni, P., de Lope, F. & Møller, A.P. 1997. Haematocrit correlates with tail ornament size in three populations of barn swallow (*Hirundo rustica*). *Funct. Ecol.* **11**: 604–610. https://doi.org/10.1046/j.1365-2435.1997.00131.x

Thavarajah, N.K., Tickle, P.G., Nudds, R.L. & Codd, J.R. 2016. The peacock train does not handicap cursorial locomotor performance. *Sci. Rep.* **6**: 36512. https://doi.org/10.1038/srep36512

Thomas, A.L.R. & Rowe, L.V. 1997. Experimental tests on tail elongation and sexual selection in swallows (*Hirundo rustica*) do not affect the tail streamer and cannot test its function. *Behav. Ecol.* **8**: 580–581. https://doi.org/10.1093/beheco/8.5.580

Trappett, A., Condon, C.H., White, C., Matthew, P. & Wilson, R.S. 2013.

Extravagant ornaments of male threadfin rainbowfish (*Iriatherina werneri*) are not costly for swimming. *Funct. Ecol.* **27**: 1034–1041. https://doi.org/10.1111/1365-2435.12097

Tubaro, P.L. 2003. A comparative study of aerodynamic function and flexural stiffness of outer tail feathers in birds. *J. Avian Biol.* **34**: 243–250. https://doi.org/10.1034/j.1600-048X.2003.03084.x

Turner, A.K. 2006. *The barn swallow.* London: T & AD Poyser.

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

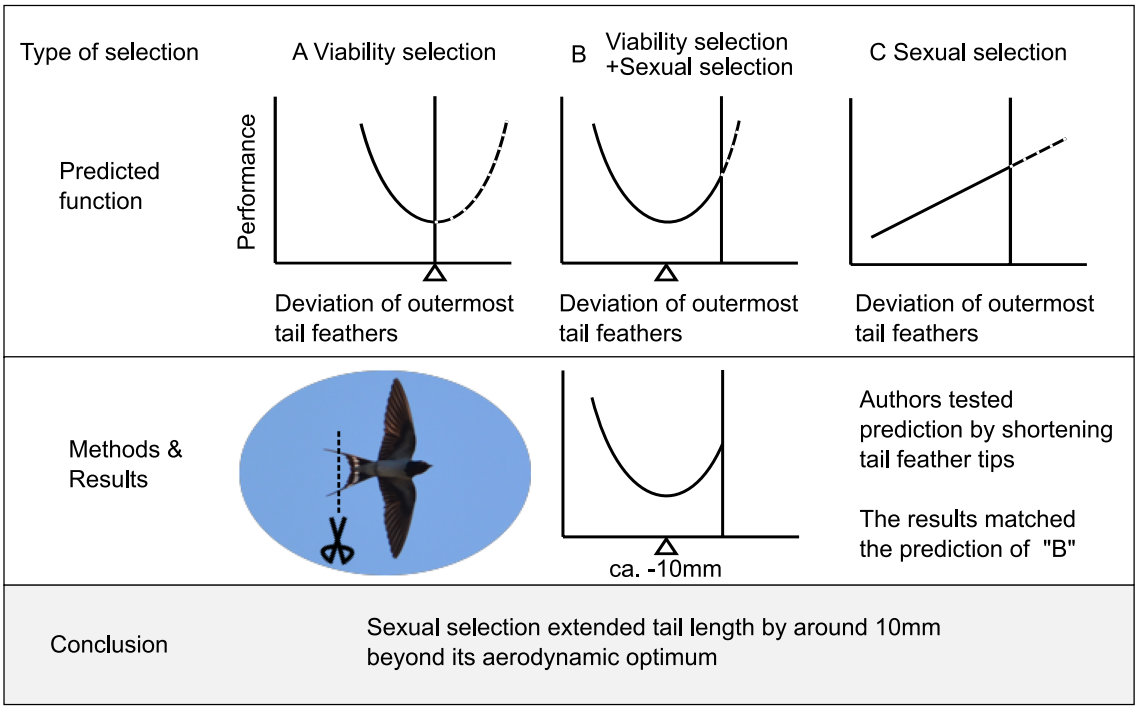


Figure 1. Details of manipulation experiment of Evans and colleagues (see Evans 1998; Buchanan & Evans 2000; Rowe *et al.* 2001 for original figures; also see Evans & Thomas 1997; Thomas & Rowe 1997 for similar predictions). The vertical line in each plot indicates current ornament expression, and the 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.

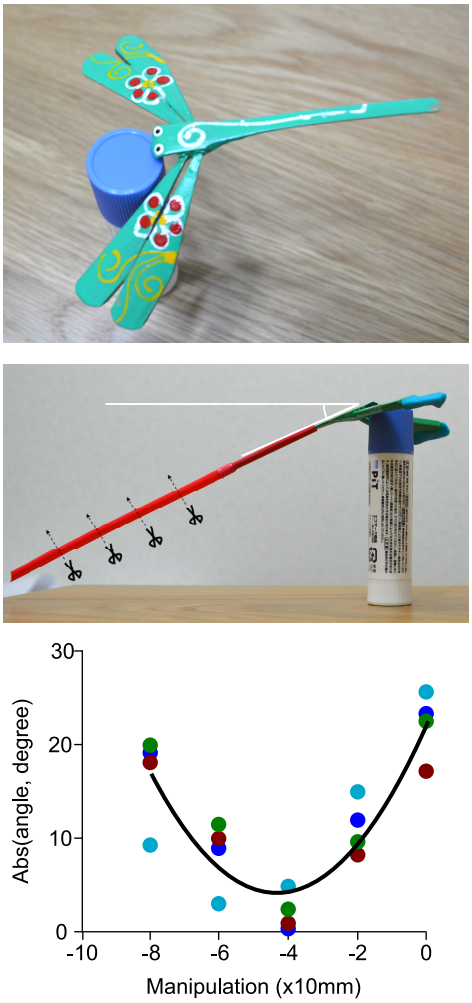


Figure 2. Chuonchuon (upper panel), manipulated chuonchuon with elongated tails and extended wings (middle panel), and results of chuonchuon experiment (lower panel). A simple quadratic regression line is denoted (see Table 1 for a formal analysis). Individual identity was denoted by different coloration. 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), and, not surprisingly, 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).

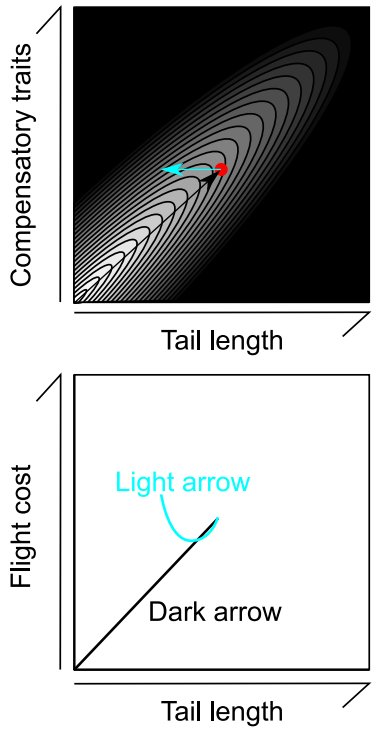
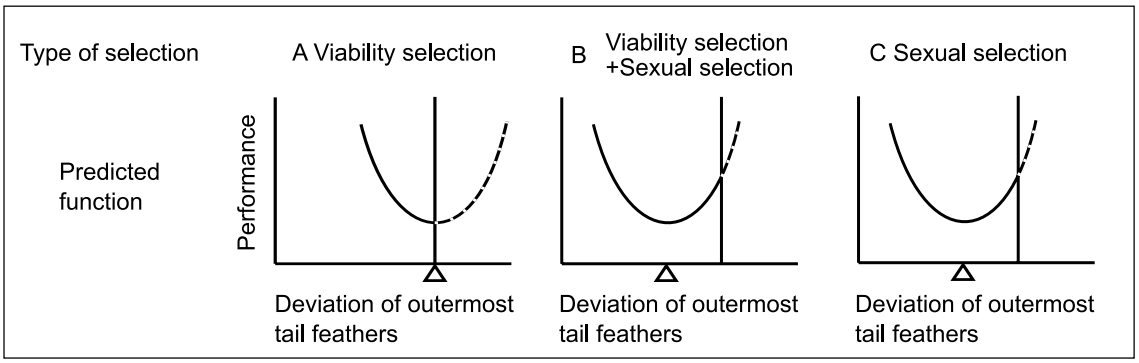
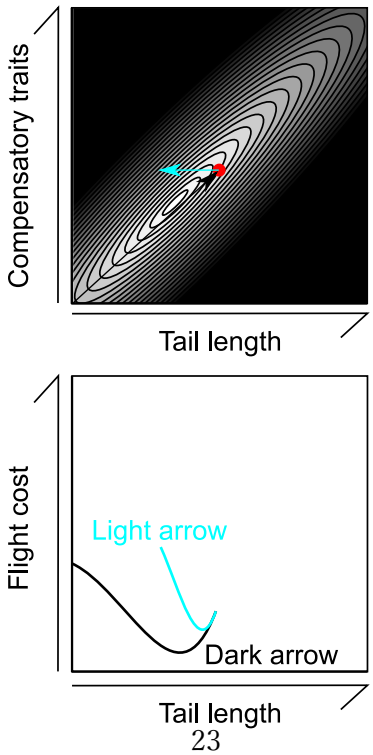


Figure 3. Schematic illustration of conceptual fitness landscape measured as flight performance in relation to tail length and phenotypic expression of compensatory traits (upper panel). Darker background coloration indicates lower flight performance (note that the best flight performance is attained in the lower left corner). Dark arrow indicates hypothetical evolutionary pathway to the current state (filled circle). Light arrow indicates phenotypic change when researchers experimentally reduced tail length (in which compensatory traits remain unchanged). Lower panel shows flight cost measurement in relation to tail length along with dark or light arrows. The evolutionary pathway on this fitness landscape is biased toward right side because of intense sexual selection favoring long tails (i.e., actual evolutionary pathway depends on sexual selection in addition to viability selection due to flight cost and other costs, such as production costs of tail length and compensatory traits; see text). Narrow contour width indicates that small deviation from integrated, co-opted trait sets had a strong negative effect on flight performance, as predicted by Norberg (1994).

Figure S1. The "corrected" predictions for manipulation experiment of Evans and colleagues under the presence of compensatory traits. Note that two type of scenarios (B and C) cannot be distinguished. See text and Fig. 1 for detailed explanations (also see Figs. 3 & S2).



537 **Figure S2.** Schematic illustration of conceptual fitness landscape
538 measured as flight performance in relation to tail length and phenotypic
539 expression of compensatory traits (upper panel). Darker background
540 coloration indicates lower flight performance (note that the lightest
541 background located near the current state, shown as a filled circle, in this
542 example). Dark arrow indicates hypothetical evolutionary pathway to the
543 current state. Light arrow indicates phenotypic change when researchers
544 experimentally reduced tail length (in which compensatory traits remain
545 unchanged). Lower panel shows flight cost measurement in relation to tail
546 length along with dark or light arrows. The evolutionary pathway on this
547 fitness landscape is biased toward right side because of intense sexual
548 selection favoring long tails (i.e., actual evolutionary pathway depends on
549 sexual selection in addition to viability selection due to flight cost and other
550 costs, such as production costs of tail length and compensatory traits; see text).
551 Narrow contour width indicates that small deviation from integrated, co-
552 opted character sets had a strong negative effect on flight performance, as
553 predicted by Norberg (1994).