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Subject: Response to PeerJ Submission #2013:08:741:1:0:REVIEW “Evolution of male life histories and age-dependent sexual signals under female choice”

Dear Editor,

I have made the requested (hopefully) final edits to my manuscript. I want to sincerely thank the reviewers and editors again for improving the manuscript and getting it closer to publication. I have worked for a long time on this manuscript and I find it refreshing to get helpful comments from journal reviewers. I hope that my edits meet the satisfaction of the reviewers and editors.

My responses are *emphasized* below the corresponding comment, with quotations of the revised text accompanying my responses.

Sincerely,

Joel J. Adamson

Cite Rands et al. Chief among these suggestions is that I would like to see acknowledgement of the paper “The Dynamics of Honesty: Modelling the Growth of Costly, Sexually-Selected Ornaments” by Rands et al. from PLoS One in 2011, as well as discussion of how your findings differ from theirs. They also seem to find (in line with the Kokko, and Proulx et al. papers you cite) that at younger ages, high-quality males are likely to have smaller orna-

ments, while at older ages the reverse is true. They use a stochastic dynamic programming approach rather than your major gene model, so it would be interesting if you would compare the results and approaches, either in the Introduction or the Discussion (or both, as you currently do with the other papers mentioned).

I thank the reviewer for mentioning this paper. I have inserted references into the second paragraph of the Introduction

Life-history theory suggests that sexual selection theory could benefit from modeling more complex life-histories. Low adult mortality leads to a stable strategy of age-dependent male reproductive effort. Kokko (1997) found evolutionarily stable strategies for age-dependent strategies under fairly broad conditions. Proulx et al. (2002) found that males benefit from increasing mating effort as they age and reproductive opportunities decline. They predicted that condition should be positively correlated with delays in investment. High condition males signal more at older ages. A third, more recent study employing similar techniques found that optimal higher-quality males will postpone trait growth until the onset of breeding (Rands et al., 2011).

and the fifth paragraph of the Discussion. See below for further changes to this paragraph.

Abstract: “Evolution of age-independent traits depends on trait size, whereas evolution of age-dependent traits depends on strength of selection and growth rate (i.e. size)” This reads like you’re saying “Evolution of age-independent traits depends on size, whereas evolution of age-independent traits depends on size”. Seems a bit strange. So maybe stress that the former depends ONLY on trait size, while the latter depends on two parameters.

I have amended this sentence to something clearer: “Evolution of age-independent traits depends only on trait size, whereas evolution of age-dependent traits depends on both strength of selection and growth rate.”

p6, line 110: “mean males of a particular genotype” Consider amending this to “mean that males...” since the juxtaposition of “mean” and “males” after the parentheses might make the insufficiently careful reader think you are referring to a specific kind of average male, rather than what larger values of b mean.

I thank the reviewer for pointing out this confusion. You’ll now find that the word “mean” has only one meaning within the manuscript. The sentence in question now reads: “A larger value of b in a particular population (i.e. simulation) signifies that males of a particular genotype attain larger trait values than they would in populations with smaller b -values.”

p7, Equation (2): I’m afraid I still don’t follow your logic for t_{bar} . Firstly I don’t understand the sentence “I calculated \bar{t} at each iteration such that males carrying F_2 contributed to the population mean as if their traits were age-dependent”. I apologise if I have confused matters further with my comments last time around. I thought that F_2 males (in this instance) are simply defined regardless of their age as having an ornament size equal to the mean ornament size for age-dependent males of their condition? But you now seem to be saying that F_2 males

all have ornament size equal to the mean ornament size of F₂ males, regardless of condition. Or maybe not?

The reviewer saw correctly that I was not clear about condition-dependence in the case of F₂. I have reorganized these paragraphs to better relate the whole story of how this procedure worked. Please see below for the full revised passage.

Denominator of Equation (2) Further, I still don't see why there is the denominator of $y_{max} + 1$. If $f(t)$ is the frequency of males with trait size t , and the sum in the numerator is over all possible discrete trait sizes t , then isn't \bar{t} the numerator already the mean trait size in the population?

I now see where the confusion arose. I am glad the reviewer pointed this out before the paper went to publication. Many of the equations in the paper were imitations of procedures found in the computer algorithm, written in C, where the data was stored in arrays for each age class. The frequency referred to is actually the frequency of a particular size in a particular age class, and not the frequency in the general population, as hitherto written in the manuscript. If I had deleted the denominator, I would have an equivalent expression for the values used in the simulation, but for the sake of "algorithmic transparency," I will spell out the equation as the C algorithm performed it. I have adjusted the equation so that the actual quantity used reflects this:

For the third set of simulations, where F₂ males carried $t = \bar{t}$, I updated \bar{t} in every iteration. My goal was ensuring that a class of males of intermediate attractiveness persisted in the population. Therefore all males (regardless of condition) carrying F₂ received \bar{t} as their trait value for a particular episode of mating, then I updated their values in the next iteration, following changes in \bar{t} . Furthermore, the value of \bar{t} used in these simulations reflected the full range of variation in condition, despite the lack of condition-dependence for F₂ males. I therefore calculated the mean trait as

$$\bar{t} = \frac{\sum_{t=0}^{t_{max}} t f(t, y)}{y_{max} + 1}$$

where $f(t, y)$ describes the frequency of males with trait value t at age y over $y_{max} + 1$ age classes. The average is taken over all males, from unornamented males to the maximum trait size of $t_{max} = be^{\mathcal{C}y_{max}}$, where \mathcal{C} represents the largest possible number of condition alleles (i.e. number of condition loci). Males carrying F₂ contributed to the population mean as if their traits were age-dependent, i.e. contributing $t(C, y) = be^{\mathcal{C}y}$ to the calculation in Equation (2). If the trait allele (T₂) were to spread, then a contribution of \bar{t} by F₂ males would depress the trait value for F₂ males and produce a delay in following phenotypic changes. Although these procedures reduced biological realism from an individual perspective, they maintained the population genetic conditions relevant to the question at hand.

p8, line 158: "represents the traits size" typo, should be "trait size"? Unless you want to adopt "the trait's size" throughout, which I would personally advise against.

Simple typo, now fixed.

p11, line 206: maybe add “initial” before the word “size” in your parenthetical explanation of parameter b ?

I hesitate to use “initial size” since this paragraph discusses both age-dependent and age-independent traits. The parameter b does not equal the initial size of traits in the age-independent males discussed in the paragraph. Instead I hope the reviewer will find a reference to Equation (1) satisfactory. This should at least point readers in the right direction, perhaps if they skipped reading the Model section. The sentence now reads: “The area of parameter space where the trait fixes depends on three parameters: α (strength of preference), b (“growth coefficient”; see Equation (1)) and v (strength of selection; Figure 4).”

p13, line 252: “The left-hand column of Figure 5” Right-hand, surely?

Yes, the reviewer is correct about this. This has been fixed.

p15, line 300: Maybe point the reader to Figure 1?

I have inserted a parenthetical reference to Figure 4, that contains the result referred to in the sentence.

p16, line 341-2: “avoid viability selection, by contrast, avoid selection...” Probably should remove the redundant repetition here.

The repetition is much clearer when taken out of context. I have revised the sentence as follows: “Age-dependent males that avoid viability selection, by contrast, do become more attractive.”

p17, lines 357-360: I’m afraid I still don’t quite get the comparison between Proulx et al and Kokko. Is the conclusion in both papers that poor condition young males should signal more than good condition young males?

Yes, the reviewer is correct that I intended a strict comparison of these two papers. I have updated the paragraph to make it more clear to readers that the conclusions of the two papers were very similar. The paragraph now reads:

The results here support the strategic modeling literature of age-dependent signals (Rands et al., 2011; Proulx et al., 2002; Kokko, 1997). Proulx et al. modeled the situation where male longevity and reproductive opportunities increase — e.g. under a low adult mortality environment — and found that high-condition males downplay their signaling relative to lower condition males, preserving resources for survival. Kokko came to the similar conclusion that young males of lower condition should signal more than their higher-condition cohorts, thus obscuring the observed relationship between genetic quality and trait value. Both studies find that (optimally) males of a given condition signal inversely proportional to number of remaining reproductive attempts (a predictor of condition in any age-class). Selection then favors females that prefer to mate with older males, since they are more likely to be of high condition. These studies model competing

strategies, whereas my study uses a condition-dependent and age-dependent trait function to model variation. When selection weakens enough, with a particular developmental trajectory, age-dependent signaling and female preferences evolve in a population genetic model. The evolutionary dynamics, in this case, do mirror the conclusions of the optimization models. These results suggest that with the needed life-history conditions and genetic variation we can expect selection on life-histories to produce age-dependent signaling.

p18, line 389: Put the Evans citation in parentheses?

Whoops! This was a minor error in a citation command that eluded all of the authors' 102 revisions.