CMSE 802 Final Project
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Link to GitHub Repository
https://github.com/Jonahbranding/cmse802_project/tree/main

Background and Motivation
The Handicap Principle (HP) in evolutionary biology claims that apparently maladaptive traits
("handicaps"), such as conspicuous coloration patterns or long tails, can evolve as a means of "honestly
signalling" mate quality (Zahavi 1975). If a male peacock has a long heavy tail, so the logic goes, then his
long tail signals to females that he is capable of surviving, even *with* such an obvious handicap. If females
have a preference for this handicap, then the trait can become fixed in a population, because handicapped
males will have increased fecundity. In this way, sexual selection can provide a path for harmful traits to
evolve, despite their increasing individual mortality.

However, HP suffers from a logical problem (identified by Penn & Számado [2021]): it appears to
artificially "separate out" the male's fitness *with* the handicap from his fitness *without* the handicap.
Fitness is a property of the whole organism, including the handicap. So, if a male is able to survive with a
long tail, but only because he's super strong, he is not necessarily any more fit than a less strong male,
who lacks the handicap. Since HP assumes handicaps are heritable, offspring of handicapped males will
therefore have no advantage over those of non-handicapped males. One way to solve this problem would
be to consider only sex-linked handicaps: those where a son will inherit the handicap, though his sisters
will not. In this case, handicaps could become widespread due to their benefits to *daughters*.

A model proposed by John Maynard-Smith (1976) showed that even in cases of sex-linkage, a
single-locus Mendelian allele for a handicap will go extinct within a few generations. One limitation of
Maynard-Smith's model, however, is that it only considers discrete handicaps (i.e. there's some allele, and
if you have the allele, you're handicapped, whereas if you don't, you are not). Most known handicaps are
not like this. Rather, they're quantitative traits: traits which can have higher or lower values (e.g. longer or
shorter horns, brighter or duller coloration), and are under the control of many different genetic loci. A
question I had was: would Maynard-Smith's model still give us grounds to reject HP, if we extend it to
consider *quantitative* traits?

Methodology
I began by implementing Maynard-Smith's original model in python. I confirmed his suggestion
(unsubstantiated with figures) that a Mendelian handicap will be driven to extinction in just a few
generations. Then, I considered how a quantitative handicap could evolve, under two different
circumstances: (1) when the handicap is sex-linked, and (2) when it's not. I measured "success" as
occurring when, after some number of simulations, the mean trait value is driven to its maximum possible
value, given a manually set constraint. I used unit testing to ensure that the model of primary interest (the
sex-linked, quantitative model) performed well in three different edge cases: (i) when the mutation rate is
zero, and the handicap is initially set to zero (expecting: the handicap will not evolve), (ii) when the
handicap is set to zero with a non-zero mutation rate (expecting: the handicap will pick up from zero and

go to its maximum value), and (iii) when the trait is set to its maximum value (expecting: the trait value will stay there). All unit tests were passed.

Results

I found that (1) John Maynard-Smith's claim that a Mendelian handicap would not evolve selected against was correct, but (2) in the case of a quantitative handicap evolving under constraint, sex-linkage can in fact make the difference for whether the mean trait value goes to its maximum, or remains around zero. This is illustrated by Fig's (1) and (2).
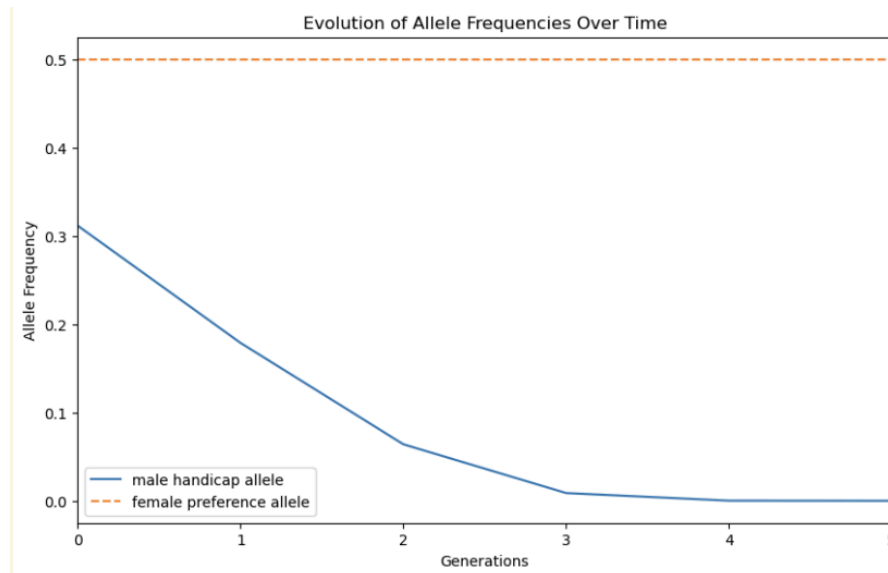

Fig. 1: If the handicap is Mendelian, it is rapidly selected against.
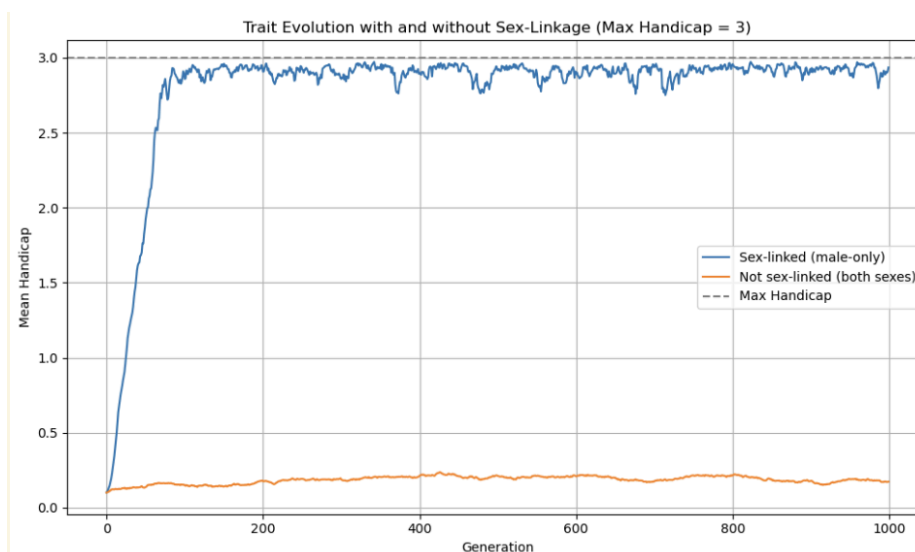

Fig. 2: However, if the trait is quantitative, it can evolve to its maximum mean trait value, so long as it's sex-linked.

Synthesis and Discussion

One obstacle I ran into occurred when I observed a handicapped trait exhibiting some strange oscillating behavior, instead of going to fixation at the maximum trait value (Fig. 3). The reason was that, in the case where a harmful trait can become exaggerated to extreme values, there was a mass die-off, and the population was saved by the handful of mutant males who had relatively small handicaps. I overcame this problem by adding in more biological realism: traits cannot become arbitrarily large, but instead are subject to developmental constraints (e.g. peacocks cannot evolve to have arbitrarily long tails, but instead must go to some maximum that can be physically supported by their development).
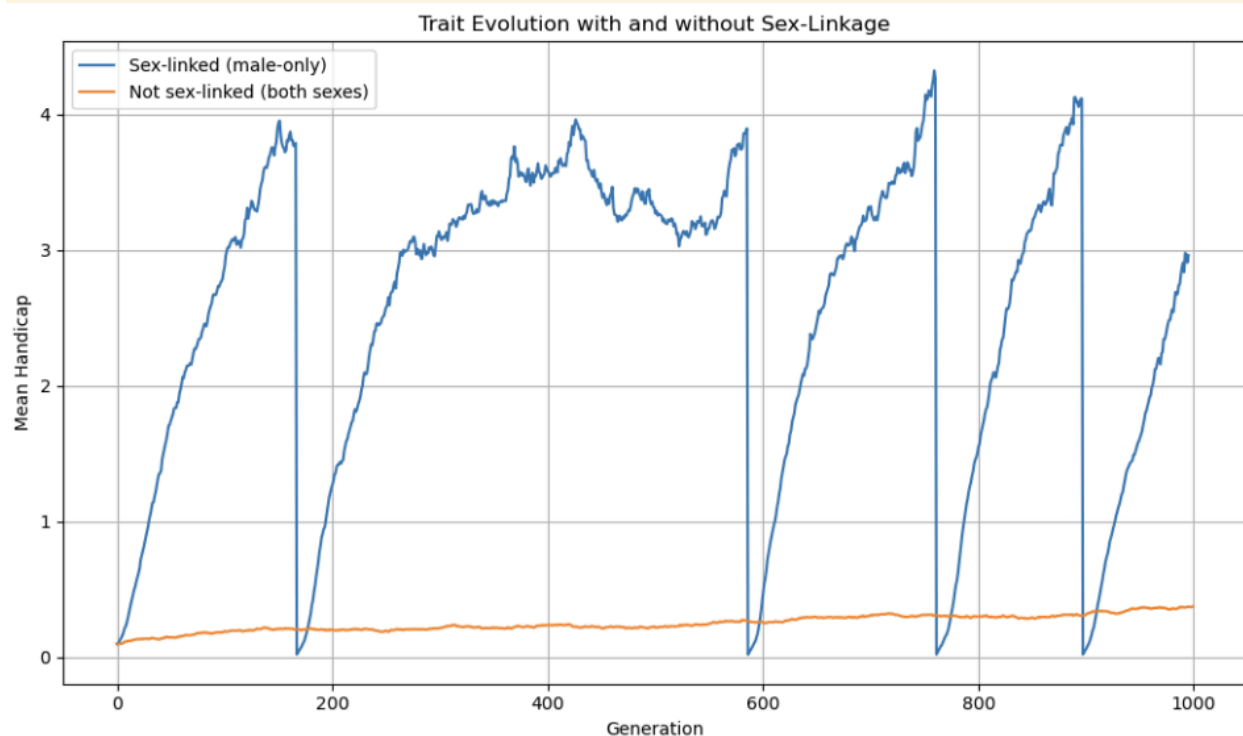

Fig. 3: Without developmental constraint, we see a strange oscillating pattern.

I found that so long as the maximum trait value was lower than the threshold point at which the mass-die offs become highly likely (which, in the model, is in turn a function of the parameter k, which gives the cost of the handicap at various trait values), the handicap would go to the maximum and remain there, instead of initiating this strange cyclical behavior.

One thing I learned from this model is, contrary to some recent suggestions in the literature, there may be more hope for HP as an explanation of maladaptive traits than we previously thought, due to their potential benefit to daughters. In other words, the answer to the question of "Can sex-linkage make a difference to whether a quantitative handicap can evolve to its maximum value?" is: "Yes, so long as there is a reasonably small developmental constraint on the trait value."

Next time, I would like to expand the model in a couple of ways. First, I would like to introduce random mortality, which would likely turn this oscillating behavior into a simple collapse: if the few

non-handicapped males happen to die at the point where the blue line dips, then the population would go to extinction. This is a classic case of an "evolutionary trap": a situation in which progressive, unsustainable evolution in one direction ultimately leads to a crash. Second, I would like to introduce female preference as a parameter that itself can vary; if one could show how strong daughters can drive an increase in both the mean trait value of the handicap, *and* the preference for the handicap, then this would go a substantial distance toward showing that HP is a plausible, and biologically realistic, principle.

Works Cited

Maynard-Smith, J. 1976. Sexual selection and the handicap principle. *Journal of Theoretical Biology*, 57: 239-242.

Penn, D. & Számadó, S. 2020. The handicap principle: How an erroneous hypothesis became a scientific principle. *Biological Reviews*, 95: 267-290.

Zahavi, A. 1975. Mate selection--A selection for handicap. *Journal of Theoretical Biology*, 53: 205.