Homework #3

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1. Introduction

Brief project overview/significance of the problem

One way of explaining apparently maladaptive traits--such as coloration patterns that are conspicuous to predators, or non-functional ornaments like long tails or horns--has been through Amotz Zahavi's "Handicap Principle" (HP). The principle holds that maladaptive traits serve as "handicaps" to display quality to potential mates. A cardinal who can survive predation, even standing out quite obviously against a white snowy background, so the reasoning goes, "honestly advertises" his fitness to potential mates, as he would require other beneficial adaptations (e.g. speed, intelligence) to evade predators, given such a great handicap. For females looking to maximize the fitness of their offspring, mating with such a male could provide obvious benefits. Thus, handicaps can become fixed in a population in spite of their costs to individual mortality.

A key problem with HP, however, is that handicapped males are *not* "fitter" than other potential males; fitness is a property of the whole organism, including the handicap. Mating with a handicapped male would mean not *only* passing on the positive traits that counterbalance the handicap (e.g. speed, intelligence) but also the handicap itself (e.g. conspicuous coloration). It is therefore not clear *why* a female would choose a handicapped over a non-handicapped mate. One way around this problem is to note that most handicaps are sex-linked; only sons, for example, inherit the bright red coloration of male cardinals. Meanwhile, the daughters will inherit the counterbalancing traits (speed, intelligence) *without* having to bear the handicap. So, perhaps handicaps could become fixed in a population, due to their benefits to *daughters*. Call this a "strong daughters" model.

This idea was considered, and rejected, in a 1976 paper by John Maynard-Smith, which is still cited as evidence that a strong daughters model cannot work. However, Manard-Smith's original paper had no accompanying figures, and only considered a highly unrealistic case, in which a discrete handicap is under the control of a single-locus Mendelian allele.

Problem statement and objectives

In light of these limitations, I decided to (1) implement Maynard-Smith's original model in Python, and (2) go on to consider whether a modified version, which looks at more biologically realistic *quantitative* traits, might be able to drive a handicap to fixation in a population, due to benefits to daughters.

Scope and limitations

One limitation of the model I developed is to consider no evolutionary change on female preferences; in a more realistic model, alleles for preferences would vary just as alleles underlying the preferred trait itself would vary. One can view the account provided here, then, as an explanation of how maladaptive traits can become fixed, *assuming* some preference already exists. The preference itself then requires some other, context-specific explanation (e.g. drift, sensory drive, etc.).

2. Project Implementation

Architecture and component overview

I implemented three related models: (1) Maynard-Smith's original discrete handicap model, (2) A model of quantitative handicaps *without* sex-linkage, and (3) a model of quantitative handicaps *with* sex linkage. The purpose of (1) was to reproduce results reported by Maynard-Smith in his original paper. The purpose of (2) and (3) was to see whether, in the cases of quantitative handicaps, sex linkage can "make a difference" to the evolution of a trait. Here is a brief list of the major components:

Original Handicap Model

- Mendelian genotype frequencies (e.g. AaB, AAB, ABc) determine traits.
- Viability selection (i.e. a method describing who survives to breeding age), which is deterministic, and based on the fitness of the genotypes per Maynard-Smith's original specification.
- Female choice, which is binary, and in which *C* females display a preference for males with *B* alleles.
- Update rule, which is given by the Hardy-Weinberg-based allele frequency updates, as is common practice in population-genetic models

Non-Sex-Linked Quantitative Trait Model

- Handicap is a trait with a continuous trait value, expressed in both males and females
- Uses softmax-based mating and exponential survival function (as is common in population-genetic models).

Sex-Linked Quantitative Trait Model

- Handicap is a trait with a continuous trait value, expressed only in males
- Survival
- Also uses softmax-based mating/survival

Implementation Status

Everything is now complete.

Key algorithms and methods used

I created a class with the following major components algorithms/methods:

a. A method to calculate survival probabilities
b. A method to calculate mating probabilities among survivors
c. A method to update the simulation over generations

Technical challenges and solutions

Upon implementing these models, I found a strange oscillating behavior--it seemed sex-linkage *cannot* drive a trait to fixation, because at high levels, there is an increased viability cost, and the population crashes. This, then, could be an example of what has elsewhere been called an "evolutionary trap." However, when I manually introduced a *constraint* (i.e. a stipulation that trait values cannot exceed some viable threshold), the oscillation went away, and the trait went to fixation.

Any changes from the original plan in HW2

The biggest change is the introduction of developmental constraints, to solve the problem above. Since all evolution does happen under constraints (e.g., as pigs can't evolve wings without major changes elsewhere in their anatomy), it is interesting that this increase in realism makes the model actually work.

3. Technical Optimization

Performance bottlenecks

- Bottlenecks don't really appear in the original model, but in my modification, they can occur if population size, or number of generations, are too high.

Optimization Techniques

- Vectorization with NumPy
- Increased memory efficiency, by tracking only mean trait values, instead of the full trait distribution

Quantitative Performance Improvements

Not necessary; the models as I ran them returned results in under 1 second.

Error Handling and Robustness Measures

In an edge case where survivors = 0, the simulation resets to zero trait values. Also, inputs such as mutation rate and maximum handicap are checked to be >= 0, and > 0, respectively.

4. Validation and Testing

Validation Methodology

I used Python's built-in unittest function to test model robustness over a few biologically realistic edge cases and boundary conditions (described below).

Test cases and coverage

I considered three test scenarios:

a. Initial traits at maximum
b. Initial trait at zero
c. Lethal handicap at all trait values

Quantitative validation results

All three of these tests were passed successfully: traits remained less than or equal to the maximum constraint, the mean trait value increased from zero, and when the trait value was lethal at all values, the population crashed.

Analysis of accuracy and reliability

I take these tests to demonstrate that the model is reliable under at least several major biologically realistic test conditions.

5. Results and Discussion

Key findings and outputs

Here I'll report several interesting visualizations.

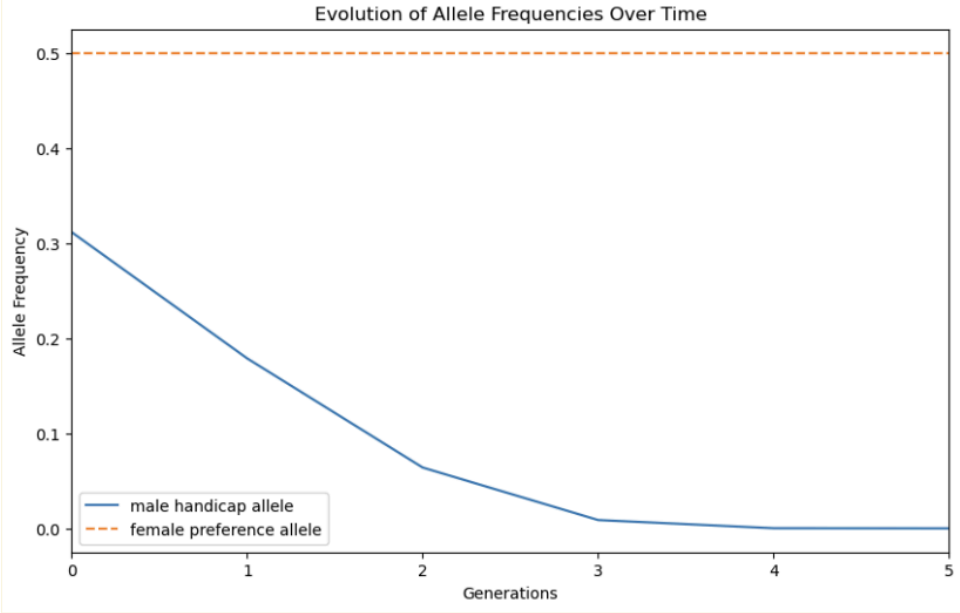

Fig. 1: Maynard-Smith's original model: As predicted, handicap goes extinct within five generations.

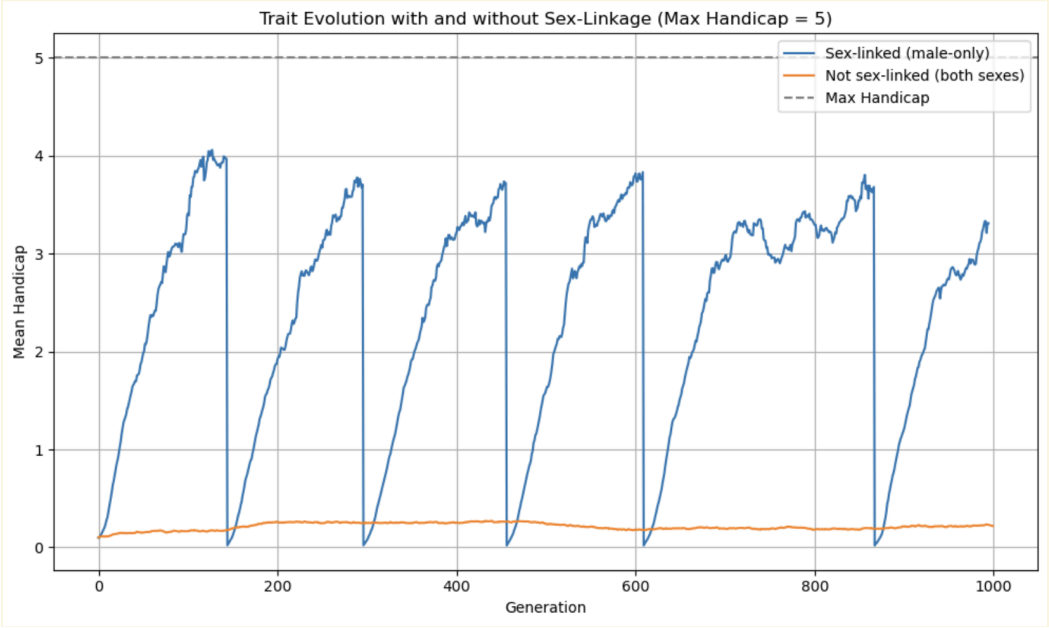

Fig. 2: Sex-linked handicap without viable developmental constraint - oscillating behavior observed.

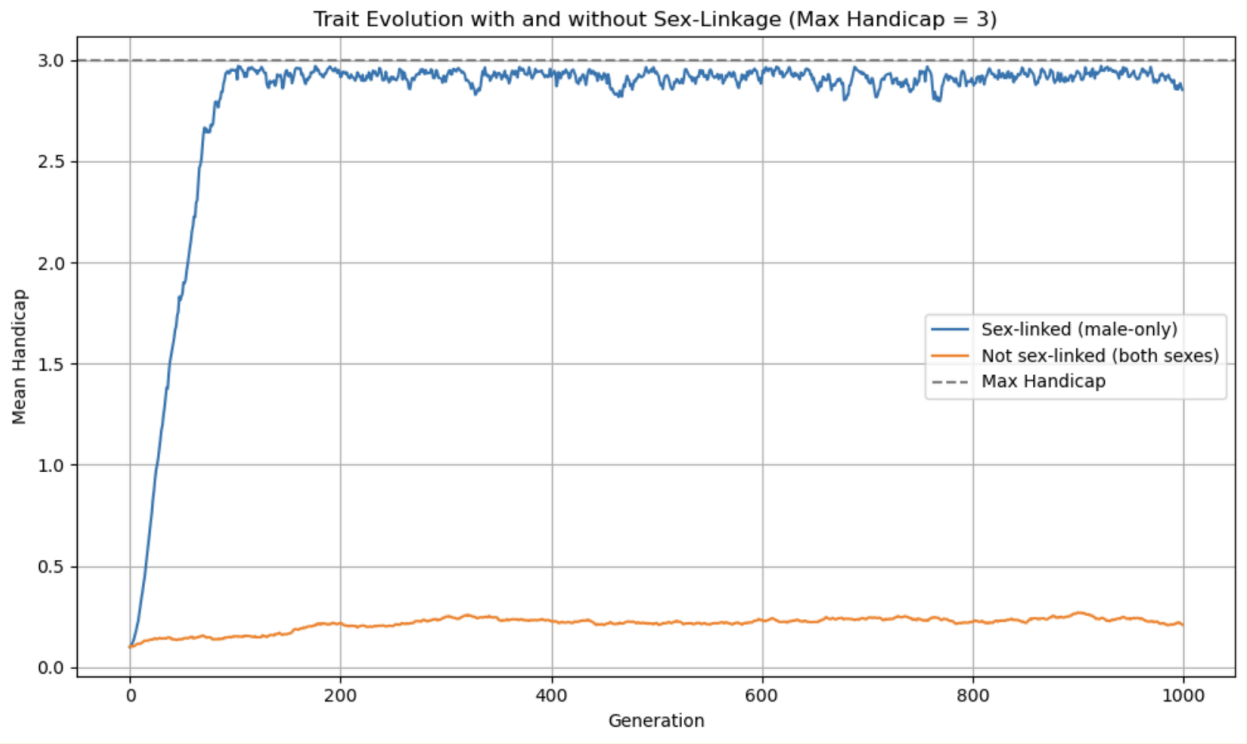

Fig. 3: Sex-linked handicap with viable developmental constraint - the handicap goes to the maximum value, and stays there indefinitely

Analysis of results

The model I ran suggested that, assuming a developmental constraint below a viable maximum trait value, and sex-linkage, a "strong daughters" model can, *contra* the expectations of much of the literature, drive a handicap to fixation.

Interpretation in context of project goals

I successfully implemented an old model from the 1970's, which is thought to show that a Strong Daughters model of HP cannot work. After validating the predictions of the original model, I went on to describe how a more realistic modification, which incorporates quantitative, instead of Mendelian, traits can make a Strong Daughters model work.

Limitations and future improvements

As stated above, this model must assume a background preference for the handicap trait. A future model could investigate how these preferences themselves can evolve, in cases where they're underlied by a heritable genetic architecture.

6. Conclusions

Summary of achievements

Here, I showed how incorporating additional biological realism into an old "Strong Daughters" model of HP can make the process work. In particular, it can respond to what has been identified as the principle problem of HP: how can without-handicap fitness be decoupled from with-handicap fitness, which appears to be the relevant measure of fitness? The answer: sex linkage, for quantitative traits, under developmental constraint.

Evaluation of approach

The virtues of this approach was both the reproduction of earlier results, and the interesting difference that was found when additional, more realistic, assumptions were incorporated.

Next steps for completion

No next steps required; the project is complete.

7. Works Cited

Maynard-Smith, J. 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.