Modeling the Evolution of North American Monarch Butterfly Forewing Area Since 1870

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Evolution (BIOL 461)

29 April 2022

ABSTRACT

Butterfly wings have always been fascinating to us, and one of the most well-known and loved species of butterfly is the monarch, known for its long-distance migration. Many studies have looked at how the wings of monarch butterflies have changed through time, and most find that there has been an increase in wing size of migratory butterflies throughout the period we have data for (since about 1870)2,3. This is thought to be the result of selection acting to increase wing size, which allows them to better be able to migrate2. For this project, a time series analysis was done, fitting data about the area of North American monarch butterfly wings to several common evolutionary models. The one that best fits the data is the stasis model, indicating that there is no net change in forewing area, and that instead there is an optimum value that the average forewing area tends to fluctuate around. Thus, selection may have driven the area to that optimum in the past, but for the last 150 years, there has been no real change in forewing area for North American monarch butterflies.

INTRODUCTION

Butterfly wing morphology has always been a popular topic, and while many studies have focused on the reasons behind the patterns and coloration of butterfly wings, an area of research now being examined is the shape and size of the wings. Measurements tend to focus on the forewings, and usually include aspect ratio and area. Aspect ratio is the length of the forewing divided by the width, and it is often used to give an idea of wing shape2. Area is simply the area of the forewing, and can be used as wing size, but some papers have used more complex methods to make a model that incorporates data such as the aspect ratio into the overall size 3. Having various shapes and sizes of wings can give butterflies advantages in certain habitats or flying conditions8. For example, wings that are larger and longer can help them to fly greater distances, and shorter, more rounded wings may give butterflies the ability to fly more nimbly2.

Monarch butterflies, *Danaus plexippus*, are famous for their migration that sometimes entails crossing the entirety of North America. The butterflies spend the winter in Mexico, and breed as they move north again, which can take multiple generations7. Not all monarchs migrate, however, and the migratory populations (most of the North American ones) tend to have larger wings than the ones that do not, although there is no difference in how elongated the wings are6. The larger wings are thought to be the product of selection for a trait allowing for better migration2, and over time, there has been an increase in both overall wing size (factoring in many measurements)3 and wing area2 since around 1870 for North American monarchs. Likewise, there has been a decrease in wing size for monarchs that no longer migrate, such as populations on islands3.

There have been many models created for characterizing patterns of evolution and using a time series analysis is a way to study how a trait has changed over time by comparing it to these models. One model is the generalized random walk model (GRW), which works for data that shows directional change over time, with the trait either showing a consistent increase or decrease4. On the other hand, a trait following unbiased random walk (URW) evolution could increase or decrease within each interval of time looked at, which results in increased variation over time. It has historically been used somewhat like a null hypothesis for directional change4. The stasis model shows that there has been no net change over time, and that there is some value for the trait that works best that the other values tend to stay close to, although they can vary slightly around it4. The Ornstein–Uhlenbeck model (OU) model tends to fit a trait that reaches an optimum value and then stays near it or data showing stabilizing selection, although recent adaptations of the model can also be used for directional selection1. These models can be compared by looking at a modified version the Akaike Information Criterion (AIC), called the AICc, which also includes the sample size in the calculations. It shows which model matches the data best through a series of calculations such as the log likelihood of each model, and also looks at how complicated the model is4. The Akaike weight is also used, and it shows how probable each model is when they are compared to one another. Typically, a relatively low AICc and high Akaike weight indicates a better fitting model4.

Based on the studies previously mentioned demonstrating an increase in wing size over time, my hypothesis is that in the last approximately 150 years North American monarch butterfly forewings have evolved to be larger in area through random walk evolution.

MATERIALS AND METHODS

The butterfly wing data used here came from a paper that used both butterflies caught in the wild for this study and previously caught museum specimens, allowing there to be data for around the last 150 years3. The wings were photographed or scanned with a scale bar and then a program called ImageJ v1.5110 was used to get measurements of forewing area, in square centimeters3. For the purposes of this paper, only the North American specimens were used, and any that were missing parts of the relevant data were excluded, leaving 2,327 data points spanning from 1870 to 2018. The left and right forewing area measurements were averaged together for each butterfly to give the average area of one forewing for each, which is what was used for this analysis. All data analysis was carried out using R version 4.1.39, and the dplyr package11 was used for sorting the data to get just the North American monarchs. The data was then fit to evolutionary models using the paleoTS package5, which was also used to plot the best-fitting model.

After storing the data as a paleoTS object that took the average of the samples for each year, with the variance of the data being represented by the total variance of the data set, the simpleFit function was used to fit the data to four different evolutionary models: GRW, URW, stasis, and OU. The compareModels function was then used to directly compare the four models. The stasis model had the lowest AICc and the highest Akaike weight, so it was then plotted to see how the data fit to a 95% confidence interval projected by that model. The number of butterflies collected each year was also plotted to reveal any bias introduced by having more specimens collected in some years.

RESULTS

Out of the four models tested, the best fit for North American monarch butterfly forewing area, based on the data used here, was the stasis model, which had an AICc of 170.5069 and an Akaike weight of 0.885 (Table 1). The only other model that had a Akaike weight not equal to 0 was OU (=0.115), which had a slightly higher AICc value of 174.5839 (Table 1).

Table 1: Results of the compareModels function for the data used here. The model that fits the North American monarch butterfly forewing area data best is the stasis model, with the lowest AICc and highest Akaike weight.



A plot was then made showing the data along with a 95% confidence interval based on the stasis model (Figure 1). Both the GRW and URW models had Akaike weights of 0, and their AICc’s were higher (199.4080 and 197.3534, respectively) (Table 1), meaning they were not as good of a fit for the data.

A picture containing chart

Description automatically generated

Figure 1: A plot of North American butterfly forewing area data fit to a 95% confidence interval for the stasis model of evolution.

Because of the nature of the data, with much of it being collected many years before this study was done, the number of butterflies collected each year was plotted (Figure 2). This shows that the largest numbers of specimens included here were caught between 1930-1990, with a few larger samples taken after 2000, but that before about 1950 and after 2000, for the most part, the numbers of butterflies caught was relatively comparable.

Chart, scatter chart

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Figure 2: The number of monarch butterfly specimens caught each year used in this study.

DISCUSSION

As previously described, the idea of the stasis model is that there is no net evolutionary change over time, and by seeing it graphed this way, it becomes clear that there was no real change in this data. Like the model would predict, there appears to be an optimum forewing area that the data fluctuates around periodically, but that it always seems to return to. This means that within this span of time, there has not been any real evolutionary change in forewing area for the North American population of monarch butterflies.

Using a time series analysis forces one to make choices about the way to handle the data, which was unevenly distributed throughout the time, with some years having many specimens, some few, and some none. The variance of the data therefore can be greatly different depending on the way it is calculated. Although it causes the data to lose some accuracy for individual years, the total variance was used here to even out the data slightly and allow for better comparisons of the models. Something else worth considering is that the data is not evenly split between males and females and can be very differently distributed between sexes each year. Because of the limited and very uneven data for each sex alone, males and females were combined for this analysis. Sex was found to be a major determining factor in the size of monarch wings2, and once again the total variance was used in order to help accommodate the variation that unevenness can cause. The data was about half male and half female when looked at as a whole, so using the total variance thus gave us a more generalized view of this subpopulation. However, doing this made it harder to see the true variance each year, which could have deviated from the total variance year-by-year and if used for the modeling may have given different results.

The model seems to fit the data best during the period of time from around 1930 to 1980, and a plot of the number of specimens collected each year shows that during much of that time period, some of the largest numbers of specimens were caught, giving a more accurate depiction of the trend in forewing area for those years. The other years could vary in the number of specimens used, and thus sampling error made worse by smaller samples could have caused those years to be less reflective of the true forewing area and possibly led to some of the deviance from the model. There is also a chance of geographic bias based on the historical specimens likely being caught locally to the museum they are housed in or being focused in certain areas depending on where they went to collect specimens, but it is unlikely since there appears to be a good distribution of museum locations.

This finding of evolutionary stasis differs from that of the other papers written using this data and is different from what was hypothesized to be happening. Both of the other papers cited an increase in the size of North American monarch butterfly wings2,3. Looking at how they analyzed their data can reveal the reasons why the results differ. One of them was simply testing to see if the year a butterfly was caught was correlated with the size of the wings, and thus if the year could be used to explain some of the variation in wing area2. The other used a time series analysis for a different measurement of size, one that incorporated many other factors3. Both of these papers, however, by doing this, made assumptions about the evolutionary processes at work, and one even mentions that selection could be causing the wings of the migrating butterflies to be larger2. This project was meant to determine what type of, if any, evolution was actually happening during this relatively short period of time, although it should be remembered that this does not imply anything about the forces, such as selection, working here. It can only be inferred from these results that there appears to be an optimum forewing area for these butterflies, and that over time, although it has sometimes fluctuated greatly, that optimum has remained the same, at least for this span of time. Along those lines, this was a relatively short period of time, and one could argue that selection may have acted to get the butterfly forewing area to that optimum size, but that this may have happened in the distant past, long outside the range of data for this project. However, more data from further in the past would be needed to provide evidence for that, so the only firm conclusion that can be drawn is that out of the models tested here, the change in area of North American monarch butterfly forewings appears to fit the stasis model of evolution best, implying there has been no change in the last 150 years.

DATA AVAILABILITY

All data and code are available on GitHub at (<https://github.com/RLaRochelle/Tasks/tree/master/Project>).

ACKNOWLEDGEMENTS

I would like to thank Dr. Jonathan Mitchell for his guidance throughout the entirety of this project. This project would not have been possible without his help, especially with the coding for the analysis and plot.

REFERENCES

1. Bartoszek K, Glémin S, Kaj I, Lascoux M. Using the Ornstein–Uhlenbeck process to model the evolution of interacting populations. Journal of Theoretical Biology. 2017;429:35–45. doi:10.1016/j.jtbi.2017.06.011

2. Freedman MG, Dingle H. Wing morphology in migratory North American monarchs: characterizing sources of variation and understanding changes through time. Animal Migration. 2018;5(1):61–73. doi:10.1515/ami-2018-0003

3. Freedman MG, Dingle H, Strauss SY, Ramírez SR. Two centuries of monarch butterfly collections reveal contrasting effects of range expansion and migration loss on wing traits. Proceedings of the National Academy of Sciences. 2020;117(46):28887–28893. doi:10.1073/pnas.2001283117

4. Hunt G. Fitting and Comparing Models of Phyletic Evolution: Random Walks and beyond. Paleobiology. 2006;32(4):578–601.

5. Hunt G. paleoTS: Analyze Paleontological Time-Series. 2019.

6. Li Y, Pierce AA, Roode JC de. Variation in Forewing Size Linked to Migratory Status in Monarch Butterflies. Animal Migration. 2016;3(1):27–34. doi:10.1515/ami-2016-0003

7. Monarch Butterfly. National Wildlife Federation. [accessed 2022 Apr 5]. https://www.nwf.org/Home/Educational-Resources/Wildlife-Guide/Invertebrates/Monarch-Butterfly

8. Montejo-Kovacevich G, Smith JE, Meier JI, Bacquet CN, Whiltshire-Romero E, Nadeau NJ, Jiggins CD. Altitude and life-history shape the evolution of Heliconius wings. Evolution. 2019;73(12):2436–2450. doi:10.1111/evo.13865

9. R Core Team. R. The R Foundation for Statistical Computing; 2022.

10. Schneider CA, Rasband WS, Eliceiri KW. NIH image to ImageJ: 25 years of image analysis. Nat. Methods. 2012;9:671–675.

11. Wickham H, Francois R, Henry L, Muller K. dplyr: A Grammar of Data Manipulation. 2022.