Annotated Bibliography- Sexual Dimorphism CURE

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Background on Pieris rapae & Wing Melanization

Gilbert, N., & Raworth, D.A. (2005). Movement and migration patterns in *Pieris rapae* (Pieridae). *Journal of the Lepidopterists' Society*, *59*, 10-18. https://images-peabody-yale-edu.proxy.lib.pdx.edu/lepsoc/jls/2000s/2005/2005(1)10-Gilbert.pdf

This paper discusses non-migratory movement and migration patterns of *Pieris rapae*. This article is an example of the kind of reference and background research necessary to interpret the data attached to museum specimens. Since *Pieris rapae* is a migratory species, time of year is an important part of the data to record and account for when it comes to analysis. It also means some further research will be necessary to know what the expected range for this species should be – having this kind of data will help students pick out outliers.

Kingsolver, J.G. (1985). Thermoregulatory significance of wing melanization in Pieris butterflies (Lepidoptera: Pieridae): Physics, posture, and pattern. *Oecologia, 66*(4), 546-553. https://doi.org/10.1007/BF00379348

This paper explains the thermoregulatory significance of wing melanization and basking posture. It presents data from lab and fields studies and is one of the first studies demonstrating the relationship between the color of the entire wing surface and thermoregulation in insects. The Introduction of this paper provides good background for other articles that discuss thermoregulation and wing melanization in Lepidoptera, although the rest is a little physics-heavy and includes a mathematical model.

Kingsolver, J.G., & Wiernasz, D.C. (1987). Dissecting correlated characters: Adaptive aspects of phenotypic covariation in melanization pattern of Pieris butterflies. *Evolution, 41*(3), 491-503. https://doi.org/10.1111/j.1558-5646.1987.tb05820.x

The authors measure melanization patterns in *Pieris* from cooler North American environments and compare to their expectations based on an adaptive hypothesis. Their results suggest that melanization in *Pieris* is adaptive. This study can be used to introduce the method of measuring covariance of traits to determine whether traits are adaptive. The authors also review wing melanization patterns in *Pieris* with useful diagrams. This is also a great example of an older study and is written in a style that may be more accessible to students with little experience reading primary literature.

Stoehr, A.M., & Goux, H. (2008). Seasonal phenotypic plasticity of wing melanisation in the cabbage white butterfly, *Pieris rapae L.* (Lepidoptera: Pieridae). *Ecological Entomology*, *33*(1), 137-143. https://doi.org/10.1111/j.1365-2311.2007.00931.x

This paper introduces the concept that darker wing patterns affect thermoregulation in butterflies. The authors quantify the degree of phenotypic plasticity in forewing melanization in *Pieris rapae* and compare to other *Pieris* species. Their results conformed to the expectations in males but differed in females. They report seasonal differences in melanization for most of the melanized areas on *Pieris* wings. This paper provides background information about the focal species of the CURE, *Pieris rapae*, and focuses on wing patterns. The methods described are likely similar to how most of the specimen records the students are working with were generated. The results presented in this paper are also similar to what students might expect they will be able to conclude from the data they are collecting.

Stoehr, A.M., Walker, J.F., & Monteiro, A. (2013). Spalt expression and the development of melanic color patterns in pierid butterflies. *EvoDevo*, *4*(1), 1-11. https://doi.org/10.1186/2041-9139-4-6

Spalt (Sal) is a transcription factor that has been associated with the development of wing patterning in *Pieris rapae*. The authors test whether Sal is involved in the development of wing patterning in other pierid butterflies using immunohistochemistry tagging. They demonstrate that Sal is involved in dense wing melanization across pierid species, but not in vein melanization or diffuse wing melanization. Sal expression is sexually dimorphic, consistent with difference in spot sizes between males and females. Sal is also implicated in eyespot patterning in nymphalid butterflies, but more work needs to be done to determine whether development of pierid spots and nymphalid eyespots is convergent. This study looks at wing melanization from a genetic perspective and demonstrates the kind of follow-up studies that can result from measurement studies, like the one the students of the CURE are involved in. Gene expression is not related to the CURE material, but may help tie CURE activities to other course material and encourages students to think more broadly about the implications of the data they are collecting.

Stoehr, A.M., Hayes, K., & Wojan, E.M. (2016). Assessing the role of wing spots in intraspecific communication in the cabbage white butterfly (*Pieris rapae L*.) using a simple device to increase butterfly responses. *Journal of Insect Behavior*, *29*(3), 243-255. https://doi.org/10.1007/s10905-016-9556-2

This is a behavioral study utilizing a model butterfly to test responses in real butterflies. The authors demonstrated that small wing pattern elements play a role in communication. They tested responses in both lab-reared and wild populations of male and female *Pieris rapae* butterflies and found that females only respond to male models, while males will respond to female models and male models that have been manipulated so their wings match female patterning.

Sexual Dimorphism & Sexual Selection

Allen, C.E., Zwaan, B.J., & Brakefield, P.M. (2011). Evolution of sexual dimorphism in the Lepidoptera. *Annual Review of Entomology*, *56*, 445-464. https://doi.org/10.1146/annurev-ento-120709-144828

This paper provides a review of Sexual dimorphism in moths and butterflies, that covers sexual dimorphism in life history, morphology, and behavior. It focuses on sexual selection and natural selection as two forces that shape the evolution of sexual differences in moths and butterflies and discusses the possibility of their opposing or synergistic roles. The article begins with a good introduction to sexual selection vs. natural selection debate, provides examples of sexual dimorphism in butterflies (with images), and goes through the different kinds of sexual dimorphism and how they are regulated. It finishes with a discussion of the consequences of sexual dimorphism. This review reads as a textbook chapter and should be a great introduction to the topic of sexual dimorphism for beginning and advanced students. Students should have a basic understanding of evolution and natural selection before reading.

Izzo, A.S., & Tibbetts, E.A. (2012). Spotting the top male: Sexually selected signals in male *Polistes dominulus* wasps. *Animal Behaviour*, *83*(3), 839-845. https://doi.org/10.1016/j.anbehav.2012.01.005

This paper introduces sexual selection in social insects (the wasp *Polistes dominulus*) and lek-based mating systems. The authors demonstrate through physical manipulation of spots that females prefer males with smaller, elliptically-shaped abdominal spots compared to males with larger or irregularly-shaped spots. Males with smaller spots were also dominant over other males and won a greater proportion of fights. This paper is a great introduction to sexual selection research and behavioral studies. In particular, this paper demonstrates that sexually dimorphic, variable traits may be demonstrably linked to other traits that impact fitness. This is a good introduction to sexual selection research and requires little background knowledge beyond a basic introduction to ornamentation in insects and an introduction to sexual selection.

Oliver, J.C., Robertson, K.A., & Monteiro, A. (2009). Accommodating natural and sexual selection in butterfly wing pattern evolution. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1666), 2369-2375. https://doi.org/10.1098/rspb.2009.0182

In this study, the authors demonstrate that dorsal wing characters in *Bicyclus* butterflies evolve faster and demonstrate more sex-based differences than ventral wing characters, supporting the hypothesis that dorsal traits are used for mate signaling while ventral characters are used for predator avoidance. This work is a good example of evolutionary research methods, including phylogenetic reconstruction and calculating evolutionary rates. This paper is more advanced and assumes substantial background knowledge from the reader, such as familiarity with phylogenetic inference methods and ancestral character state reconstruction. This is a good reference for answering student questions regarding why certain characters display sexual dimorphism while others do not.

Wiernasz, D.C. (1989). Female choice and sexual selection of male wing melanin pattern in *Pieris occidentalis* (Lepidoptera). *Evolution*, *43*(8), 1672-1682. https://doi.org/10.1111/j.1558-5646.1989.tb02617.x

This work was among the first studies to demonstrate the effect of female choice on male wing patterns in butterflies. The author provides a nice figure of the variation in *Pieris occidentalis* wing patterns. This paper can be used as an introduction to some of the concepts that are thematic to the CURE in a closely related species. It is a great example of older ecological field studies and manipulation studies. This paper should be presented with Wiernasz (1995) below.

Wiernasz, D.C. (1995). Male choice on the basis of female melanin pattern in Pieris butterflies. *Animal Behaviour, 49*(1), 45-51. https://doi.org/10.1016/0003-3472(95)80152-9

This is a partner study to Wiernasz (1989), demonstrating the effect of male choice on female wing patterns in butterflies. These papers should be presented together.

Wiernasz, D.C., & Kingsolver, J.G. (1992). Wing melanin pattern mediates species recognition in Pieris occidentalis. *Animal Behaviour, 43*(1), 89-94. https://doi.org/10.1016/S0003-3472(05)80074-0

This paper presents a hybridization study that demonstrates wing melanization is important for mate choice and conspecific mate identification. The authors artificially manipulate the wing melanization of *Pieris protodice* and *P. occidentalis* to demonstrate that interspecific mating success increases when melanization of male *P. protodice* is more similar to that of *P. occidentalis*. This study is an example of an interesting approach to studying behavior with a clever study design.

Evolution of Eyespots in Lepidoptera

Oliver, J.C., Tong, X.L., Gall, L.F., Piel, W.H., & Monteiro, A. (2012). A single origin for nymphalid butterfly eyespots followed by widespread loss of associated gene expression. *PLOS Genetics, 8*(8), e1002983. https://doi.org/10.1371/journal.pgen.1002893

The authors score phenotypes in 399 nymphalid butterfly species and test eyespot gene expression in 21 species to determine that eyespots in this group have a single origin approximately 90 million years ago. They demonstrate changes to expression of eyespot genes in certain lineages that do not correspond with eyespot loss, indicating that the genes controlling the eyespot have undergone substantial evolution since the origin of the eyespot, possibly to remove genes that are not necessary for expression of the novel trait. This study is an excellent demonstration of exploring the evolution of a novel trait and underlying gene evolution in a phylogenetic context. It is most appropriate for advanced students, or students that have been given substantial background in trait evolution and genetics.

Tokita, C.K., Oliver, J.C., & Monteiro, A. (2013). A survey of eyespot sexual dimorphism across nymphalid butterflies. *International Journal of Evolutionary Biology*, *2013*. http://dx.doi.org/10.1155/2013/926702

The degree of eyespot dimorphism is quantified in ~400 nymphalid butterflies. The authors summarize prevalence of male- vs. female-based dimorphism, where dimorphism occurs (e.g. ventral vs. dorsal, forewing vs. hindwing), and compares placement of sexually dimorphic vs. non-sexually dimorphic eyespot placement. This is a good reference for students to understand the variation in sexual dimorphism across species and get a sense of the trends in eyespot dimorphism in this particular clade of butterflies. It should be emphasized that *Pieris rapae*, the species used in the CURE, is *not* a part of this clade of butterflies, and is less well-studied – so the kind of discoveries that have been made in nymphalid butterflies may be waiting to be discovered in *Pieris*. The kinds of statistics presented in this paper may also give students a good idea of what they will be able to conclude from the data they are collecting for the CURE.

Phenotypic Plasticity

Bhardwaj, S., Jolander, L.S.H., Wenk, M.R., Oliver, J.C., Nijhout, H.F., & Monteiro, A. (2020). Origin of the mechanism of phenotypic plasticity in satyrid butterfly eyespots. *Elife*, *9*, e49544. https://doi.org/10.7554/eLife.49544

This paper discusses phenotypic plasticity of eyespots in the butterfly *Bicyclus anynana* as a response to temperature. The introduction gives a good overview of plasticity and the debate surrounding the origin of plasticity in a lineage (i.e. is it a derived trait or a “pre-adaptation” that is present in most organisms). The authors demonstrate that plasticity in the eyespot size of *Bicyclus anynana* is due to variations in temperature. They present their results from 12 different species of nymphalid butterflies and show that the plastic response of eyespots in this species is due to expression levels of certain hormones, and that sensitivity of the eyespots to those hormones appears to have evolved gradually as nymphalid butterflies diversified. This paper is a great introduction to how phenotypic plasticity is studied. It could be used as an introduction to phenotype-to-genotype methods, developmental methods, and evolutionary research methods more generally. Students will need to understand the concept of phenotypic plasticity and should have been introduced to phylogenies: how to read them properly and map traits onto them. This paper can give students context for the importance of measuring the occurrence of phenotypic plasticity and how it can lead to further research. Quantifying the degree of phenotypic plasticity, and sexual dimorphism, is the endeavor that they are contributing to when they measure museum specimens for this CURE. This paper should also give them an idea of how important it is to make accurate measurements, as these traits are small and small differences are important.

Prudic, K.L., Jeon, C., Cao, H., & Monteiro, A. (2011). Developmental plasticity in sexual roles of butterfly species drives mutual sexual ornamentation. *Science*, *331*(6013), 73-75. https://doi.org/10.1126/science.1197114

Similar to Bhardwaj et al. (2020), this paper explores sexual dimorphism in *Bicyclus anynana*, but instead of focusing on the morphological characters, this paper focuses on temperature-induced plasticity in larval rearing behavior. The authors demonstrate the males and females will switch their rearing roles depending on the temperature. This switch corresponds to the wet and dry seasons in the wild, and the authors conclude that this is a consequence of seasonal plasticity of ornamentation. This is a nice demonstration of how sexual dimorphism in morphology (such as wing ornamentation) can impose consequences on the organism and drive sexual dimorphism in behavior. This paper is short and accessible to students with a basic background in sexual selection and trait evolution.

Data Management

Michener, W.K., Brunt, J.W., Helly, J.J., Kirchner, T.B., & Stafford, S.G. (1997). Nongeospatial metadata for the ecological sciences. *Ecological Applications*, *7*(1), 330-342. https://doi.org/10.1890/1051-0761(1997)007[0330:NMFTES]2.0.CO;2

This study highlights the importance of preserving metadata, especially as data is increasingly shared between scientists, research agencies, and the broader community. Metadata is important for understanding and accurately interpreting a particular dataset, especially if it was published long ago and/or the original researchers are deceased. This paper is included as a reference for instructors regarding how and why metadata is stored and why it is important to teach students how to access and interpret it.