

Using the Scientific Method to Understand the Brilliant Colors of Male Jumping Spiders

by

Michael E. Vickers and Lisa A. Taylor
Entomology and Nematology Department
University of Florida, Gainesville, FL



Part 1 – Introduction

Understanding the steps of the scientific method and knowing how to apply them is essential not just for those pursuing careers in the sciences, but for any career. Whether you go on to become a teacher, politician, business leader, or artist, scientific literacy and critical thinking are important for making informed and evidenced-based decisions in both your work and personal life.

Many students think of the scientific method as simply a learned protocol to write up lab reports in a biology class, rather than a series of steps that real scientists follow to make groundbreaking discoveries. As this case study will illustrate, the scientific method is the process that scientists use to answer questions about the world. Scientists are making new discoveries every day, and as they do, our understanding of the world changes. Textbooks need to be updated every few years to account for the constant acquisition of knowledge. This means that if you really want to understand science, and more specifically biology, you cannot just memorize facts; you need to understand where scientific knowledge comes from and how to interpret it.

In this case study, you will be guided through the scientific method. Usually, research begins with a simple observation of the natural world. If a biologist notices something interesting or unusual, this leads them to ask a question about how or why this observed event occurred. Based on the knowledge they already have, the biologist then proposes a hypothesis, or a possible answer to their own question. In order to assess whether their hypothesis is likely to be true, a biologist then makes predictions that follow logically from the hypothesis, and then tests these predictions with an experiment. Finally, the biologist compares the results of their experiment with their predictions to draw a conclusion. If their results match their predictions, then their hypothesis is supported. If their results do not match their predictions, their hypothesis is not supported, and they may need to revise their original hypothesis, or come up with a new one altogether. It is important to note that results from an experiment can only ever provide support for or against a hypothesis; they can never prove or disprove a hypothesis with absolute certainty. For this reason, researchers conduct many different types of experiments to test their predictions again and again, and the more support they find for their hypothesis, the more likely their hypothesis is to be true. In this case study you will see how spider biologists use this scientific process to learn about the brilliant color patterns of jumping spiders.

Part 2 – Animal Communication, Coloration, and Jumping Spiders

Animals communicate with one another in a variety of ways and for a variety of reasons. Many male birds, such as red-winged blackbirds, sing to defend their territories from other male competitors, which increases their success in acquiring female mates (Peek, 1972; Yasukawa *et al.*, 1980; see Figure 1a below). Female moths produce airborne chemicals (pheromones) that attract males, and males have evolved elaborate featherlike antennae to detect these chemicals and locate females (Symonds *et al.*, 2012; Figure 1b below). Young treehoppers communicate with their mothers using vibrations; these vibrations travel through the branches they rest on and alert their mother of predators, so she can come to their defense (Cocroft, 1999; Figure 1c). Many animals even communicate directly with their potential predators. Vervet monkeys direct alarm calls to their leopard predators; these calls tell the hunting leopards that they have been detected and the leopards respond to these calls by retreating (Isbell & Bidner, 2016; Figure 1d). Animal signals are diverse, and this is probably because different kinds of signals work best to send different kinds of information in different kinds of environments.

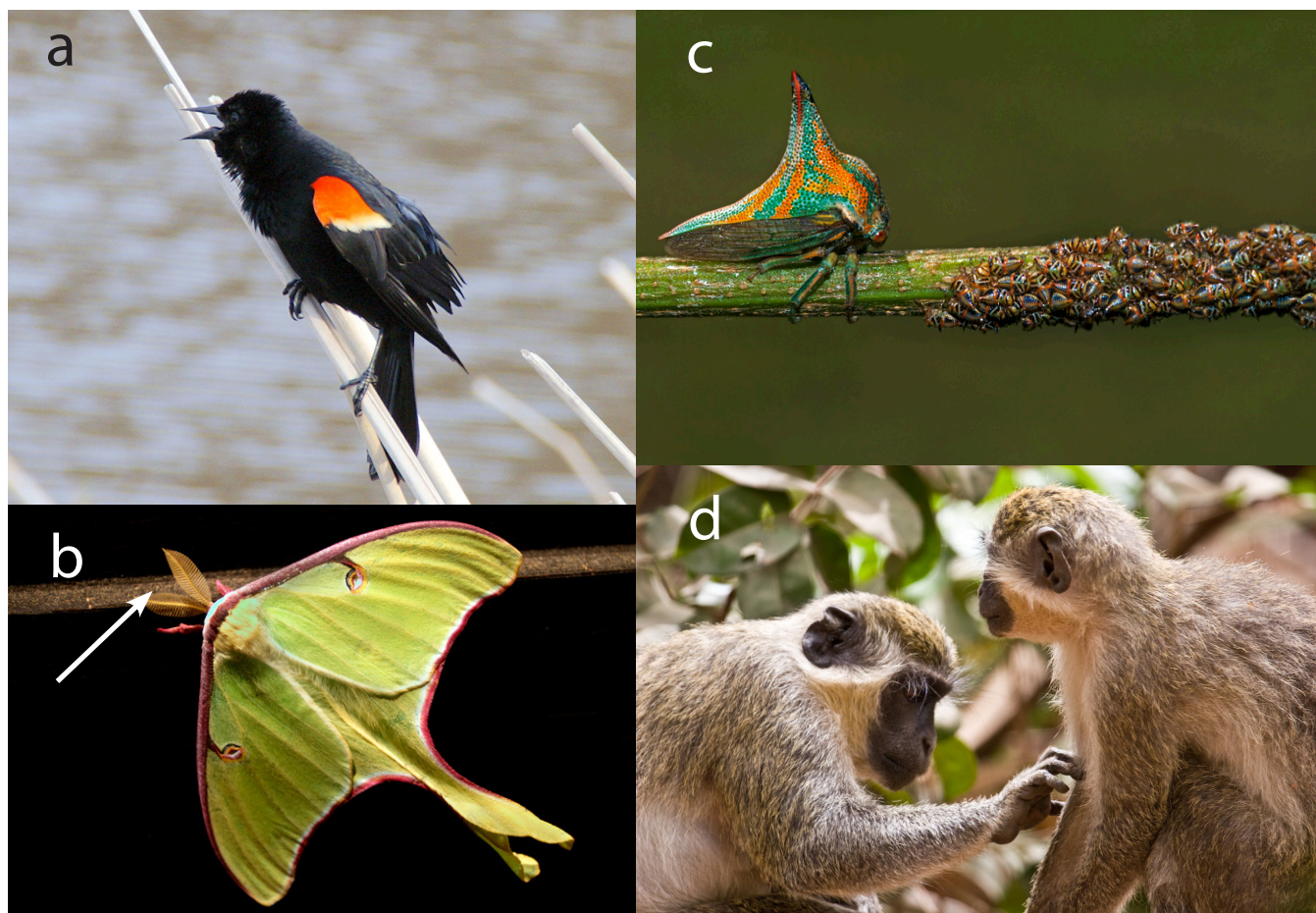


Figure 1. Communication strategies in animals. (a) male red-winged blackbird calling to defend his territory from competing males, (b) male luna moth showing elaborate antennae (indicated by the arrow) used to detect female pheromones, (c) female treehopper with her offspring that communicate with her using vibrations, (d) vervet monkeys that direct alarm calls to their leopard predators.

Credits:

- (a) red-winged blackbird by ritavida, CC BY-NC-SA 2.0, <https://www.flickr.com/photos/30336501@N03/3599915960>.
- (b) luna moth by weanders, CC BY-NC-ND 2.0, <https://www.flickr.com/photos/29032798@N05/3766344704>.
- (c) treehopper by Carlos De Soto Molinari, CC BY-NC-ND 2.0, <https://www.flickr.com/photos/33005514@N04/14047158233>.
- (d) vervet monkeys by Andrew Burrows, CC BY-NC-SA 2.0, <https://www.flickr.com/photos/78033600@N00/2417092758>.

Displaying bright colors can also be an effective way to communicate, and this strategy works well in many types of environments. Male peacocks use their brilliantly colored tail feathers to attract females, and even orient their courtship displays to take advantage of the position of the sun (Dakin & Montgomerie, 2009; Figure 2a below). Male veiled chameleons display their bright and quick-changing colors to other males to signal their motivation and fighting ability (Ligon & McGraw, 2013; Figure 2b). Monarchs feed on milkweed, which makes them toxic to many animals, and they advertise this toxicity with their bold black, white, and orange patterns that many birds avoid (Wiklund & Sillen-Tullberg, 1985; Figure 2c).

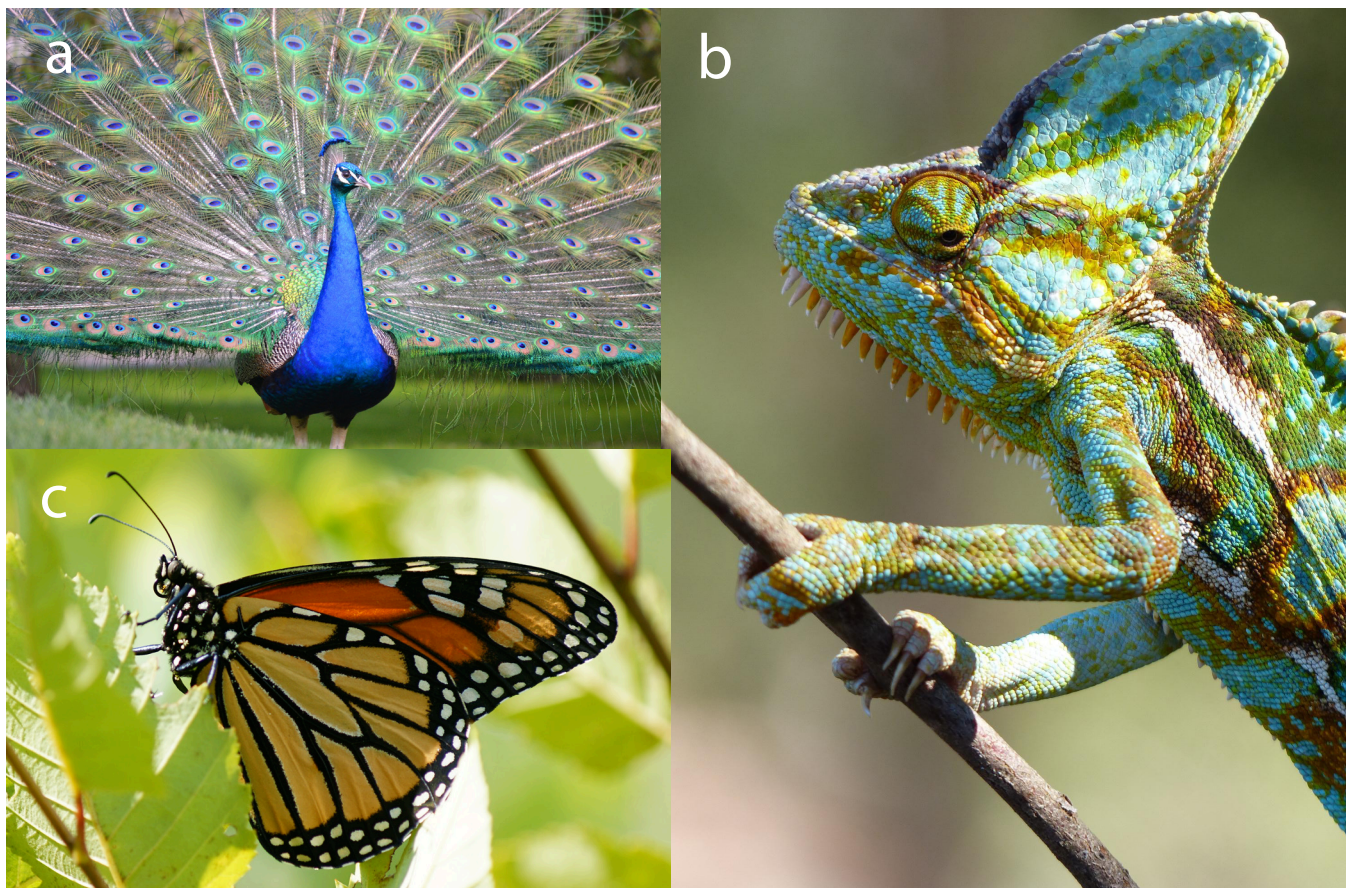


Figure 2. Using colors to communicate. (a) male peacocks display elaborate and colorful plumage to attract females, (b) male veiled chameleons rapidly change their colors during displays for other males, signaling their motivation and fighting ability, (c) monarch butterflies advertise their toxicity to predators using bold orange, black, and white patterns.

Credits:

(a) peacock by MTSOfan, CC BY-NC-SA 2.0, <https://www.flickr.com/photos/8628862@N05/8727563323>.

(b) chameleon by neeravbhatt, CC BY-NC-SA 2.0, <https://www.flickr.com/photos/74601184@N00/7738582570>.

(c) monarch by shell game, CC BY-NC-ND 2.0, <https://www.flickr.com/photos/36409008@N00/3780480957>.

Jumping spiders are an ideal group of animals to study to learn about colorful communication. There are more than 6000 described species of jumping spiders (World Spider Catalog, 2019), many of which have bright color patterns on various parts of their bodies (Figure 3, next page). They have colonized most ecosystems besides the sea and North and South Pole (Maddison *et al.*, 2008) and are common around the world in backyards and gardens, where they are voracious predators of many insect pests (Young & Edwards, 1990). They have excellent vision (Harland *et al.*, 2012), and behavioral experiments show that some species can discriminate between different colors (Nakamura & Yamashita, 2000; Jakob *et al.*, 2007; VanderSal & Hebets, 2007). Recent research is just beginning to uncover the mechanisms that jumping spiders use to see color (Zurek *et al.*, 2015). Jumping spiders use color to select their prey, and they avoid eating certain colors (e.g., reds, yellows, and black and white stripes) that are typically associated with toxicity (Taylor *et al.*, 2014; Vickers & Taylor, 2018; Powell *et al.*, 2019). Jumping spiders also engage in elaborate courtship displays

for potential mates that consist of combinations of color, movement, and even vibrations (e.g., Maddison, 1995). Experiments in a few species have shown that aspects of coloration are important in mating (e.g., Lim *et al.*, 2007; Girard *et al.*, 2011; Taylor & McGraw, 2013). One thing that is particularly interesting about jumping spiders is that females are such voracious predators that they sometimes attack and eat courting males, rather than mating with them. This makes courtship for male jumping spiders a particularly risky endeavor. Jumping spiders also have to avoid getting eaten by a variety of predators, many of which can also likely see color, such as other jumping spiders, predatory wasps, and birds (Taylor, 2012).

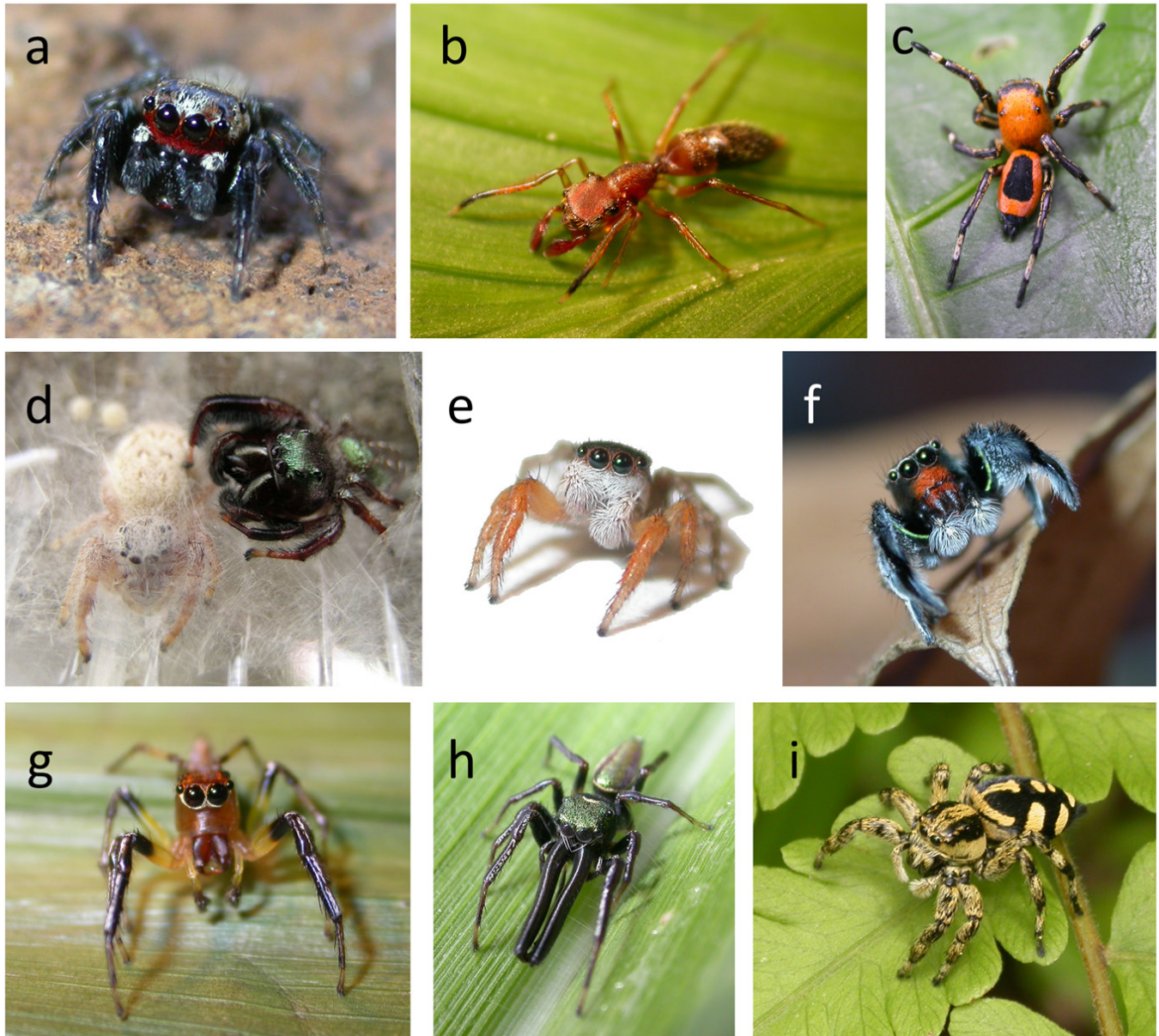


Figure 3. Diversity of color patterns in jumping spiders. (a) male *Evarcha culicivora*, Kenya, (b) female *Myrmarachne* sp., Costa Rica, (c) female *Phiale mimica*, Costa Rica, (d) female (left) and male (right) *Paraphidippus* sp., Costa Rica, (e) male *Habronattus icenoglei*, USA, (f) red-faced morph of male *Habronattus hirsutus*, USA, (g) male *Hypaeus benignus*, Costa Rica, (h) unidentified male salticid, Costa Rica, (i) female *Phiale guttata*, Costa Rica.

Credits: Photos by Lisa A. Taylor.

Part 3 – Applying the Scientific Method

3.1 Making Observations

The first step of the scientific method is simply to make observations. When it comes to studying spiders, this can be done in many places: in the field, in the lab, or even from photographs on the internet. Here we ask you to make some observations about the spiders shown in the photographs in Figure 3 (above).

In Figure 3, what do you notice about the diversity of color patterns that you see? Record anything you notice that you think is particularly interesting. For example, this could include differences between male and female colors, where specific colors are located on the spiders' bodies (e.g., face, legs, abdomens, etc.), how the spiders' colors compare to the backgrounds on which they are resting, or any other interesting things that capture your attention. Observation is a critical piece of the scientific method, so take at least five minutes to simply observe and note at least ten observations. (Note that many biologists spend years observing animals in both the field and lab over the course of their careers, and these observations lead them to new questions and ideas).

Note your observations here:

1. _____
2. _____
3. _____
4. _____
5. _____
6. _____
7. _____
8. _____
9. _____
10. _____

3.2 Generating Causal Questions

After biologists spend a lot of time observing, this leads them to ask causal questions about what they have seen. A causal question often begins with “how,” “why,” or “what causes...?” For example, you might have observed that in the pair of *Paraphidippus* sp. shown in Figure 3d, the male (the shiny green spider on the right side of the image) is more brightly colored than the female (the white spider on the left side of the image). This might lead the biologist to the causal question, *Why are males of this species more colorful than females?*

Note that causal questions are different than descriptive questions. Examples of descriptive questions include: *What color are juvenile spiders? Where do these spiders live?* These non-causal questions are perfectly valid and interesting questions and biologists spend a good deal of time asking these types of questions too, particularly during the observation stage of the scientific method. But for this activity, you will need to generate causal questions.

Now come up with three of your own causal questions that are related to the observations you recorded above.

1. _____
2. _____
3. _____

3.3 Generating Hypotheses

Hypotheses are answers to causal questions. If your causal question is, *Why are male Paraphidippus more colorful than females?*, there are several hypotheses that you could propose to answer this question. For example, one possible hypothesis is that males are more colorful than females because they use their iridescent green coloration to communicate their dominance to other males with whom they compete for females (as is the case in some birds: Parsons & Baptista, 1980; Pryke *et al.*, 2001). Another possible hypothesis is that males and females spend time in different habitats; perhaps males spend time in dense green vegetation, while females live between white rocks guarding their eggs and therefore each sex has different color patterns that are adaptive in each environment (as is the case for sex differences in coloration in some beetles: Hespeneide, 1975). There are many other hypotheses that could answer this causal question as well.

Now it's your turn to generate hypotheses. Pick one of your causal questions from section 3.2 above and come up with three hypotheses to answer it. Remember that each of your hypotheses must provide an answer to your causal question.

Restate your causal question here (from section 3.2): _____

Hypotheses:

1. _____
2. _____
3. _____

3.4 Making Predictions

Now it's time to think about how we might test a hypothesis. To do this, biologists begin by thinking about what predictions follow from each of their hypotheses. For example, one of our hypotheses stated above was that *Paraphidippus* males are bright green because males use this green coloration to signal their dominance to their male competitors. If this hypothesis is true, what predictions would we make? There are several possibilities. For example, we might predict that males will display their colors to one another during male-male interactions. We might also predict that males with their colors covered up experimentally (with paint, for example) would be less successful in male-male contests and, specifically, they might lose more fights. We might predict that males with their colors enhanced would be more successful in male-male contests and win more fights. Notice that these predictions are things that we can explicitly test in experiments; for example, we can actually count the number of fights that males win and lose.

Now we are going to tell you about a real study that was done to understand color patterns in the jumping spider, *Habronattus pyrrithrix* (a tiny jumping spider found in the southwestern United States and Mexico). In this study, Taylor and McGraw (2013) observed that males are more colorful than females (Figure 4). Males have bright red faces and green legs that they display to females during elaborate courtship dances. Interestingly, the males also “sing” for females during their displays by producing vibrations that travel through the ground or leaf litter to reach females (Elias *et al.*, 2012). Taylor and McGraw were particularly interested in the colors of males and wondered, why do males have red faces and green legs that are not present in females? One hypothesis (or possible answer to this causal question) is that the bright red facial colors and green leg colors of males are used as mating signals to convince females to mate. This is the hypothesis that they set out to test.

If this hypothesis is true, what predictions would you make? Come up with at least three specific predictions that follow logically from the hypothesis. Be sure that these predictions are specific enough that they could be tested with an experiment.

Predictions:

1. _____
2. _____
3. _____

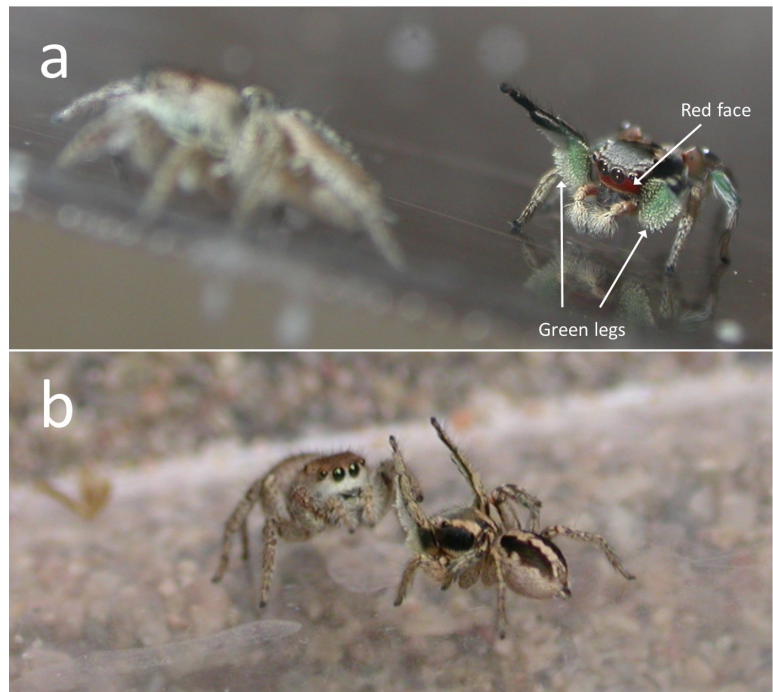


Figure 4. Coloration and courtship in *Habronattus pyrrithrix*. (a) In the early stages of courtship, the male (right) waves his green legs and displays his red face as he approaches the female (left) from a distance. (b) As courtship progresses, the male (right) cautiously approaches the female and continues to display his colors, while also producing vibrations that the female detects through the substrate. From Taylor and McGraw (2013).

3.5 Designing Experiments to Test Predictions

Now that you have a few of your own predictions in mind, we'll tell you about how Taylor and McGraw (2013) set out to test their own predictions. Taylor and McGraw predicted that if male colors were important mating signals, then females should pay attention to them during mating. More specifically, they predicted that males with either their red facial coloration concealed, or their green leg coloration concealed would be less attractive to females, and these males would therefore have lower mating success in experiments.

To test these predictions, Taylor and McGraw designed a color manipulation experiment where they used makeup to alter the males' colors (a method that has become common in jumping spider studies: Ihle & Taylor, 2019). They collected gravid females (females that were about to lay eggs) from the field in Arizona and allowed them to lay eggs in plastic boxes in the lab. When the spiderlings hatched, they were raised until adulthood and were randomly assigned to 1 of 4 experimental groups. In group 1, the males had their red facial coloration concealed with black liquid eyeliner that matched their underlying body coloration. In group 2, the males had their green coloration on their front legs concealed with tan makeup powder, so that their front legs matched the drab color of the rest of their legs. In group 3, males had both their red face and green leg coloration concealed. Group 4 was the control group; these males had none of their colors concealed (so they looked like natural males with their red and green coloration intact) (see Figure 5). Taylor and McGraw wanted to be sure that the experimental manipulation was similar across all four groups, so they used a sham treatment on the males whose colors were not concealed. A sham treatment is a procedure where the experimenters mimic the same experimental protocol, but do not actually change color of the spider's face and legs. For example, males in the control group who had their red face and green leg coloration not manipulated had black eyeliner applied to the top of their head (where the female would not be able to see it), and they had tan makeup powder applied to the second pair of legs (which did not change their appearance).

Why is this type of sham treatment important in experiments? Specifically, why is it important that all four of the experimental groups have the same amount of each type of paint applied?

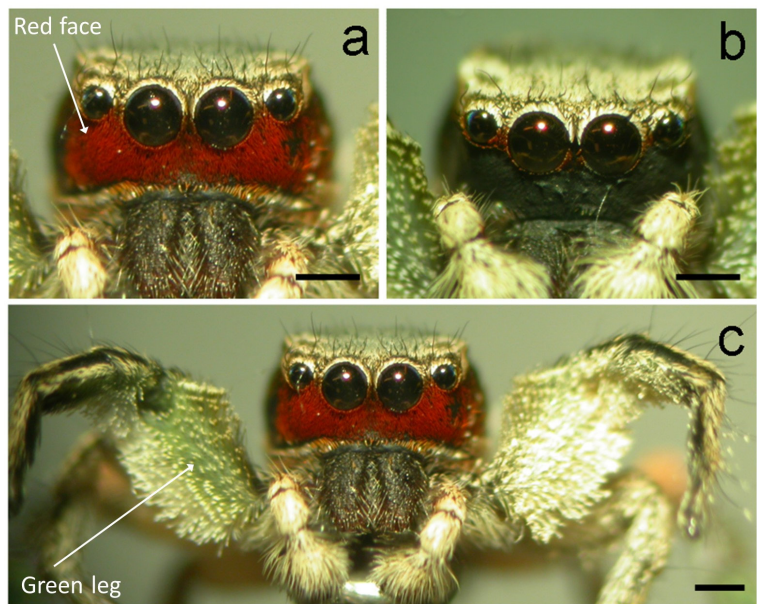


Figure 5. Experimental color manipulation in *Habronattus pyrrithrix*. (a) Unmanipulated male showing his naturally-colored red face, (b) male with his red facial coloration concealed with black liquid eyeliner, (c) male showing one leg with its natural green coloration (on the left) and the other leg covered with tan makeup powder (right). From Taylor and McGraw (2013).

Taylor and McGraw then randomly paired each of these males with a different female in individual boxes in the lab and watched to see if they mated.

Below is a bar graph (Figure 6) with only some of the data plotted. Think about the predictions that Taylor and McGraw made above and draw (directly on the figure) what you expect the rest of the data to look like. Remember: these are the data that you predict you would get if their hypothesis is true. Don't get too hung up on the exact height of each bar. The data for the control group are already shown indicating that when males don't have their colors manipulated just over 40% of them are successful in mating with a female. Now think about whether you think the other groups will be higher or lower than this control group.

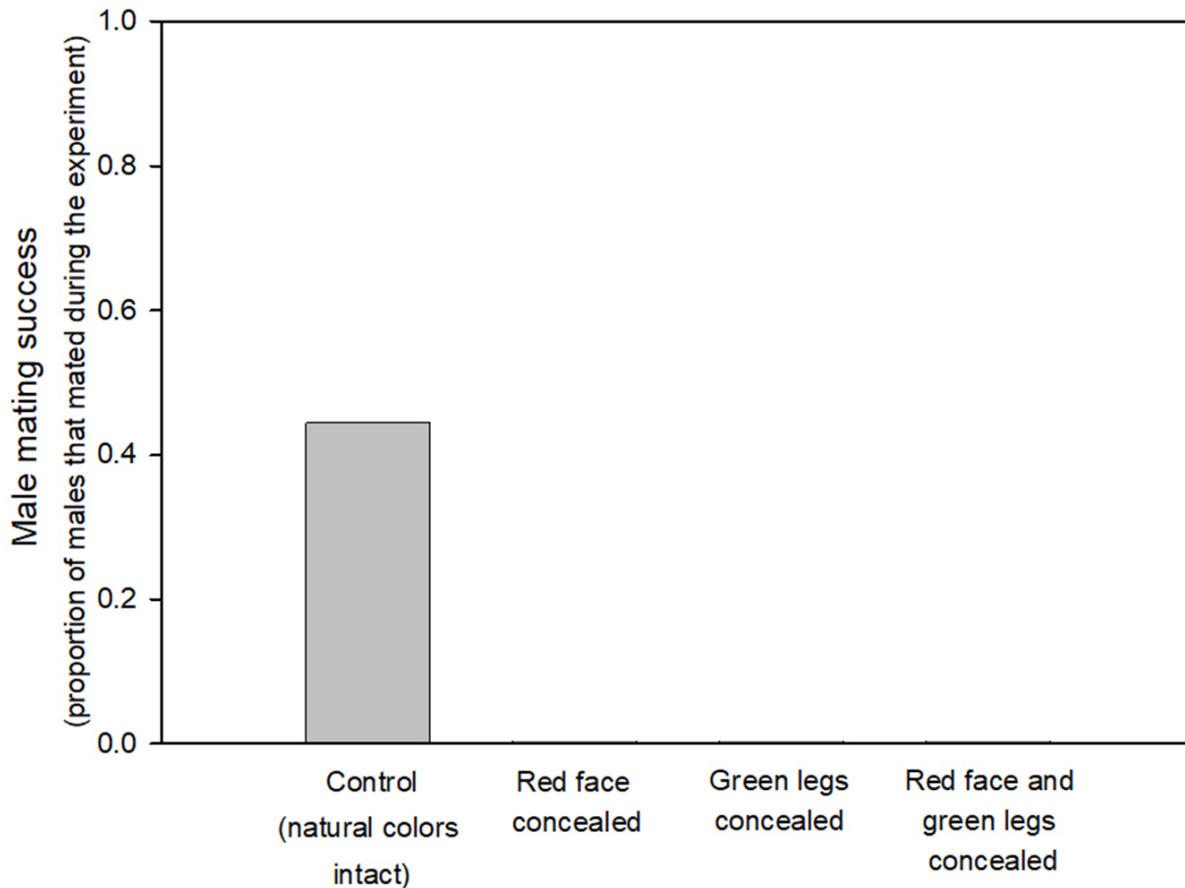


Figure 6. Bar graph showing only part of the data from Taylor and McGraw's color manipulation experiment. This is provided for you to draw the rest of the predicted results that follow from the hypothesis that a male's red facial and green coloration are mating signals to attract females and convince them to mate.

3.6 Drawing Conclusions

Once biologists have run their experiments and collected data, the next step of the scientific method is to ask whether their results match their predictions, and to draw conclusions from that. If their results do match their predictions, they conclude that their hypothesis is supported. If their results do not match their predictions, they conclude that their hypothesis is not supported. Sometimes some results match and others do not, providing partial support for a hypothesis.

Now that you have had the chance to draw your predictions, let's look at what actually happened in Taylor and McGraw's study, so you can see if these match your predictions, and use them to draw some conclusions.

Below are the actual data from their experiment (Figure 7).

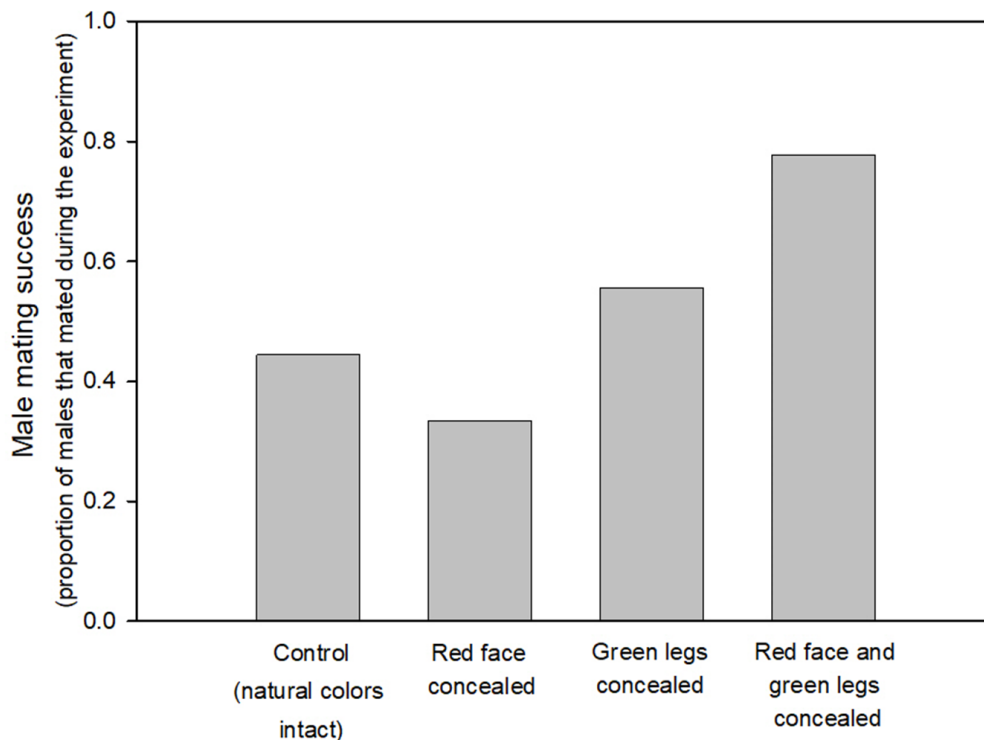


Figure 7. Experimental results showing the effect of male color manipulation on mating success under laboratory conditions. Note that none of the groups were statistically different from each other. Adapted from Taylor and McGraw (2013).

Do these results in Figure 7 match your predictions? (If not, explain how and where they differ).

What conclusions would you draw from this data so far? Was the hypothesis (that the male's red and green coloration act as mating signal) supported by these data? Why or why not?

3.7 Revising and Retesting Hypotheses

Just because the data from a single experiment does not support a hypothesis, this doesn't necessarily mean that the hypothesis is totally wrong. It may be that the experiment wasn't perfectly designed to test the hypothesis. For example, maybe the temperature in the lab wasn't quite right when the experiment was done and so the animals did not behave as they would in the wild. Likewise, just because one small set of data supports a hypothesis doesn't prove that the hypothesis is true. As biologists, our goal is to do a lot of different experiments, and even replicate experiments that have already been done. The more data we gather in support of a hypothesis, the more likely that hypothesis is to be true. And the more data we gather that contradict our predictions, the less likely that hypothesis is to be true. Just remember that no matter how well-designed our experiments are, they can never prove or disprove a hypothesis; they can only provide data to support it or not support it.

Often after an experiment is complete, a biologist will revisit and revise their hypotheses and then collect more data to test this newly revised hypothesis. This is what Taylor and McGraw did after they finished the experiment described above.

Taylor and McGraw knew from a lot of previous research (done by other researchers) in a variety of animals that an animal's ability to see colored objects depends on the light environment they are in (Kelber & Lind, 2010). We know this from our own experience too; if we are in a brightly lit room, we may be able to see colors on the wall really well, but we can't see those same colors very well if we dim the lights. Like us, many animals respond to colors differently when they are presented under low light (e.g., fish: Wong *et al.*, 2007; Heuschele *et al.*, 2009; butterflies: Obara *et al.*, 2008).

Taylor and McGraw wondered if the female spiders in their experiment didn't respond to the males' color as expected because they were tested under artificial lab lighting. Maybe they would be more responsive if they had the opportunity to view them under bright natural sunlight, like the real sunlight found in the spiders' natural habitat in Arizona. While they attempted to acquire the best lab lighting possible for their first study, they decided it would be best to present males to females outdoors under the real Arizona sun.

Based on what they had learned from their first study, and what they knew from watching these spiders interact in the field, Taylor and McGraw modified their original hypothesis and came up with a new, revised hypothesis: *Male colors in Habronattus pyrrithrix function as a mating signal to convince females to mate, but this signal only works when males are courting in the bright sunlight where females can see these colors well.*

To test this hypothesis, they designed a follow-up study. This time, they focused just on the male's red facial coloration and not the green leg coloration. There were several reasons (both logistical and theoretical) that they just focused on the red coloration; if you are interested, you can read more about these reasons in the original research publication (Taylor & McGraw, 2013). As before, they randomly assigned males to have their red face coloration either concealed with eyeliner or left intact (using the same sham treatment described above). Then they ran half of the tests in the sun and half in the shade. They predicted that if their hypothesis was true, red-faced males (with their natural red facial color intact) should be more successful in courtship than males with their colors concealed, but only for the tests run in the sunlight. For the tests run in the shade (where females may not be able to see the colors as well), they predicted that both sets of males would perform equally well. In this study, they estimated courtship success differently than they had previously. Here, they measured how close the male was able to get to the female (as they knew from previous experiments that males that get closer to females are more successful in mating).

Figure 8 (next page) shows the results from their experiment. As you look at this graph, remember that males that were more successful got closer to females and they therefore had lower values on the *y*-axis (i.e., lower bars). This is in contrast to Figure 7 where higher bars indicated higher success.

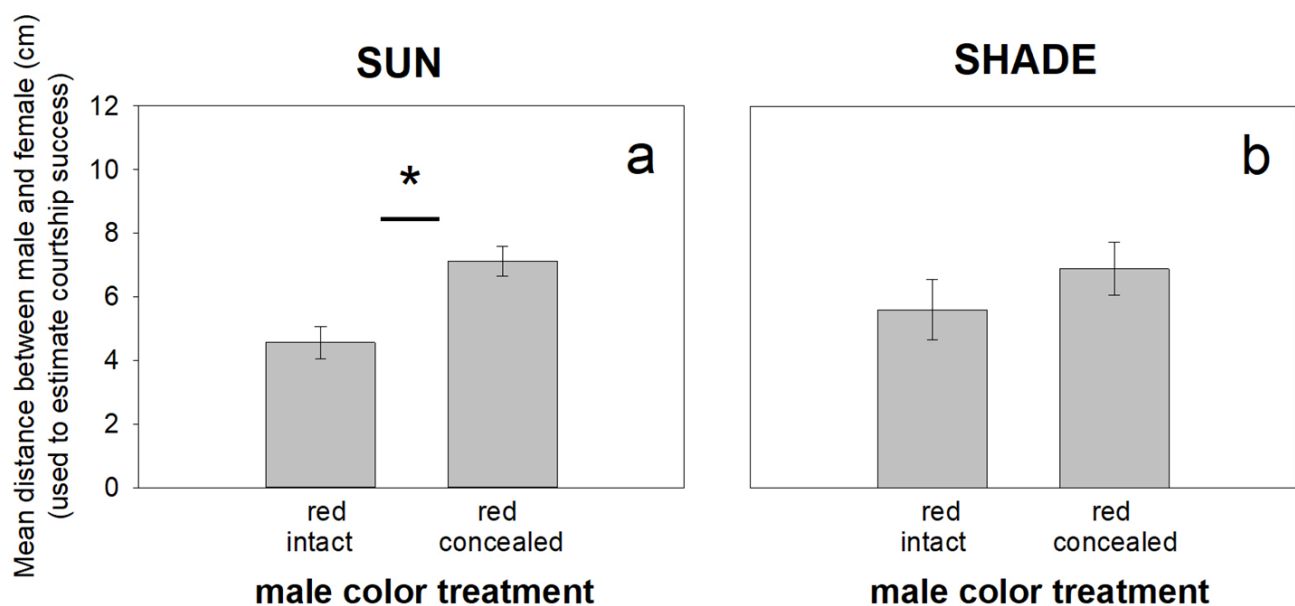


Figure 8. Experimental results showing the effect of male color manipulation on male courtship success in both the sunlight and the shade. Note that males that got closer to females, and therefore had lower values on the y -axis (i.e., lower bars) had higher courtship success. The asterisk in (a) indicates that the two treatment groups are significantly different from one another; specifically, males with their red coloration concealed were less successful than males with their red coloration intact. In (b), the two treatment groups did not differ statistically from one another (meaning that both groups were equally successful). Adapted from Taylor and McGraw (2013).

What is the overall conclusion you would draw from both of Taylor and McGraw's experiments that you read about in this case study?

Interestingly, two years after Taylor and McGraw published their 2013 study showing that *Habronattus pyrithrix* females only pay attention to the red coloration of males in the sunlight, we learned why. Taylor teamed up with a group of vision researchers and together they discovered that these spiders have a unique color vision system that differs from most other jumping spiders; this allows them to see and discriminate long-wavelength colors such as red that other jumping spiders cannot (Zurek *et al.*, 2015). This mechanism involves a red visual pigment in their eyes; the anatomy of their eyes and the location of this visual pigment now helps to explain, mechanistically, why their ability to see and discriminate red is strongest under bright light (Zurek *et al.*, 2015).

Part 4 – Designing Future Experiments

Now that you have experience developing hypotheses and predictions and designing experiments to test them, it's your turn to design your own study. Examine the photographs of *Habronattus pyrrithrix* in Figure 9 (below). Everything we have discussed so far in this case study has involved colors that males of this species clearly display to females during courtship (i.e., their red faces and green legs). But you will notice that in addition to these colors, males also have conspicuous and highly contrasting black and white patterns on their backs (that are not present in females). These patterns are oriented away from females during courtship, and therefore are unlikely to be used as mating signals. This observation leads to the causal question: *Why do males have conspicuous back patterns while females do not?*

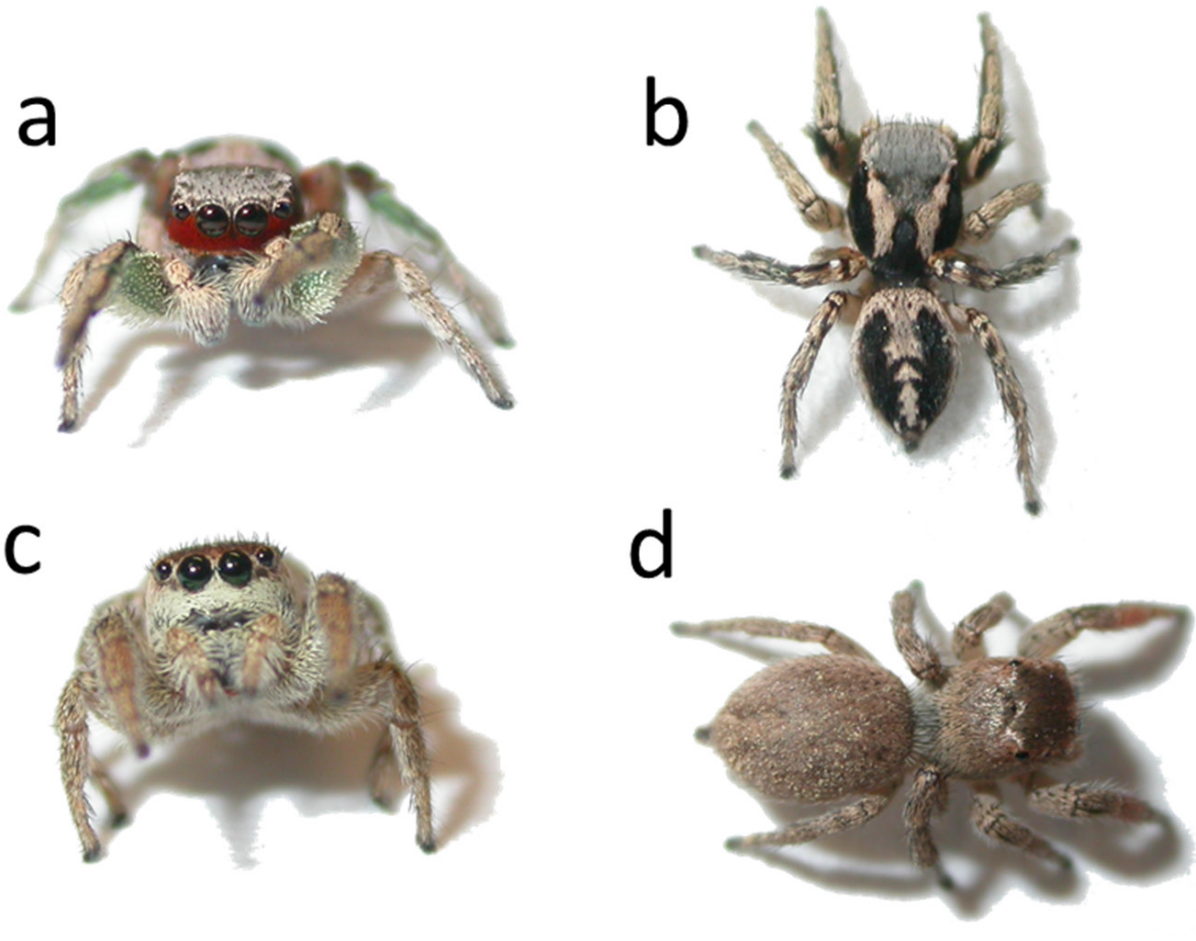


Figure 9. Sex-differences in color patterns in *Habronattus pyrrithrix* showing differences between males (a, b) and females (c, d). Notice that in addition to the facial markings (a,c) males have bright and conspicuous markings on their backs (b) that are not present in females (d).

Credits: Photos by Lisa A. Taylor.

Come up with at least one hypothesis to answer the causal question provided above (Why do males have conspicuous back patterns while females do not?). Remember that your hypothesis should be a proposed answer to this causal question.

If your hypothesis above is true, what prediction(s) would you make? Remember that your predictions should follow logically from your hypothesis. Your answer here should include at least one clear prediction (but you can list more than one if you wish).

Now design a simple experiment to test at least one of the predictions listed above.

References

Further Reading on Jumping Spider Colors

This case study is based on the following journal article:

- Taylor, L., and K. McGraw. 2013. Male ornamental coloration improves courtship success in a jumping spider, but only in the sun. *Behavioral Ecology* 24(4): 955–67. <<https://doi.org/10.1093/beheco/art011>>

For further reading on this study system (written for a general audience), see:

- Simon, M. 2018. Inside the lab where spiders put on face paint and fake eyelashes (and termites wear capes). *Wired Magazine*. <<https://www.wired.com/story/spiders-put-on-face-paint-and-fake-eyelashes/>>
- Clark, A. 2018. What does it take to understand spiders? False eyelashes, capes and face paint. *UF News*. <<https://medium.com/@UFNews/what-does-it-take-to-understand-spiders-false-eyelashes-capes-and-face-paint-6fb6c41e45e>>

To see a video of how makeup is applied to jumping spiders, see:

- Ihle, M. and L. Taylor. 2019. Manipulation of color patterns in jumping spiders for use in behavioral experiments. *Journal of Visualized Experiments* 147: e59824. (Open access article). <<https://doi.org/10.3791/59824>>

To see some beautiful and colorful jumping spider courtship videos, check out Jurgen Otto's peacock spider page on YouTube <<https://www.youtube.com/user/Peacockspiderman/videos>> as well as Daniel Zurek *et al.*'s video of *Habronattus pyrrithrix* courtship <<https://youtu.be/uGZwZlcCnDE>>.

Literature Cited

- Cocroft, R. 1999. Offspring-parent communication in a subsocial treehopper (Hemiptera: Membracidae: *Umbronia crassicornis*). *Behaviour* 136(1): 1–21. <<https://www.jstor.org/stable/4535591>>
- Dakin, R., and R. Montgomerie. 2009. Peacocks orient their courtship displays towards the sun. *Behavioral Ecology and Sociobiology* 63(6): 825–34. <<https://www.jstor.org/stable/40295406>>
- Elias, D., W. Maddison, C. Peckmezian, M. Girard, and A. Mason. 2012. Orchestrating the score: complex multimodal courtship in the *Habronattus coecatus* group of *Habronattus* jumping spiders (Araneae: Salticidae). *Biological Journal of the Linnean Society* 105: 522–47. <<https://doi.org/10.1111/j.1095-8312.2011.01817.x>>
- Endler, J. 1991. Variation in the appearance of guppy color patterns to guppies and their predators under different visual conditions. *Vision Research* 31(3): 587–608. <[https://doi.org/10.1016/0042-6989\(91\)90109-I](https://doi.org/10.1016/0042-6989(91)90109-I)>
- Girard, M., M. Kasumovic, and D. Elias. 2011. Multi-modal courtship in the peacock spider, *Maratus volans* (OP-Cambridge, 1874). *PLoS One* 6: e25390. <<https://doi.org/10.1371/journal.pone.0025390>>
- Harland, D., D. Li, and R. Jackson. 2012. How jumping spiders see the world. In: Lazareva O., Shimizu T., Wasserman, E. (eds) *How Animals See the World: Comparative Behavior, Biology, and Evolution of Vision*. Oxford University Press, New York, pp 133–164. <<https://doi.org/10.1093/acprof:oso/9780195334654.001.0001>>
- Hespenheide, H. 1975. Reversed sex-limited mimicry in a beetle. *Evolution* 29(4): 780–3. <<https://doi.org/10.1111/j.1558-5646.1975.tb00873.x>>
- Heuschele, J., M. Mannerla, P. Gienapp, and U. Candolin. 2009. Environment dependent use of mate choice cues in sticklebacks. *Behavioral Ecology* 20(6): 1223–7. <<https://doi.org/10.1093/beheco/arp123>>
- Ihle, M., and L. Taylor. 2019. Manipulation of color patterns in jumping spiders for use in behavioral experiments. *Journal of Visualized Experiments* 147: e59824. <<https://doi.org/10.3791/59824>>
- Isbell, L., and L. Bidner. 2016. Vervet monkey (*Chlorocebus pygerythrus*) alarm calls to leopards (*Panthera pardus*) function as a predator deterrent. *Behaviour* 153(5): 591–606. <<https://doi.org/10.1163/1568539X-00003365>>
- Jakob, E., C. Skow, M. Haberman, and A. Plourde. 2007. Jumping spiders associate food with color cues in a T-maze. *The Journal of Arachnology* 35: 487–93. <<https://doi.org/10.1636/JOA-ST06-61.1>>

- Kelber, A., and O. Lind. 2010. Limits of colour vision in dim light. *Ophthalmic and Physiological Optics*. 30:454-459. <<https://doi.org/10.1111/j.1475-1313.2010.00721.x>>
- Ligon, R., and K. McGraw. 2013. Chameleons communicate with complex colour changes during contests: different body regions convey different information. *Biology Letters* 9: 20130892. <<https://doi.org/10.1098/rsbl.2013.0892>>
- Lim, M., M. Land, and D. Li. 2007. Sex-specific UV and fluorescence signals in jumping spiders. *Science* 315(5811): 481. <<https://doi.org/10.1126/science.1134254>>
- Maddison, W. 1995. Salticidae section of the Tree of Life Web Project, Version 01. <<http://tolweb.org/Salticidae/2677/1995.01.01>>. Accessed 3 July 2019.
- Maddison, W., M. Bodner, and K. Needham. 2008. Salticid spider phylogeny revisited, with the discovery of a large Australasian clade (*Araneae: Salticidae*). *Zootaxa* 1893: 49–64. <<https://doi.org/10.11646/zootaxa.1893.1.3>>
- Nakamura, T., and S. Yamashita. 2000. Learning and discrimination of colored papers in jumping spiders (*Araneae, Salticidae*). *Journal of Comparative Physiology A* 186: 897–901. <<https://doi.org/10.1007/s003590000143>>
- Obara, Y., H. Koshitaka, and K. Arikawa. 2008. Better mate in the shade: enhancement of male mating behaviour in the cabbage butterfly, *Pieris rapae crucivora*, in a UV-rich environment. *Journal of Experimental Biology* 211: 3698–702. <<https://doi.org/10.1242/jeb.021980>>
- Parsons, J., and L. Baptista. 1980. Crown color and dominance in the white-crowned sparrow. *The Auk* 97: 807–15.
- Peek, F. 1972. An experimental study of the territorial function of vocal and visual display in the male red-winged blackbird (*Agelaius phoeniceus*). *Animal Behaviour* 20: 112–8.
- Powell, E., C. Cook, J. Coco, M. Brock, L. Holian, and L. Taylor. 2019. Prey colour biases in jumping spiders (*Habronattus brunneus*) differ across populations. *Ethology* 125(6): 351–61. <<https://doi.org/10.1111/eth.12859>>
- Pryke, S., S. Andersson, and M. Lawes. 2001. Sexual selection of multiple handicaps in the red-collared widowbird: female choice of tail length but not carotenoid display. *Evolution* 55(7): 1452–63. <<https://doi.org/10.1111/j.0014-3820.2001.tb00665.x>>
- Symonds, M., T. Johnson, and M. Elgar. 2012. Pheromone production, male abundance, body size, and the evolution of elaborate antennae in moths. *Ecology and Evolution* 2(1): 227–46. <<https://doi.org/10.1002/ece3.81>>
- Taylor, L. 2012. Color and communication in *Habronattus* jumping spiders: tests of sexual and ecological selection. Arizona State University (PhD dissertation).
- Taylor, L., E. Maier, K. Byrne, Z. Amin, and N. Morehouse. 2014. Colour use by tiny predators: jumping spiders show colour biases during foraging. *Animal Behaviour* 90: 149–57. <<https://doi.org/10.1016/j.anbehav.2014.01.025>>
- Taylor, L., and K. McGraw. 2013. Male ornamental coloration improves courtship success in a jumping spider, but only in the sun. *Behavioral Ecology* 24(4): 955–67. <<https://doi.org/10.1093/beheco/art011>>
- VanderSal, N., and E. Hebets. 2007. Cross-modal effects on learning: a seismic stimulus improves color discrimination learning in a jumping spider. *Journal of Experimental Biology* 210: 3689–95. <<https://doi.org/10.1242/jeb.009126>>
- Vickers, M. and L. Taylor. 2018. Odor alters color preference in a foraging jumping spider. *Behavioral Ecology* 29(4): 833–9. <<https://doi.org/10.1093/beheco/ary068>>
- Wiklund, C., and B. Sillen-Tullberg. 1985. Why distasteful butterflies have aposematic larvae and adults, but cryptic pupae: evidence from predation experiments on the monarch and the European swallowtail. *Evolution* 39(5): 1155–8. <<https://doi.org/10.1111/j.1558-5646.1985.tb00456.x>>
- Wong, B., U. Candolin, and K. Lindstrom. 2007. Environmental deterioration compromises socially enforced signals of male quality in three-spined sticklebacks. *The American Naturalist* 170(2): 184–9. <<https://doi.org/10.1086/519398>>
- World Spider Catalog 2019. World spider catalog. Natural History Museum Bern [cited 2019 July 3]. <<http://wsc.nmbe.ch>>

- Yasukawa, K., J. Blank, and C. Patterson. 1980. Song repertoires and sexual selection in the red-winged blackbird. *Behavioral Ecology and Sociobiology* 7:233–8. <<https://doi.org/10.1007/BF00299369>>
- Young, O., and G. Edwards. 1990. Spiders in United States field crops and their potential effect on crop pests. *Journal of Arachnology* 18(1): 1–27. <<https://www.jstor.org/stable/3705574>>
- Zurek, D., T. Cronin, L. Taylor, K. Byrne, M. Sullivan, and N. Morehouse. 2015. Spectral filtering enables trichromatic vision in colorful jumping spiders. *Current Biology* 25(10): R403–4. <<https://doi.org/10.1016/j.cub.2015.03.033>>

Internet references accessible as of June 21, 2021.

