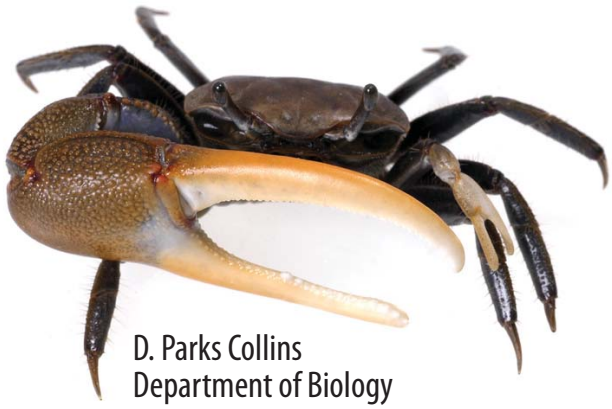
En Garde!

Animal Structures and What They Mean



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Part I – Unexpected

"This looks like the perfect spot to pitch the tent," Pete yelled to his dad.

"Let's back up about 15 feet, right to the edge of the trees," John replied.

John, a college professor, and his son Pete, a high school freshman, had both been intrigued by animal combat. They had seen both bull elk *(Cervus canadensis)* and bull moose *(Alces alces)* fight on numerous television documentaries. They had even witnessed two bighorn rams (*Ovis canadensis*) battling each other while on vacation in Montana two years ago.

On this particular weekend, John had decided to take Pete camping on the coast of South Carolina. The plan was to set up camp and spend the afternoon exploring and playing in the ocean. The afternoon was sunny and beautiful. John and Pete had the opportunity to survey the sand for shark teeth and remnants of horseshoe crabs. They also laughed with excitement as they observed brown pelicans dive into the ocean in hopes of stunning a fish for food. This was fun and exciting, but the real reason they made this trip was because of what happened there at night.

When evening came it was completely black. Even though darkness dominated, the beach would come alive at night. John had picked this place to observe and study how fiddler crabs *(Uca pugilator)* use their large claws in battle. Male fiddler crabs have one large claw that is sometimes just as big as the rest of their body (see Figure 1). John knew they had these extraordinary weapons, but he wanted to see them fight in person.

John and Pete watched as thousands of crabs littered the beach. Some stood by a burrow, ready to dart for cover if a predator got too close. Others wandered around rapidly, occasionally approaching and challenging the "residents" of the burrows. John noticed that these "residents" would wave their claws up and down, again and again. John and Pete had hoped to see male fiddler crabs fighting.

There was just one problem; the crabs did not engage. When two males faced each other, more times than not, there was no fight at all. The "wanderers" would simply walk away. This puzzled John.

"Dad," Pete said quietly. "I have some questions."

"So do I, buddy. So do I," John responded. "Let me hear your questions."

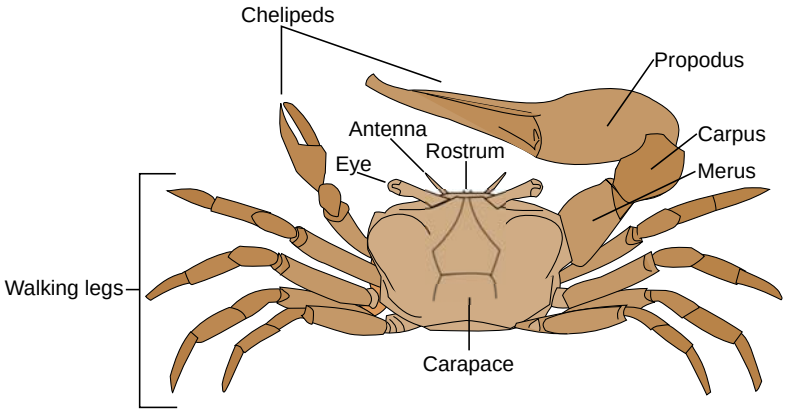

Figure 1. Anatomy scheme of a Fiddler crab. *Source:* Christopher Thomas, https://commons.wikimedia.org/wiki/File:Fiddler_crab_anatomy-en.svg, CC BY-SA 3.0.

Questions

1. Charles Darwin wrote the following in *The Origin of Species* in 1859:

   How low in the scale of nature this law of battle descends, I know not; male alligators have been described as fighting, bellowing, and whirling round, like Indians in a war-dance, for the possession of the females; male salmons have been seen fighting all day long; male stag-beetles often bear wounds from the huge mandibles of other males. The war is, perhaps, severest between the males of polygamous animals, and these seem oftenest provided with special weapons.

   Explain why the last sentence would make sense.

2. These crabs, however, were not using their "special weapons" to fight. This seems to run contrary to what Darwin observed in other species. If these male crabs have allocated resources towards growing and maintaining these claws, why would they not be using them primarily for fighting?

Part II – Trade-offs

"If the claws aren't being used to fight, why do the crabs have them?" Pete continued. "Besides elk, moose, bighorn rams and these crabs, are there any other animals that have big parts growing from their bodies that you can think of, dad?"

"Those are really great questions, Pete," John replied. "There are other types of animals that have body parts that seem to be weapons. As for the 'how' and 'why' behind the structures, let's talk about that later."

Let's turn our focus to the possible benefits and costs of having large structures.

Questions

1. List as many specific animals you can think of that have elaborate structures that could be used as weapons. Also, describe whether these structures are found in both males or females or just one sex.

2. Brainstorm as a group, and list all the possible purposes for these structures. What about benefits vs. costs? Fill out the chart below to answer this question.

Benefits of having elaborate structures	*Costs of having elaborate structures*

Part III – Data Analysis

"Hey Pete," John said. "Before we try to guess why some animals have extreme structures like these claws, we need to establish whether or not these structures are costly to the individual. Let's look at this paper."

Allen and Levinton (2007) tested the endurance capacity of crabs by running them on treadmills at a certain velocity until fatigue (see Figures 2 and 3). Fatigue was defined as the time when a crab no longer was able to maintain the pace of the treadmill. In experiment (a), all crabs that were used were similarly sized males. Treatment groups for experiment (a) included the following: (1) crabs with their major claw intact (shown as a filled-in circle); (2) crabs with no major claw and no added weight (shown as an open triangle down); and (3) crabs with no major claw but equivalent mass added to the carapace (shown as an open circle).

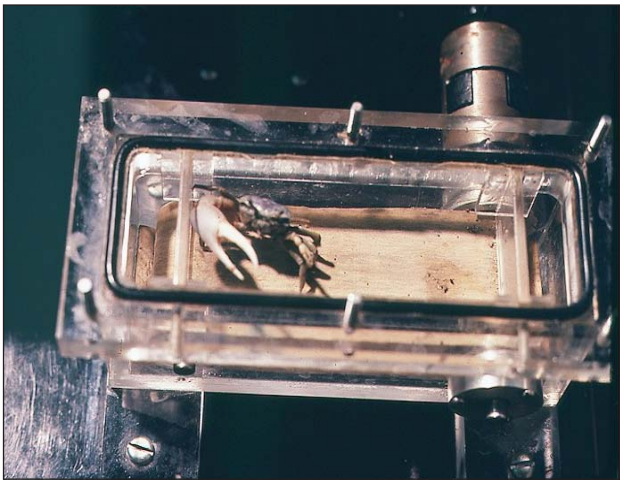

Figure 2. Fiddler crab on treadmill. Photo courtesy of Clyde Herreid.

For experiment (b), all crabs had their major claw still intact. Treatment groups for this experiment were as follows: (1) crabs with weight added to their carapace (shown as an open square); (2) crabs with weight added to their claw (shown as an open diamond); and (3) crabs with no weight added (shown as a filled-in circle).

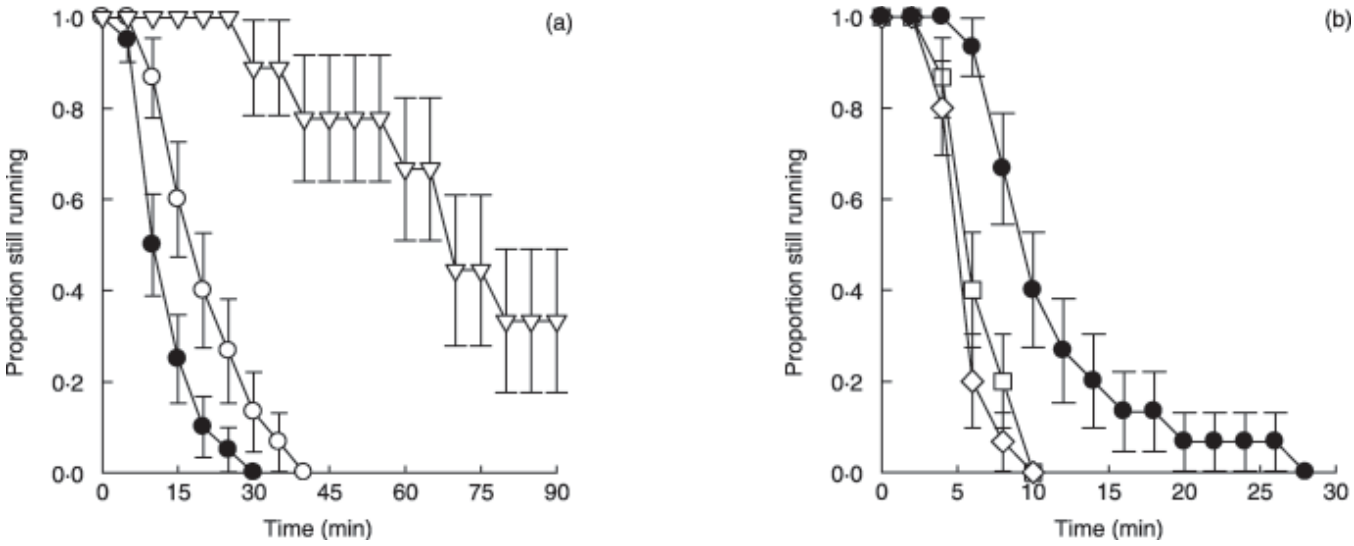

Figure 3. Proportion (± SE) of male fiddler crabs continuing to run at 4 m min^{-1} in the (a) first [intact major claw (filled circle); no major claw (open triangle down); and no major claw, weight added to carapace (open circle)], and (b) second [weight added to carapace (open square); weight added to claw (open diamond); and no weight added (filled circle)] treadmill endurance experiments. In the first experiment, n = 20 (intact claw) and 15 (no claw and no claw, weight added to carapace). In the second experiment, n = 15. P-values are from Wilcoxon's signed ranks tests: (a) < 0·001; (b) < 0·001. *Source:* Allen and Levinton, 2007. Used with permission of John Wiley and Sons.

Questions

1. Identify the control groups in both experiment (a) and (b). Why are these control groups important to the experiment?

2. What do the data say about the endurance capacity of fiddler crabs?

3. Would you be willing to say that larger size (and presumably extra weight) is costly? Please explain your answer.

"So if the large claw is costly to a male fiddler crab, why weren't the males using them for fighting? How do they benefit from the claws?" Pete asked.

"Here's another paper that may explain our fiddler crab observations, Pete," John replied.

Hyatt and Salmon (1978) observed interspecific battles of the Atlantic Sand Fiddler Crab *(Uca pugilator).* They defined each individual as either a "Resident" (one who currently has a burrow) or a "Wanderer" (one who is looking for a burrow). The researchers measured the width of the carapace (see Figure 1 in Part I) to determine large or small crabs. The width of the carapace typically has a positive correlation with length and width of claw. Analyze the observations below and then answer the questions that follow.

Observations

- Wanderers fought larger residents – 151 times (residents won 150/151 of these fights)
- Wanderers fought equal-sized residents – 44 times (residents won 41/44 of these fights)
- Wanderers fought smaller residents – 208 times (residents won 158/208 of these fights)

Questions

4. What do the data tell you? Is it what you would expect?

5. Is it possible that male fiddler crabs can tell how big their claws are compared to other potential competitors? If so, would the largest-clawed males have to fight as often or could they simply rely on deterring their potential rivals with their large claw (waving)?

6. Male moose allocate important minerals like phosphorus and calcium to growing antlers. When they engage in combat, male fiddler crabs are out in the open. How could engaging in a fight leave a bull moose and a male fiddler crab vulnerable? Would it be possible for these elaborate structures to be used mostly to deter, or warn, rival males?

Reference

Allen, B.J., and J.S. Levinton. (2007). Costs of bearing a sexually selected ornamental weapon in a fiddler crab. *Functional Ecology* 21(1): 154–161. DOI: 10.1111/j.1365-2435.2006.01219.x http://onlinelibrary.wiley.com/doi/10.1111/j.1365-2435.2006.01219.x/full

Part IV—The Result of Evolution?

"Even though large, elaborate structures are costly to an animal from an energy investment perspective, sometimes these structures are necessary because they are beneficial when it comes to deterring a competitor to eventually mate," John explained. "This is especially important if having a large structure leaves the individual vulnerable in other areas, like a huge bull moose with brittle bones or a male fiddler crab not being able to eat as efficiently. So, deterrence may be another option to fighting. Maybe the large, elaborate structures allow them the opportunity to not have to fight."

"How did evolution produce these extreme weapons?" Pete asked.

"Well, Pete," John said. "The drive to be the breeder is so strong that these animals are willing to incur the costs that come with growing and maintaining these structures, even if they do not always use them as weapons. In the case of evolution, it's important to not only understand natural selection, but also sexual selection."

Questions

1. Scientists often work hard to understand the connection between structure and function to fitness/evolutionary potential. When it comes to the fiddler crab, explain how structure complements function and also how structure limits function.

2. Explain sexual selection. How would you be able to guess whether or not extreme weapons in animals such as fiddler crabs, bull elk and moose, and bighorn rams are the result of sexual selection? Think about which sex displays these elaborate weapons. (*Hint:* Look back at Question 1 in Part II.)

3. In the table below, indicate whether or not you think the following structures are a result of sexual selection:

	Elk antlers	Moose antlers	Bighorn ram's horns	Fiddler crab's large claw	Narwhal's tusk	Saber-toothed cat's tooth
Sexual selection? (Yes or No)						

4. Doug Emlen, in his book *Animal Weapons*, states the following:

   > *As weapons get bigger they select for increasingly elaborate deterrence, and deterrence, in turn, selects for bigger and bigger weapons. Arms races and deterrence push each other forward, escalating in an evolutionary spiral.*

   Please explain this statement.