Agonistic interactions in crayfish: what factors determine who wins?

Introduction

When important resources, such as food, mates or shelter, are limited, individuals of the same species will compete for that resource. This interaction is called **intraspecific competition**. Intraspecific competition can take one of two forms: **scramble competition** or **contest competition**. Scramble competition, which is also called exploitation competition, occurs when individuals compete for shared, limited resources but there is no direct interaction among individuals. As a result of the competition, no individual receives enough of the resource to grow, survive and reproduce. Contest, or interference competition, involves direct interaction between competitors so that one competitor actively interferes with the ability of the other to access the resource. This usually involves aggressive interactions. This results in some individuals obtaining enough of the limiting resource for growth, survival, and reproduction while others do not. Contest competition is the focus of this study.

A major consequence of intraspecific competition is a suppression of the growth rate of the population. This suppression occurs because the growth and development of each individual is negatively impacted due to reduced access to resources. If enough individuals are affected, then the population as a whole is affected and population growth declines.

So, individuals will compete for a limiting (i.e., required) resource when it's limited. But what determines which individual will win during an aggressive encounter? Two factors appear to be most important in deciding which combatant wins and gains access to a resource. The first is **fighting ability**. When fighting ability differs, the poor fighter will accrue costs at a faster rate than good fighters. Such costs include serious injury or death. Either of which could decrease the individual's future survival and reproduction (i.e., fitness). Thus, it is expected that poor fighters avoid fighting good fighters or, if fighting ensues, will give up the fight more quickly than good fighters. The second factor that is important in determining which of the competitors will win the contest is **resource value**. If the value of the resource differs among the competitors, it is expected that the individual that attributes the greater value to the resource will fight harder to gain or maintain access to that resource. In general, individuals that already hold a resource will attribute a greater value to it than a competitor. This is because the resource holder has already expended energy and has taken risks to secure and hold that resource. The resource holder also "knows" the true value of that resource. The competitor is "guessing" that the resource has value and does not know the magnitude of that value.

Based on the above, individual A should give up and retreat when:

$$V_A/K_A < V_B/K_B$$

Where V is the value of the resource to competitors A and B, and K is the rate at which each individual accrues costs during the contest.

Good fighters will accrue costs at a slower rate than poor fighters. Thus, when **V is the same for both competitors**, **K will determine the winner. And when K is equal, V will determine the winner.**

Objectives

The objective of this study is to determine the factors that affect outcome of agonistic interactions in crayfish. Crayfish are freshwater crustaceans that inhabit burrows that they dig inside the banks of streams. The burrows are important resources for crayfish because they offer them protection from predators. Therefore, shelters are a valuable resource for crayfish. We will use the presence/absence of a shelter (clay flower pot) to vary V. Studies of crustaceans and other animals indicate that size is an accurate indicator of fighting ability (K), so, we will hold size constant (and thus K).

Specifically, we will test the following hypotheses:

H_0: Resource value does not affect the outcome of an agonistic interaction in crayfish
H_A: Resource value affects the outcome of an agonistic interaction in crayfish

We predict that crayfish that are defending shelters should persist and win the contest because the resource is more valuable to the resource holder.

Methods

Crayfish have been isolated for at least one week and have been maintained in filtered water and fed algal disks daily. The crayfish have been separated into 2 groups. The first group consists of resource holders (RH) defending a resource (i.e., shelter). These have been kept individually in plastic tanks. The second group will be the competitors (C) that, hopefully, will compete with the RH crayfish for the shelter. These crayfish (C) have been kept in communal tanks.

You will mark each crayfish with an identifying number by drying the carapace with a paper towel and painting a section of it with “white-out.” When the “white-out” has dried, write a unique number write on the painted area with a “sharpie.”

Work in groups of two or three. Choose an RH crayfish and measure it body size. Move its tank to a position in the room where you will be conducting your observations, ideally not neighboring another crayfish tank. Then select a C crayfish that is no more than 10% difference in size. If possible, choose one that is the same sex as the resident. To determine size, measure carapace (Fig. 1A) length of each crayfish using calipers or a plastic ruler. Sex is determined by looking at the swimmerets. The fist two swimmerets are hardened in males and function as sperm transfer organs (Fig. 1B). On the front board write down the numbers of the pair of crayfish that you will be matching to ensure that this is a unique match that no other students will repeat. Place the C crayfish into the RH crayfish’s tank so that the crayfish are facing each other. Record their behaviors over 15 minutes using the data sheet provided (Appendix 1). One student should be the official timekeeper, another the official observer, who provides commentary to the official recorder. After the trial is finished, place the intruder back into its original tank. Be sure also to record general observations on the behaviors that the crayfish exhibit during the contest.

Repeat this with a unique pair of crayfish (see data on front board indicating which crayfish have already been paired). If you need to re-use an intruder, wait 15 minutes to allow it to recover from the first trial.

Data Analysis

Dominance Index

Each of the behaviors has been assigned a value that reflects relative aggressiveness (Appendix 1). Values range from +2 (aggressive behaviors) to –2 (submissive behaviors). You will use this to calculate a Dominance Index (DI), using the following formula:

$$DI = \sum S / \sum N$$

where S is the number of occurrences of each behavior multiplied by its aggressiveness value and $\sum N$ is the total of all behaviors.

The crayfish with the greater DI is the dominant individual (the other is considered the submissive individual) and is considered the winner of the contest. Remember, DI is a relative value. You can only use it to compare individuals that had competed. You cannot use it to compare individuals across trials.

Statistical Analysis

Even though we have determined the winner of a particular contest, we still need to know whether the finding is consistent across trials. Think sample size. Each contest is a sample point. By combining class data, we increase the power of detecting if a relationship exists between holding a resource and winning a fight.

But, how should we analyze the data? To answer that, we need to determine what type of data we collected. We determined winners vs. losers. So, we have discontinuous, or discrete, variables (e.g., we can have 5 winners but never 5.50 or 5.55 winners) collected as frequencies – how many times a particular *type* of crayfish won the contest. To test hypotheses about frequencies, we use either the **CHI-SQUARE TEST** or the **G-TEST**. Specifically, we need to conduct a **GOODNESS-OF-FIT TEST** (using either the Chi-square or the G-test) because (1) the data are arranged based on a single criterion (i.e., outcome of contest) and (2) because we are testing whether the outcomes (*observed* frequencies) match *expected* frequencies. These expected frequencies can be due to hypotheses extrinsic or intrinsic to our data.

Chi-square test

The Chi-square (X^2) test is straightforward. We want to determine how closely our data fits what is expected (or how far it departs from what is expected). Thus,

$$X^2 = \sum^{a} (O_i - E_i)^2 / E_i$$

where a is the number of classes, O_i is the observed frequency for *class i* and E_i is the expected frequency for *class i*.

Once you calculate X^2, you then need to determine the P –value to determine whether we must reject or accept H_0. Remember, the H_0 that is being tested is that our data fits the expected distribution of values (think about this!). To do this we need to know the number of degrees of freedom (*df*) we have. A (very) simple definition of "degrees of freedom" is that degrees of freedom are the number of classes that are free to vary. For X^2, *df* = a-1.

Once you have the X^2 value, to determine P, you lookup the X^2value for the appropriate *df*. This is known as the X^2 critical value. If the calculated X^2value is greater than the value in the table, the result is significant. See attached table of Chi-square probabilities.

G-TEST

The X^2 test is the traditional method taught to students to test hypotheses based on frequency data. The primary reason is that it makes intuitive sense. To determine whether collected data fit some expectation, we subtract the two. However, there is a computationally easier statistic (especially when analyzing complex data sets) that is more accurate. That's right, the G-test. **This is the test we want you to use.** So, why did we introduce the X^2 test? Primarily to give you an intuitive feel for the G-test. The G-test is interpreted the same as the X^2. We use it to determine whether our observed data are significantly different from what is expected. And the same table is used to determine the P value and *df* = a-1, when a = number of classes.

The formula for the G-test is:

$$G = 2 \sum^{a} f_i \ln (f_i / \hat{f}_i)$$

where a is the number of classes, f_i is the observed frequencies and $\hat{f}_i$ is the expected frequencies.

So, to analyze our data, we first must decide:

1. how to categorize crayfish *type* (i.e., class)
2. how many classes of crayfish do we have
3. what are the expected frequencies
4. how many degrees of freedom do we have.

So…..?

X^2 Critical Values

df	0.995	0.99	0.975	0.95	0.90	0.10	0.05	0.025	0.01	0.005
1	---	---	0.001	0.004	0.016	2.706	3.841	5.024	6.635	7.879
2	0.010	0.020	0.051	0.103	0.211	4.605	5.991	7.378	9.210	10.597
3	0.072	0.115	0.216	0.352	0.584	6.251	7.815	9.348	11.345	12.838
4	0.207	0.297	0.484	0.711	1.064	7.779	9.488	11.143	13.277	14.860
5	0.412	0.554	0.831	1.145	1.610	9.236	11.070	12.833	15.086	16.750
6	0.676	0.872	1.237	1.635	2.204	10.645	12.592	14.449	16.812	18.548
7	0.989	1.239	1.690	2.167	2.833	12.017	14.067	16.013	18.475	20.278
8	1.344	1.646	2.180	2.733	3.490	13.362	15.507	17.535	20.090	21.955
9	1.735	2.088	2.700	3.325	4.168	14.684	16.919	19.023	21.666	23.589
10	2.156	2.558	3.247	3.940	4.865	15.987	18.307	20.483	23.209	25.188
11	2.603	3.053	3.816	4.575	5.578	17.275	19.675	21.920	24.725	26.757
12	3.074	3.571	4.404	5.226	6.304	18.549	21.026	23.337	26.217	28.300
13	3.565	4.107	5.009	5.892	7.042	19.812	22.362	24.736	27.688	29.819
14	4.075	4.660	5.629	6.571	7.790	21.064	23.685	26.119	29.141	31.319
15	4.601	5.229	6.262	7.261	8.547	22.307	24.996	27.488	30.578	32.801

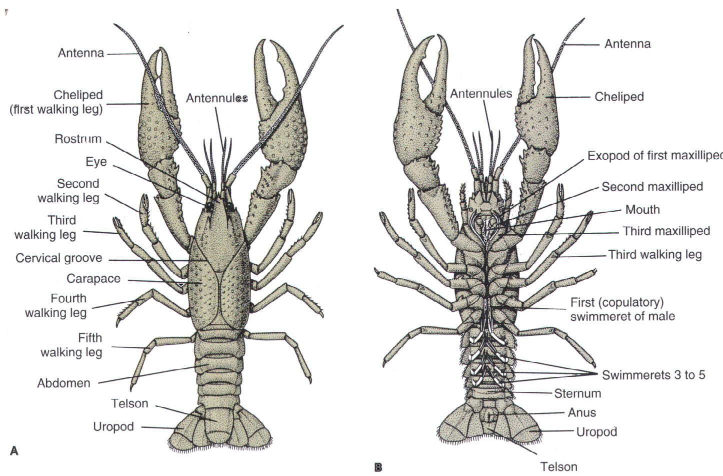

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Fig. 1 Crayfish anatomy showing (A) dorsal view and (B) ventral view. Note the modified swimmerets indicating that this crayfish is a male. Modified from http://crayfish.byu.edu/crayfish_biology.htm