Handedness during feeding in the green shore crab, *Hemigrapsus oregonensis*

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Abstract

Asymmetries offer important insights into the impacts of extrinsic environmental factors and intrinsic genetic factors in the development of organisms. In this study, *Hemigrapsus oregonensis* was tested for handedness, an asymmetrical behavioural preference to the left or right side, through a feeding experiment. The research question was: 'Will *Hemigrapsus oregonensis* exhibit handedness? If so, what patterns will the population of studied crabs show; for example, will handedness be a sexually dimorphic trait (trait that differs between males and females of the same species)?' Specimens were fasted for three days then fed pieces of *Mytilus trossulus* to observe the behaviour of the chelipeds (claws) during feeding. The number of times the left and right claws were used was tallied and analysed as a percentage of total observations. The results of this study show that 99% of *H. oregonensis* exhibit handedness ($p=0.4372$), with this being split equally between left-dominant and right-dominant individuals ($p=0.6226$). Both left-dominant and right-dominant crabs use their claws in approximately equal frequencies. However, males exhibit stronger handedness tendencies than females do, with males using their dominant 63% of the time, compared to 58% for females. Due to the fact that handedness may be a cause of fluctuating asymmetry (FA: a subtle, random departure from bilateral symmetry), and FA is a measure of developmental stability, this study was able to begin to investigate the possible causes of handedness. It was suggested that handedness may have developed at some point during the life cycle of the crab due to a possible extrinsic trigger. This adaptive response to external stimuli may have caused claws to become asymmetrical, which, in *H. oregonensis* is consistent with FA. Also, males may have stronger handedness tendencies than females do because an environmental factor may have caused them to begin using their claws differently than females.

Introduction

Over the past 40 years, patterns of asymmetry have led to an evaluation of the impact of both extrinsic environmental factors and intrinsic genetic factors on the development of an organism. Extrinsic environmental factors include, but are not limited to, temperature, salinity and pollution, while intrinsic genetic factors refer to, but are not limited to, intense selection and inbreeding (Chippindale and Palmer 1993) (Palmer 1997).

Crucial to the understanding of symmetries and asymmetries are some key terms:

1. Symmetry, also known as bilateral symmetry in some animals, is the 'zero' state in which no left-right preferences are present in an individual, in both appendage size and function (such as handedness) (Crawford 2006).
2. Asymmetry, which may be referred to as dimorphism or morphological differences. These terms refer to a distinction or difference in the size of the bodily structure of an organism. One important subset of asymmetries referred to in this study is fluctuating asymmetry (FA), which represents the "minor, random deviations from symmetry that occur during the development of otherwise symmetric traits" (Sneddon and Swaddle 1999). It is a form of subtle asymmetries, which are asymmetries not visible to the naked eye (Palmer 2002). An example is the claw dimensions of the purple shore crab (Chippindale and Palmer 1993).

Handedness is caused by a behavioural preference towards the sinistral or dextral side in bilaterally symmetric species, including humans (Smith and Palmer 1994). It may be viewed as a type of asymmetry in function, rather than in form. According to Palmer (2004), left-right differences originate from a fundamental switch that causes the mediolateral (side to side) axis on one side of the body to differ from the opposite side. "Left and right...are separate mediolateral axes that originate at and extend in

opposite directions away from the midplane [of the body]" (Palmer 2004). In humans, this switch is manifested in a correlation between the infant's preferential head orientation during the neonatal period and hand use after birth. (Butterworth and Hopkins 1993). Butterworth and Hopkins (1993) also note however, that handedness may be an evolutionary trait resulting from the infant having to turn its head to pass through the birth canal or cradling infants on the left arm. However, *Hemigrapsus oregonensis* and *Homo sapiens* are largely different animals, and one must be careful to not draw too many connections between the handedness exhibited in brachyuran crabs and in primates. The key point is that handedness will be exhibited in some bilaterally symmetric species due to a switch of the mediolateral axes.

Smith and Palmer (1994) have found recent value in studying handedness, because "...behavioural biases (handedness) towards one side, could...promote the evolution of claw dimorphism". In some species, claw dimorphism takes the form of FA as it is random, subtle, and not visible to the naked eye. Therefore, by examining handedness, one may investigate FA and its causes. Because FA is a measure of developmental stability one may begin to examine how extrinsic and intrinsic factors play a role in determining handedness, which leads, to a degree, to FA (Chippindale and Palmer 1993). Thus, by studying handedness, it may be possible to investigate the developmental and evolutionary history of a species.

Hemigrapsus nudus, the purple shore crab, is a brachyuran (true crab) that exhibits both handedness and FA (Crawford 2006) (Chippindale and Palmer 1993). In the present study, a close relative of *H. nudus*, *Hemigrapsus oregonensis*, the green shore crab, was examined. *H. oregonensis* is easily distinguished from *H. nudus* by the presence of hairs on its legs, the lack of purple spots on its chelipeds (first pair of legs with claws; pincers), as well as its smaller, squared, olive-coloured carapace (shell) (Appendix 1) (Lester B. Pearson UWC of the Pacific 2005). The carapace has a width of up to 35

mm for males and 29 mm for females (Lester B. Pearson UWC of the Pacific 2005). *H. oregonensis* is commonly found together with *H. nudus* in protected, slow current areas in the low to high intertidal zone of bays and estuaries from Resurrection Bay in Alaska to Bahia de Todos Santos in California (Lester B. Pearson UWC of the Pacific 2005). Both *H. nudus* and *H. oregonensis* feed mainly at night with diets consisting of sea lettuce, diatoms, algae, and meat when available (Lester B. Pearson UWC of the Pacific 2005) (National Oceanic and Atmospheric Administration 1997).

Due to the fact that *H. nudus* is a bilaterally symmetric invertebrate that exhibits handedness, the purpose of this study was to examine the research questions: "Will *Hemigrapsus oregonensis* exhibit handedness? If so, what patterns will the population of studied crabs show; for example, will handedness be a sexually dimorphic trait (trait that differs between males and females of the same species)?" (Crawford 2006). It was hypothesised that 100% of *H. oregonensis* would exhibit handedness, and within the population the proportion of left-dominant and right-dominant individuals would be 50:50, as there was no literature to suggest that another trend would be present in this population and species. Also, because FA, and therefore handedness, is a population level characteristic, it was further hypothesised that there would be no gender differences in the trait (Crawford 2006).

In order to test these hypotheses, a feeding experiment was designed in which crabs were fasted for three days. Crabs were individually offered 4 cm x 2 cm x 0.5 cm pieces of *Mytilus trossulus* (Pacific Blue Mussel) meat and observed to determine the number of times their right and left claws were used to eat over a 7 minute period.

Methodology

Thirty-seven male and 32 female *Hemigrapsus oregonensis* were collected from a rocky shore below Lester B. Pearson College (123° 33' W, 48° 20' N) on Pedder Bay, British Columbia, Canada. Only

crabs with carapace width greater than 10 mm were collected. Males and females were separated into two clear plastic Rubbermaid™ containers, each 40 cm x 27.5 cm x 14 cm, along with 10 to 15 *M. trossulus* of approximately 5 cm to 7 cm in length. Rocks of approximately 10 cm in width containing no algal or other growth on the surface and handfuls of rockweed (*Fucus gardneri*) were also collected in a separate pail. The specimens and materials were then transferred to one of the biology laboratories at Pearson College.

Crabs were divided into single gender groups of 7 to 10 and placed in 8 clear plastic containers measuring 13 cm x 13 cm x 6 cm. On opposite faces, openings measuring 5.5 cm x 3.5 cm were cut and covered with window screen. A small handful of rinsed rockweed was placed with the crabs, and the containers were suspended in a seawater table supplied with a constant flow of fresh seawater (mean temperature 10.1°C; mean salinity 32.0 parts per thousand (ppt)). The containers were placed so that a small portion near the top of the container was filled with air, enabling the amphibious crab to climb on the rockweed and thus come clear of the water. Holes cut into the sides functioned as vents, allowing both the seawater in the lower portion and the air in the top portion of the container to circulate. The lids of each container were marked for identification, and the natural photoperiod was respected. Mussels were placed in another container in the bottom of the seawater tank. The rocks were thoroughly washed, rinsed and inspected to ensure no algal or other growth was present.

The crabs were fed approximately every 2 days with *M. trossulus* meat, a natural food source. Pieces of meat were placed in each container allowing the crabs to scavenge. Prior to the fasting period and upon the following feeding period, old excess meat was removed from the containers. Containers were cleaned in hot water with mild dish soap and chlorine bleach, and rinsed thoroughly every 3 days. Rockweed was replaced several times throughout the research phase.

Three days prior to testing, 4 to 5 crabs were placed in a 40 cm x 27.5 cm x 14 cm clear plastic Rubbermaid™ container filled approximately 75% full with fresh seawater (mean temperature 10.1°C; mean salinity 32.0 ppt). Over 3 days, the water warmed to a mean room temperature of 19.5°C at a mean salinity of 32.2 ppt, which is a preferable temperature for crabs acclimatized to 10°C water (McGaw 2003). Rocks previously collected and cleaned were placed in the aquarium to simulate a natural environment, and the natural photoperiod was respected. An air stone connected to an air pump was also placed in the aquarium. No food was given to the crabs after placement in these fasting containers until they were individually tested. This gave the crabs an opportunity to become hungry enough to wish to eat during the testing phase of the experiment. The 3 day fasting period was predetermined as an appropriate length in a trial run of the experiment conducted prior to the main experiment. Also, 24 hours before a set of crabs was to be tested, another identical sized container was filled approximately 75% full with seawater. An air stone was placed in this container, but no rocks. As this was to be the testing aquarium, it was covered with black garbage bags on all sides and on the bottom to create a darker environment, because it has been shown that crabs tend to be more active at night (Symons 1964). Garbage bags also helped to block the crab from visualizing the observer. Temperature and salinity of the testing container was monitored to ensure it was consistent with the fasting container.

On the day of testing for a batch of crabs, the fasting aquarium and the testing tank were moved to a lab bench. [1] Four centimetre long pieces of mussel meat were placed in one end of the aquarium. A single crab was taken from its aquarium and placed in the testing tank on the opposite end, facing the food, approximately 25 cm from it. A timer was started, and for a period of 5 minutes the crab was

[1] A maximum of 5 crabs were studied each night for a period of approximately 2.5 weeks until a total of 58 crabs had been studied. In this way, three aquariums for fasting were set up, each with 4 to 5 crabs to be studied on a forthcoming evening.

observed as it moved around the tank in search of food. If it did not locate and begin eating the food within the 5 minute period, the crab was removed from the tank and placed in a completed container, and 'VOID' was marked on the data sheet. If the crab did reach the food and begin eating within the 5 minute period, the timer was stopped and a new timer set for 7 minutes was started while the crab ate uninterrupted. The number of times the crab used its left claw and its right claw to eat was recorded. Usage for a claw was defined as:

1. Using the claw to place a piece of food in its mouth
2. Using the claw to drag the food to a new location
3. Ripping, shredding, tearing, or in any other way manipulating the food
4. Picking up residual food particles in the water and eating them

After 7 minutes the crab was removed from the tank, measured across the carapace, and placed in the completed container. A new piece of meat was placed in the testing container. This was repeated for all crabs in a batch. Once all crabs in a batch had been completed, they were placed back in their storage containers in the seawater table with rockweed and generous amounts of food.

During analysis of data, data sheets were organised so that the counted number of times each claw was used in feeding was a percentage of total observations (Appendix 2). This allowed crabs to be categorised as right-dominant, left-dominant or symmetric, based on the proportion of times the left or right claw was used out of the total number of observations. Crabs that used both left and right claws equally were categorised as symmetric. Crabs that lost interest in eating after approximately two minutes were excluded from analysis because they yielded too few observations to determine their handedness characteristics with confidence.

Using Statistix v8.0 (Analytical Software, Tallahassee, FL), a descriptive statistical breakdown was performed to compare the proportion of times the left claw was used versus the right claw for both left-dominant, right-dominant, and symmetric animals. Microsoft Excel 2007 (Microsoft Corporation, Redmond, WA) was used to create pie charts showing the actual distribution of the recorded data. A Multinomial Test was used to test that the proportion of handed and symmetric crabs was 100:0 percent respectively. This hypothesis was rejected, so it was modified to 99:1 percent handed versus symmetric, which was accepted. Then, a Multinomial Test was used again to test that the distribution of handed crabs between left-dominant, right-dominant and symmetric was 50:50:0 percent, respectively. The Multinomial Test rejected this distribution, as there was one symmetric crab present in the data set. However, the distribution of left-right individuals was modified to 49.5:49.5:1 percent and was accepted. Then, for each crab the strength of its left-right tendency (a gradient measure of how left-dominant or right-dominant an individual crab is) was determined. Finally a General Analysis of Variance (GANOVA) was used to determine if the strength of the left-right tendencies differed by the handedness category (left-dominant, right-dominant, or symmetric), or gender (male or female).

Results

Out of a total of 72 crabs collected, 58 were tested for handedness. Unfortunately, 14 crabs died in captivity, which is a limitation that future studies might find worthwhile to consider. Of 58 crabs studied, 51 cooperated to produce some form of result. Forty-seven crabs produced a result that could be used in analysis (Appendix 2) (4 crabs were excluded, as they lost interest in eating after 2 minutes, thus not producing enough of a result to determine their handedness with confidence). The average number of times the left claw was used in feeding was 29.65, while the average number of times the right claw was used was 29.40, out of a total of an average of total observations for each crab of 60.15. It took the crabs an average of 53.22 seconds to reach the food and to begin eating.

Table 1

Table 1: Percent of crabs exhibiting symmetry, left-dominance or right-dominance based on the criterion of a ratio between the percent of times one claw was used in feeding compared to the percent of times the other claw was used.

Criterion	**Symmetric**	**Left-dominant**	**Right-dominant**
50:50	2.128	53.19	44.68
55:45	23.40	38.30	38.30
60:40	46.81	29.79	23.40
75:25	93.62	4.255	2.128
100:0	100.0	0.000	0.000

Table 2

Table 2: Number of crabs exhibiting symmetry, left-dominance or right-dominance based on the criterion of a ratio between the percent of times one claw was used in feeding compared to the percent of times the other claw was used.

Criterion	**Symmetric**	**Left-dominant**	**Right-dominant**
50:50	1	25	21
55:45	11	18	18
60:40	22	14	11
75:25	44	2	1
100:0	47	0	0

Due to the fact that there is no definition in literature sources stating what percentage of claw use in feeding defines handedness, the present study considered what proportion of the studied crabs would exhibit handedness based on *various* criteria (Table 1) and (Table 2). For example, with a defined criterion that handedness equals more than 50% usage for one claw, 2.128% (1) of crabs are symmetric and 97.87% (46) are handed. The present study used a criterion of 50:50 to thoroughly test handedness, although accurate studies could have been conducted with the use of other criteria. Using 50:50 as a criterion, the Multinomial Test rejected the hypothesis which stated that '100% of crabs were handed (p=0.0000)'. [2] This was due to the fact that one of 47 crabs from the sample population was found to exhibit symmetrical characteristics. Therefore, it was determined that the data must fit some other pattern, so when the hypothesized proportion was modified to '99% of *H. oregonensis* exhibit handedness', the hypothesis was accepted (p=0.4372). That is, the data fit a distribution of 99:1 percent handed versus symmetric.[3] Then, in accordance with this result, a pie chart was created to demonstrate the actual distribution of the data (Figure 1).

[2] N.B.: The Multinomial test differs from many other statistical tests in the fact that a *low* p-value is evidence to reject the hypothesis.
[3] N.B.: The one symmetric crab cannot be excluded from the results solely for the fact that it demonstrates symmetry. In fact, it contributes just as validly to final results as the rest of the crabs do.

Figure 1

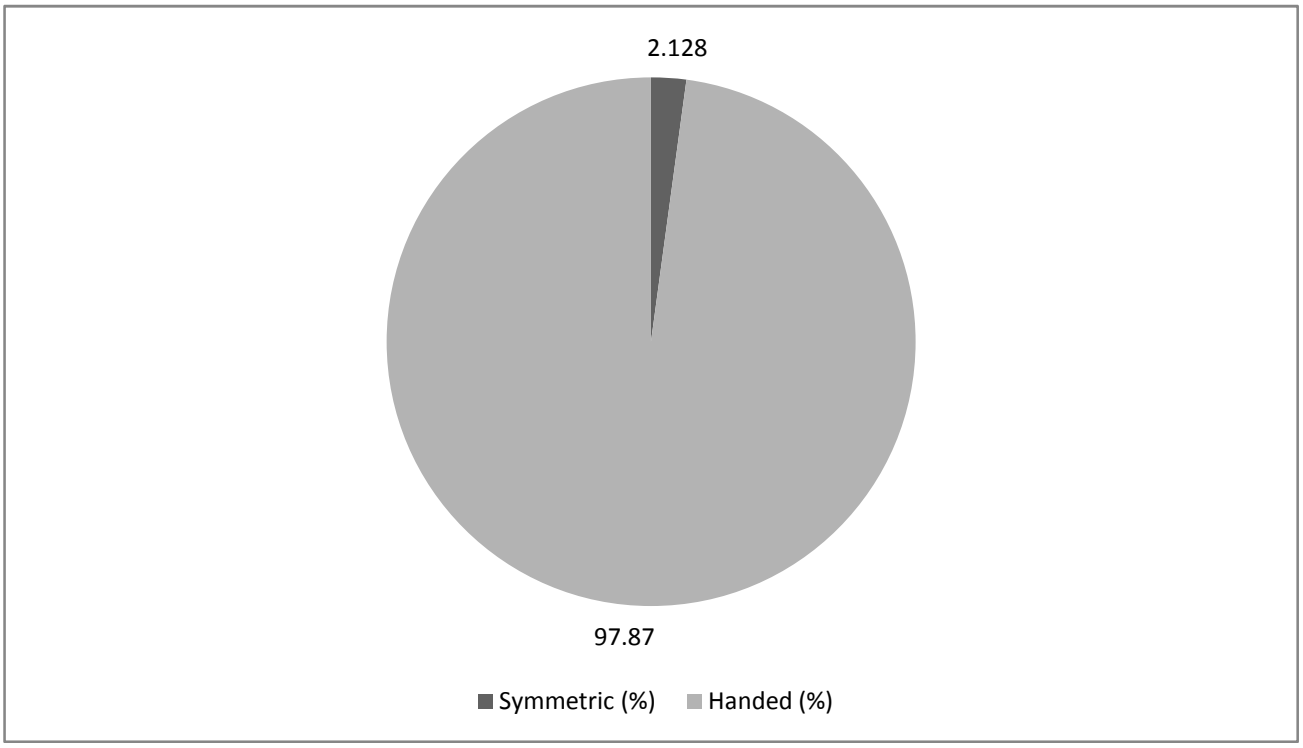

Figure 1: Percentage of crabs exhibiting handedness based on a criterion of handedness being more than 50% usage of one claw

A Multinomial Test was also used to examine a second hypothesis: the population of crabs is split equally between left-dominant and right-dominant crabs. With a hypothesised proportion of 0.50 for left-dominant crabs, and 0.50 for right-dominant, the hypothesis was rejected (p=0.0000). This is again due to one symmetric crab present in the results, which means the distribution cannot be exactly 50:50:0 percent. However, the hypothesised proportion was revised to 49.5:49.5:1 percent left-dominant, right-dominant, and symmetric respectively, and was accepted (p=0.6226). Hence, there is evidence here to accept a revised hypothesis: the sample population of crabs is, in fact, split equally between left-dominant and right-dominant individuals, with 1% of the overall sample being symmetric. A pie chart was then created to illustrate the actual trend in the recorded data (Figure 2).

Figure 2

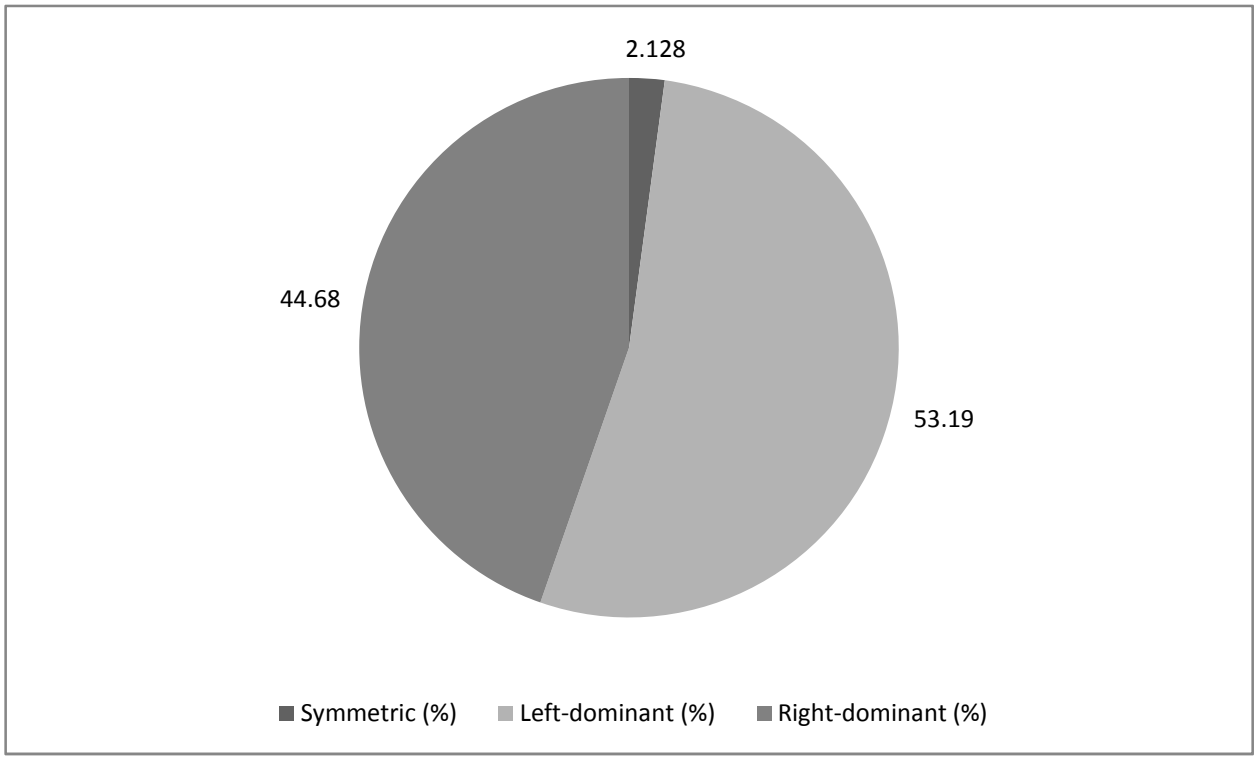

Figure 2: Percentage of crabs exhibiting left-dominant, right-dominant or symmetric traits based on handedness being more than 50% usage of one claw

A descriptive statistical breakdown of the population of studied crabs showed that both left-dominant (LPC=0.6158) and right-dominant (RPC=0.6194) crabs used their dominant claw in approximately equal frequencies, where LPC is the mean proportion of times that the left claw was used by left-handed crabs, and RPC is the mean proportion of times that the right claw was used by right-handed crabs (Appendix 3).

A GANOVA was used to analyse strength, which is essentially a gradient measure of how left-dominant or how right-dominant an individual is. Both gender and category (i.e. left-dominant, right-dominant, or symmetric) were tested to determine if either of these significantly affected the strength of the handedness. Category (p=0.6049) did not significantly affect strength, but gender (p=0.0709) suggested a tendency towards significance. Gender was then tested apart from category and was determined to be significant (p=0.0467). A Bonferroni All-Pairwise Comparisons Test was then used to examine the significance in gender, and it found that males (mean=0.1388) have much stronger tendencies towards their handedness than females do (mean=0.0853). In practical terms, this means that males used their dominant claws 63.88% of the time, whereas females used their dominant claws 58.53% of the time.

Discussion

The purpose of this study was to investigate whether *H. oregonensis* would exhibit handedness, and to investigate the distribution and possible determinants of handedness in the population. It was originally hypothesised that 100% of *H. oregonensis* would exhibit handedness. However, this was later revised to 99%, and statistically supported. The distribution was originally hypothesised to be 50% right-dominant and 50% left-dominant, but again, this was revised to 49.5% and 49.5% with 1% being symmetric, and was statistically supported. The key point however, is that the number of left-handed and right-handed individuals was the same.

Crawford (2006) conducted a similar study on *Hemigrapsus nudus*, and found, overall, that the population of crabs was right-handed. Crawford (2006) also studied whether handedness in *H. nudus* was a sexually dimorphic trait. It was found that both males and females used their right claw more than their left claw, although females used their right claw on average more than the males used their right claw (Crawford 2006).

The data from the present study shows that the H. oregonensis population studied is evenly split in its left-right usage, although males have stronger tendencies than females do. The exact reasons for the differences are not entirely clear, but it is a fact that the results of this study do not agree with Crawford's. Due to the fact that Crawford's population is a different species and is located approximately 125 km north of the studied population, environmental and genetic factors may have played a role in creating the differences.

As stated previously, Smith and Palmer (1994) found that handedness may be a component of the formation of claw dimorphism, which, in *H. oregonensis*, takes the form of fluctuating asymmetry. Chippindale and Palmer (1993) found that fluctuating asymmetry is an expression of developmental instability caused by stressors such as temperature, food deprivation, pesticides, pollution, intense selection, or inbreeding depression. Therefore, differences in environment (although the macro-environment is largely the same, the micro-environment may differ in items such as pollution, pesticides and food deprivation) and gene pools may explain different trends between this study's and Crawford's (2006) data. In fact, in a study by Palmer and Strobeck (1986) it was determined that deviations from symmetry (whether form or function) *in a particular direction* of an otherwise symmetrical trait have little or no heritable basis, while the likelihood that an individual departs from bilateral symmetry and the degree to which it departs may have a heritable basis. This suggests that the number of left-handed

and right-handed individuals is largely due to environmental factors such as those listed above, while the strength of the tendencies is due to genetic factors.

Thus, in the population of crabs investigated in the present study, an environmental factor may have caused the crabs to preferentially begin using either their left or right claw. This preferential usage may represent a mediolateral axis switch (Palmer 2004). Thereafter, these short-term adaptive responses could have promoted the evolution of claw dimorphism (Smith and Palmer 1994). Hence, environmental factors caused the crabs to become either left-dominant or right-dominant (in possibly both physical asymmetries and handedness). At one point, some degree of heritability may have caused handedness to translate from an environmentally induced behavioural preference to a subtle, morphological difference consistent with fluctuating asymmetry. Smith and Palmer (1994) indeed state that “asymmetrical claws might begin to evolve from symmetrical progenitors”.

The results from the present study also suggest why males have a stronger preference for their dominant side than the females have for their dominant side. For example, the males may have begun to use their dominant claw more frequently in competition fights for mating, whereas the females did not experience this particular environmental influence. This is consistent with a study by Smith and Palmer (1994) which concluded that by immobilising one claw, the other became asymmetrical. Hence, males may have developed stronger tendencies in their dominant claw usage due to this, and combined with heritability, it became an observable trend in the population (Smith and Palmer 1994) (Palmer and Strobeck 1986).

The findings of this study could have been made more significant in several ways, which would also increase the extent to which the population could be measured. First, a small sample size was used. This created possible limitations in the accuracy of the data, and similar future studies should use a larger

sample size, perhaps between 150 to 200 animals. Second, a large study period was used, which may have led to behavioural exhaustion in the specimens. In future studies, crabs should be kept in captivity for as short a time as possible. Additionally, future studies should focus on sampling animals from different locations.

The room for potential improvement gives rise to suggestions for further future studies. Firstly, handedness should be measured in conjunction with cheliped size, to see if handedness has a morphological effect on the cheliped size. Chippindale and Palmer (1993) present a novel technique for measuring chelipedal fluctuating asymmetry, which would confirm Smith and Palmer's (1994) hypothesis as to whether or not handedness is a cause of fluctuating asymmetry. This would then lead to more research being conducted in the field of the origins of fluctuating asymmetry, and handedness in particular. As well, in accordance with a study by Palmer (1996), the period of development during which asymmetries develop could be studied, as Palmer (1996) suggested that early asymmetries imply genetic factors as the cause, while later-developing asymmetries suggest environmental factors as the cause. Secondly, further studies on handedness should be expanded to encompass more behavioural outcome measurements, such as defence or breeding. Finally, future studies could examine handedness in other brachyuran crabs, such as *Pugettia producta* or *Cancer magister* to examine the extent to which conspicuous asymmetries have an effect on behavioural hand biases.

The results of this study show that *Hemigrapsus oregonensis* does exhibit handedness on the individual level, which may be due to the switch of a mediolateral axis due to preferential usage. On the population level, this translates into an equal number of left-dominant and right-dominant individuals, with a small portion of the population being symmetric. Trends within this population and between other populations are unique, perhaps due to specific determinant environmental and/or genetic factors.

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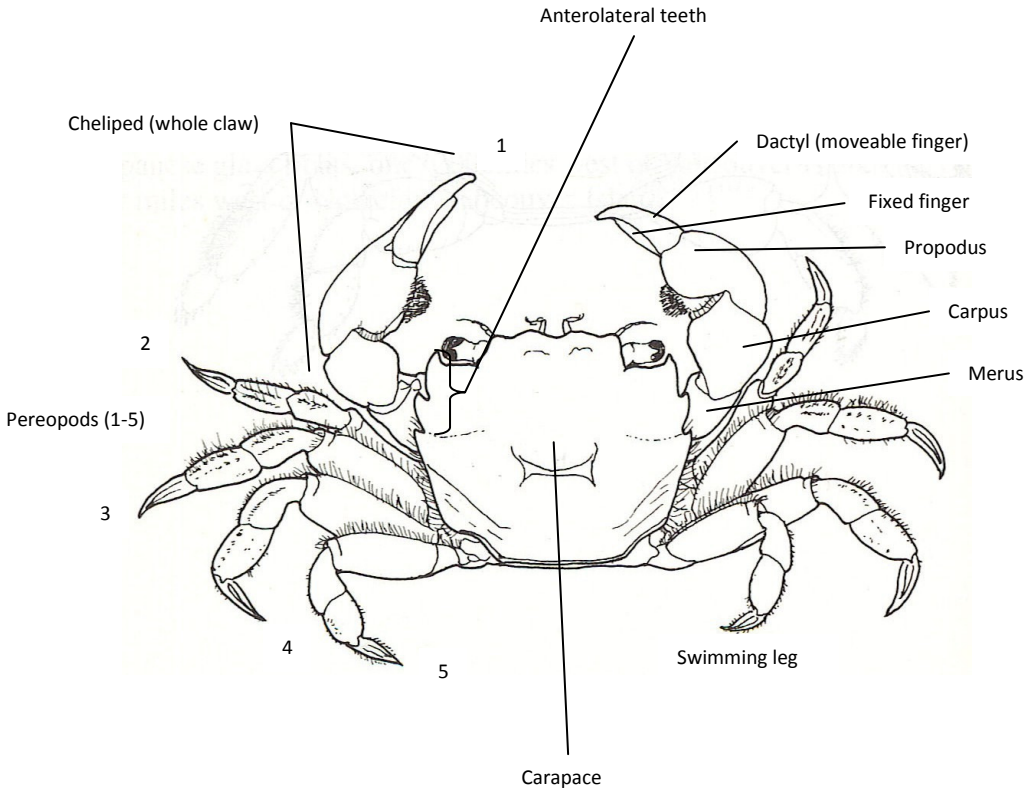
Appendix 1



Appendix 1: Important anatomical features of *Hemigrapsus oregonensis*

Hart, Josephine F L. *Crabs and their relatives of British Columbia*. Victoria: British Columbia Provincial Museum, 1982.

Appendix 2

Data collected during the study

Where:

- L = number of observations for left claw
- LPC = number of observations for left claw as a percentage of total observations
- R = number of observations for right claw
- RPC = number of observations for right claw as a percentage of total observations
- . = missing data due to voided crab

Crab #	Batch	Sex	Size (mm)	Time to reach food (s)	L	LPC	R	RPC	OBSERVATIONS
1	PBM1-A	M	14	24	9	0.290	22	0.710	31
2	PBM1-A	M	11	35	20	0.571	15	0.429	35
3	PBM1-A	M	15	60	6	0.500	6	0.500	12
4	PBM1-A	M	12	30	4	0.133	26	0.867	30
5	PBM1-A	M	12	26	24	0.522	22	0.478	46
6	PBM1-B	M	13.5	48	24	0.282	61	0.718	85
7	PBM1-B	M	13	17	18	0.529	16	0.471	34
8	PBM1-B	M	13	77	55	0.821	12	0.179	67
9	PBM1-B	M	13	.	.	.	.	.	.
10	PBM1-B	M	12	19	45	0.413	64	0.587	109
11	PBM2-A	M	11	16	9	0.500	9	0.500	18
12	PBM2-A	M	13	61	48	0.658	25	0.342	73
13	PBM2-A	M	11	107	20	0.714	8	0.286	28
14	PBM2-A	M	.	44	25	0.439	32	0.561	57
15	PBM2-B	M	12	35	21	0.438	27	0.563	48
16	PBM2-B	M	13	11	6	0.429	8	0.571	14
17	PBM2-B	M	12	79	48	0.632	28	0.368	76
18	PBM3-A	M	14	196	4	0.400	6	0.600	10
19	PBM3-A	M	13	32	25	0.481	27	0.519	52
20	PBM3-A	M	16	42	31	0.738	11	0.262	42
21	PBM3-A	M	.	.	.	.	.	.	.
22	PBM3-A	M	16	87	37	0.649	20	0.351	57
23	PBM3-B	M	13	56	19	0.528	17	0.472	36
24	PBM3-B	M	13	66	60	0.632	35	0.368	95
25	PBM3-B	M	12	26	18	0.367	31	0.633	49
26	PBM3-B	M	14	56	37	0.552	30	0.448	67
27	PBM3-B	M	11	138	34	0.895	4	0.105	38

28	PBM4-Z	M	18	50	20	0.323	42	0.677	62
29	PBM4-Z	M	.	.	.	.	.	.	.
30	PBM4-Z	M	18	58	22	0.400	33	0.600	55
31	PBM4-Z	M	15	20	32	0.533	28	0.467	60
32	PBM4-Z	M	15	99	17	0.630	10	0.370	27
33	PBF2-A	F	18	57	34	0.607	22	0.393	56
34	PBF2-A	F	15	20	44	0.611	28	0.389	72
35	PBF2-A	F	13	47	72	0.673	35	0.327	107
36	PBF2-A	F	13	50	44	0.620	27	0.380	71
37	PBF3-A	F	14	42	15	0.375	25	0.625	40
38	PBF3-A	F	16	29	29	0.558	23	0.442	52
39	PBF3-A	F	14	37	8	0.381	13	0.619	21
40	PBF3-A	F	14	57	38	0.418	53	0.582	91
41	PBF3-A	F	13	83	44	0.557	35	0.443	79
42	PBF2-B	F	13	53	56	0.434	73	0.566	129
43	PBF2-B	F	14	28	23	0.397	35	0.603	58
44	PBF2-B	F	11	17	37	0.507	36	0.493	73
45	PBF2-B	F	10	209	68	0.511	65	0.489	133
46	PBF3-B	F	.	.	.	.	.	.	.
47	PBF3-B	F	.	.	.	.	.	.	.
48	PBF3-B	F	.	.	.	.	.	.	.
49	PBF3-B	F	11	16	18	0.529	16	0.471	34
50	PBF1-Z	F	19	12	5	0.385	8	0.615	13
51	PBF1-Z	F	15	10	16	0.254	47	0.746	63
52	PBF1-Z	F	15	51	21	0.618	13	0.382	34
53	PBF1-Z	F	15	15	6	0.333	12	0.667	18
54	PBF4-Z	F	12	100	17	0.472	19	0.528	36
55	PBF4-Z	F	11		52	0.441	66	0.559	118
56	PBF4-Z	F	10	51	45	0.500	45	0.500	90
57	PBF4-Z	F	11	133	39	0.494	40	0.506	79
58	PBF4-Z	F	11	.	.	.	.	.	.

Appendix 3

Descriptive statistical breakdown of the population of studied crabs showing the average proportion of times the crabs used their dominant claw compared to their non-dominant claw.

Statistix 8.0 Data sheet-05Jul08, 7/5/2008, 9:40:34 AM

Descriptive Statistics for Category = Symmetric

Variable	N	Mean	SD	Minimum	Maximum
L_PC	1	0.5000	M	0.5000	0.5000
R_PC	1	0.5000	M	0.5000	0.5000
Observ	1	90.000	M	90.000	90.000
Strength	1	0.0000	M	0.0000	0.0000

Descriptive Statistics for Category = Left dominant

Variable	N	Mean	SD	Minimum	Maximum
L_PC	25	0.6158	0.0970	0.5070	0.8950
R_PC	25	0.3842	0.0970	0.1050	0.4930
Observ	25	59.680	26.231	27.000	133.00
Strength	25	0.1158	0.0970	7.000E-03	0.3950

Descriptive Statistics for Category = Right dominant

Variable	N	Mean	SD	Minimum	Maximum
L_PC	21	0.3807	0.0869	0.1330	0.4940
R_PC	21	0.6194	0.0869	0.5060	0.8670
Observ	21	59.286	32.373	14.000	129.00
Strength	21	0.1193	0.0869	6.000E-03	0.3670