



Female Choice

4. Female Choice

Introduction

We can use the term *choice* as the differential response to a given stimulus (provided by one mate to the other). The speed of a process that requires feedback stimuli for both genders, such as spawning can be used as a sign of choice. The great variation in spawning duration (**Table 5** in **Chapter 2**) reveals mate choice plays an important role in salmonines reproduction.

Male choice

Male mate choice is common in animals where females differ in fecundity, mainly in relation to body size (Andersson, 1994 p.186). In salmonines fecundity is related to female size (Gaudemar, 1998). Furthermore, bigger females produce bigger eggs and dig deeper nests (Crisp & Carling, 1989). However, behavioural stimuli are equally or more important than size. Several works have demonstrated that males chose to court those females more actively involved in nest activities independently of their size (Schroder, 1982 for chum salmon; Foote, 1988 for sockeye salmon; Beall & Gaudemar, 1999 for Atlantic salmon).

In addition, as demonstrated by Foote (1988) male choice is dependent on male size, small males are less discriminating than larger individuals. This idea relies in the fact that large and powerful males can potentially mate with all available females whereas weaker individuals are limited to the lowest quality ones.

Female choice

Taking into account the physiological limitations females have (ovulation, eggs' ripening) the speed at which they build their nest and release their eggs is an expression of their choice.

Differential behavioural response to male traits can be based on morphological and behavioral characters.

The effect of male size has been studied in several Salmoninae species. Females courted by relatively small males delay their spawning activities (references in **Chapter 1**). Schroder (1981) further demonstrated differential spawning velocity based on morphological traits in chum salmon. In this species, dominant males present distinctive vertical colour bars on their sides, whereas subdominant ones have a single horizontal stripe. Females courted by males with stripes slow down nest construction while those courted by males with bars took less time to construct their nests (Schroder, 1981 **Figures 1 & 2**).



Figures 1 & 2. chum salmon males with different colouration patterns showing their dominance ranking. Males are able to switch from one to the other in a matter of seconds (Groot pers. communication).

The effect of male courtship activities in female choice has not been studied in detail. The difficulty of this task relies in the complexity of studying behaviour after controlling for size and morphology. Nevertheless, females have been observed to select mates according to the intensity of their courtship (Gaudemar, et al 2000b for Atlantic salmon, discussed below).

The above explanations show what traits females choose, **Chapter 3** explains how (through differential stimuli-response) the choosing process occurs, however to answer why particular traits are chosen it is necessary to introduce sexual selection mechanisms.

Sexual selection mechanisms

Fisher's (1930) 'runaway selection' and Zahavi's (1975) 'handicap principle' have been used as alternative mechanisms of sexual selection through female choice.

In the runaway selection model females choose males based on aesthetic traits that carry no prior relation with genetic quality. The model assumes heritable variation for male traits and female preferences. Once for arbitrary reasons (any trait can start a runaway selection process if such trait confers any slight advantage to the offspring), females start to show preference for a particular male trait an evolutionary positive-feedback loop becomes established. Both male and female offspring inherit trait and preference (even though only males express the trait and only females express the preference). As long as there is a slight disagreement between the two components (e.g. salmon females prefer males with a trait larger than average; see Dawkins, 1986 p.199-209) the process will runaway *with ever-increased speed and the limits would only the ones imposed by natural selection* (Fisher, 1930 p. 152).

In the handicap principle model female choice is based on genetic quality indicators. Zahavi (1975) reasoned that an extravagant male trait implies a cost to the carrier and thus can be used as a genetic quality indicator simply because less fit males cannot incur such a cost (Grafen, 1990; Zahavi & Zahavi, 1997). By choosing males with the most developed traits *females can be sure that they have selected from among the best genotypes of the male population* (Zahavi, 1975).

This chapter investigates how the mentioned mechanisms of sexual selection through female choice may affect the salmonines reproduction. Firstly, the importance of female choice versus male-male competition is highlighted by performing an experiment in which female choice is temporarily removed in a wild population of sockeye salmon. Secondly, the male's quivering behaviour and its role in female choice are studied by relating the number of male quiverings with the velocity of female digging (choice). A formula involving both parameters is used to define (**I**) as the index of choice. Thirdly, observations are used to open a theoretical discussion about the importance of Fisherian and Zahavian models. A combination of both mechanisms is suggested to run female choice in the salmonines mating system. The rationale of some behavioural and morphological patterns is discussed accordingly. The possible significance of male aggressive displays is included.

Methods

Removing female choice

An experiment was conducted to observe what will happen if females lose the exercise of choice. That is, what will happen if females were willing to mate with any male approaching them. In order to do that, Mesalina (dummy two in **Chapter 3**) was employed.

Comparisons were made between five one-hour underwater tapes of different species (in which a nesting female was guarded by a dominant male and several subdominant ones) with two one-hour tapes of sockeye salmon in which Mesalina intermittently provided the necessary clues to spawn to any male approaching her (see **Chapter 3**).

In the first one-hour tape Mesalina was surrounded by five males. In the second one-hour tape as many as nine males were close to her. The sign for immediate mating (trembling) was performed intermittently every other minute (the trembling action was accomplished by using a rod with a fish lure attached to Mesalina's tail; see **Chapter 3**).

The number of male-male attacks on each of the types (choice versus no choice) was counted (**Table 1**).

Table 1. The effect of presence or absence of female choice in the number of male-male attacks.

species	female choice	number of male-male attacks
bull trout	yes	14
pink	yes	9
sockeye	yes	22
chum	yes	27
coho	yes	10
sockeye	no	0
sockeye	no	0

Male quiverings

Twenty one-hour underwater tapes of sockeye salmon spawning in the Cedar River, WA were used to study the effect of quiverings on female choice (**Table 2**). The frequency of quiverings and diggings was calculated in the time interval between first to last quiver or dig. Results were plotted to explore a possible correlation between both variables (**Figures 3 & 4**).

The following hypotheses were tested:

H₀1: The number of quivers performed by males has no effect in the velocity of female digging (choice).

H_a1: Females courted by males performing more quivers dig at faster rates.

The Index of choice

The quiverings-digging relation was further studied by defining (**I**) as the index of choice with the following formula:

$$I = (d/q)/T = d/qT$$

Where q is the number of quivers, d is the number of digs and T the courtship time (time, as a fraction of an hour, from first quiver or dig until last quiver or dig).

The equation was normalized between 0 and 1 using the range of the observed values by using the following conversion:

$$I_n = [(d/qT) - I_{\min}] / (I_{\max} - I_{\min})$$

Where **I_n** is the normalized Index of choice.

The same data from **Table 2** was used to calculate the (**I_n**) of twenty sockeye females (**Figure 5**). The observed (**I**) range was 4.51-0.31.

Results were then compared with the quivers per minute to visualize that even the quivering-digging relationship exists; choice is not only a function of the number of quivers (**Figure 5**).

Table 2. Spawning history of twenty different pairs of sockeye salmon species spawning at the Cedar River, WA.

one-hour tapes	diggings	quiverings	minutes	hours	d/q	d/min	q/min	Index	n index
1	64	92	60.50	1.01	.69	1.05	1.52	.69	0.09
2	33	58	60.20	1.00	.57	.55	.96	.57	0.06
3	12	23	14.30	.24	.52	.80	1.54	2.17	0.44
4	10	26	54.50	.91	.38	.18	.48	.42	0.02
5	13	32	53.00	.87	.40	.24	.52	.53	0.05
6	13	30	44.50	.74	.43	.29	.67	.58	0.06
7	21	25	48.50	.80	.84	.35	.41	1.05	0.17
8	9	14	18.00	.30	.64	.5	.77	2.14	0.43
9	9	6	20.00	.33	1.50	.45	.3	4.54	1
10	49	40	56.50	.94	1.22	0.87	.71	1.30	0.23
11	29	15	53.20	.89	1.93	.54	.28	2.17	0.44
12	13	9	33.00	.55	1.44	.39	.27	2.62	0.54
13	3	9	47.00	.78	.33	.06	.19	.43	0.03
14	16	9	59.30	.99	1.77	.27	.15	1.91	0.38
15	9	3	47.00	.78	3	.19	.06	3.84	0.83
16	6	9	41.50	.70	.66	.14	.21	.95	0.15
17	6	6	41.00	.68	1	.14	.14	1.47	0.27
18	5	16	58.70	.98	.31	.08	.27	.32	0
19	3	10	58.20	.97	.3	.05	.17	.31	0
20	30	24	28.20	.47	1.25	1.06	.85	2.65	0.55

Handicap displays

A handicap display was defined as one conferring fighting advantages to the rival. Data from five one-hour underwater tapes were used to count the relative number of handicap displays in five different salmonine species (**Table 3**).

Table 3. Type of fighting displays in five species.

species	total number of displays	number of handicap displays
brown trout	12	11
bull trout	3	3
chum salmon	7	7
sockeye salmon	16	16
pink salmon	9	9

Results and Discussion

Removing female choice

Female choice in salmonines has been thought to be overruled by male-male competition (**Chapter 1**). However, a striking difference came out when comparing the tapes with and without female choice: males mating with Mesalina showed no aggressive behaviour (**Table 1**).

This finding leads to make the following hypothesis: male-male competition is the result of females discriminating with whom to mate. According to this idea, male-male competition, at least in salmonines, is subordinated to female choice. This line of reasoning makes sense if we assume inheritance (the male offspring of a good fighter are also, relatively, good fighters). A female choosing a good male competitor is assuring to have male offspring with relatively high fighting abilities which in turn will be more successful at their time of mating. Consequently, is in the females' interest to promote male-male competition in order to facilitate themselves the choosing process.

Several facts, however, made this experiment subject of criticism. Firstly, observations with Mesalina were few in time (two hours) and in number of males observed (five males in the first tape and nine in the second). Secondly, there were no controls. Ideally, the same males mating with Mesalina should be observed mating with a real female. In addition the same female (Mesalina) should be observed exhibiting choice to the same males. Thirdly, and probably most important, even in the case that females were willing to mate with any male approaching them, they still have to build their nest and consequently males will have to wait for the mating moment. This is the critical waiting time in which we have to look for male-male aggressions.

The first problem can be solved by increasing the number of observations. The second one can also be partially solved, without manipulating the fish, by placing the dummy next to a nesting female guarded by a dominant male and several subdominant ones (during our observations there were females in the vicinity waters, but none of them was in a developing nest). This will allow us to see if there are differences in male aggression depending upon which female they interact with (real vs. dummy).

However, Mesalina, being a dummy, can not be used to reproduce the behavioural sequence of events that salmonines females perform. This makes it very difficult to solve the third and part of the second problem. In summary it is not possible to make definitive conclusions in our experiment. However, a suggested method to overcome these difficulties is to compare the spawning behaviour of closely related species in which there is no female choice.

Whitefish are salmonids from the Coregoninae subfamily considered ancestral to Salmoninae (Wilson 1997). Whitefish are broadcasters' spawners that mate in promiscuity (no female choice). The following paragraph is taken from a description of whitefish spawning behaviour by Fabricius (1954, p. 107).

“...they never showed any fighting, nipping, chasing, threatening or other aggressive behaviour. Actually, the whitefish seem to be the most peaceful species of fish we have ever watched.”

Despite all the mentioned problems, the experiment with Mesalina constitutes the first attempt to demonstrate the importance of female choice versus male-male competition in the salmonines reproduction. Further research in this line is needed in order to develop more on this idea.

Male quivering

Quivering is a common male behaviour present in all the salmonines, consisting of rapid vibrations from head to tail while approaching a female (**Chapter 2**). It is not necessary for a male to perform any quivering to spawn successfully (pers. observations). Such acts require energy to execute and an obvious question to ask is what possible advantages are responsible for the maintenance of this behaviour.

Quiverings as courtship behaviours

Most likely, quivering is a courtship behaviour that stimulates females to spawn. An indirect method to verify this is to correlate digs with quivers per unit time. If quivers were courtship behaviours, we should expect females to dig at faster rates when accompanied by males

performing more quivers. However, this correlation is complex because motivation for digging changes depending upon other female (nest building progress, eggs ripening) and male (size, morphology) variables. To minimize female variables, only the digging rates of females at the same spawning phase should be compared (**Table 4 in Chapter 2**). Similarly, to control for male size, only spawning pairs where male to female size is approximately equal should be compared.

Figures 3 & 4 examine the digging-quivering relation by using data from twenty one-hour underwater tapes of (similar size mates) sockeye salmon in which females were at the *nest probing* phase. Results show a positive correlation between both variables ($R^2 = 0.6212$). Females accompanied by males performing more quivers dig at a faster rate (**H₀₁** rejected; **H_{a1}** non rejected).

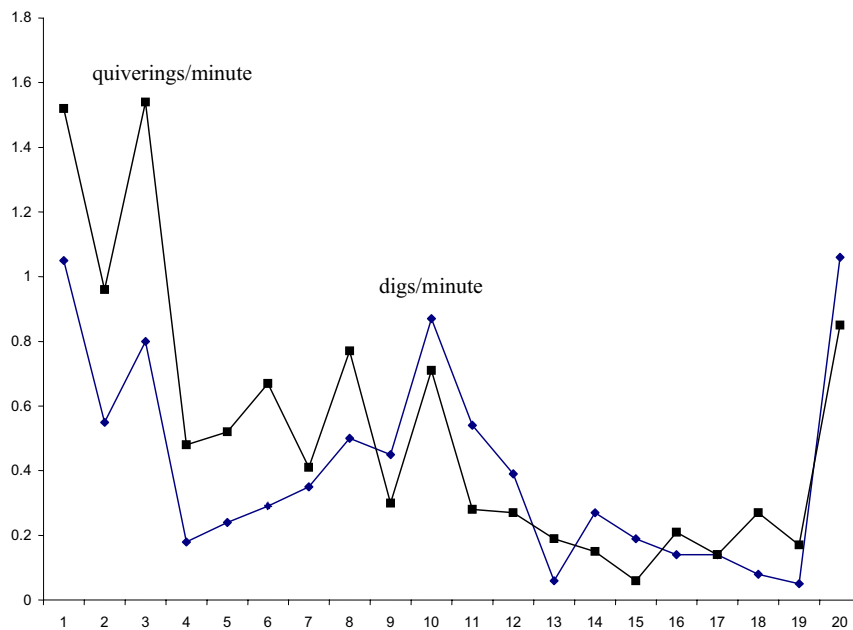


Figure 3. Number of digs and quiverings per minute in twenty pairs of sockeye salmon.

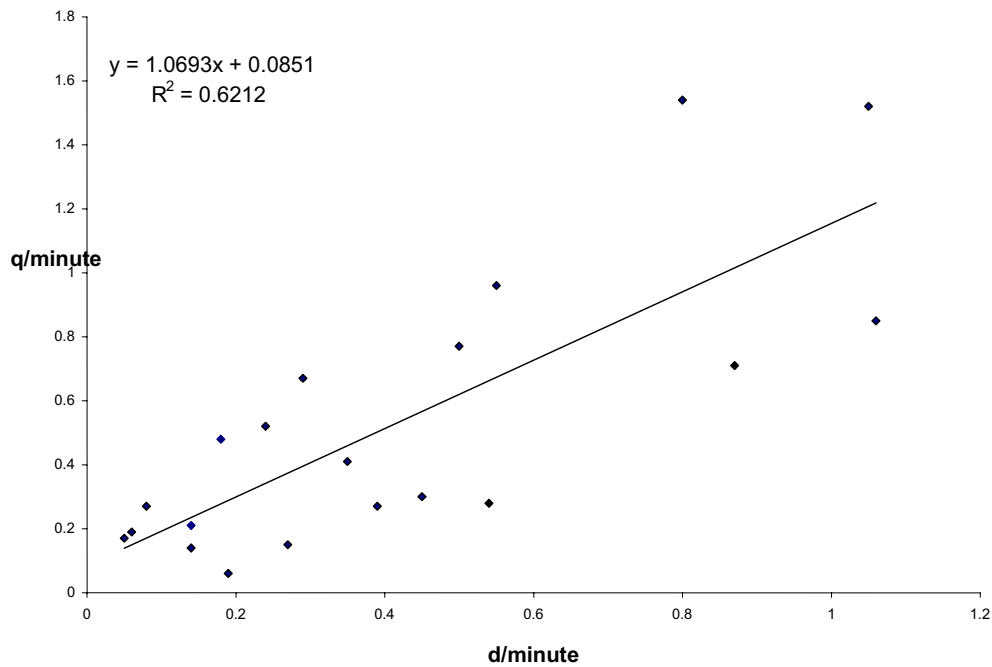


Figure 4. Correlation (showing a linear trend line) between quivers per minute and digs per minute in 20 pairs of sockeye salmon at the probing spawning phase.

Now, given that the quivering-digging relationship exists, next step is to observe if by a determinant number of quiverings two females dig at different rates. This was accomplished by defining the index of choice (**I**). The index of choice basically describes the female excitement. If a female digs more per quivering and time it means that her excitement or choice is higher.

Figure 5 uses the same data from **Table 1** to examine the Index of choice (**I**) in twenty pairs of sockeye salmon (**I** was normalized using an observed range: 4.51-.31). The greater the **I**, the greater the female excitement and consequently the greater her agreement (choice) with her mate. The variation indicates different degrees of choice in the salmon females.

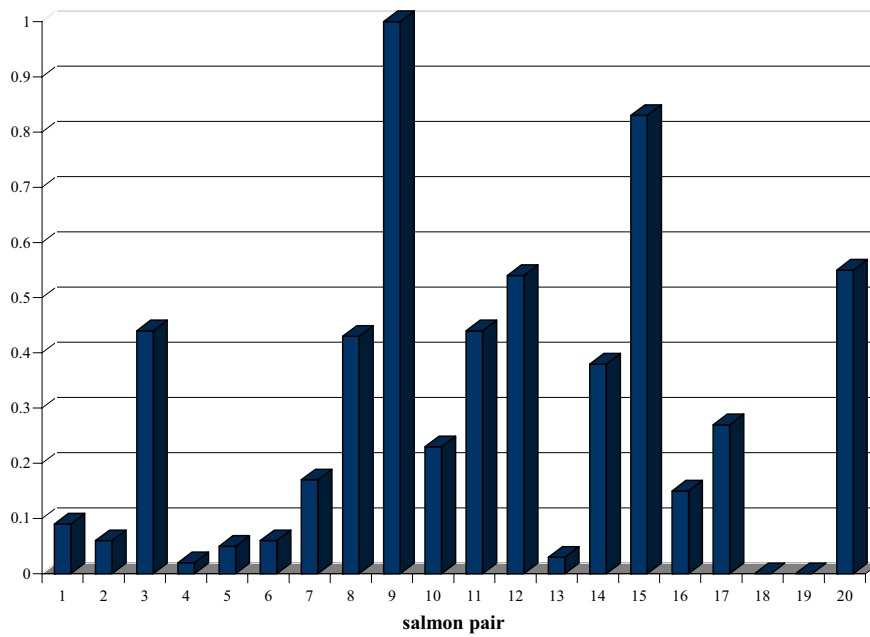


Figure 5. Index of choice (normalized) of 20 similar size pairs of sockeye salmon at the nest probing phase.

A direct method to visualize the difference on the effect of quiverings in female choice is to plot (In) with the quiverings rate (Figure 6).

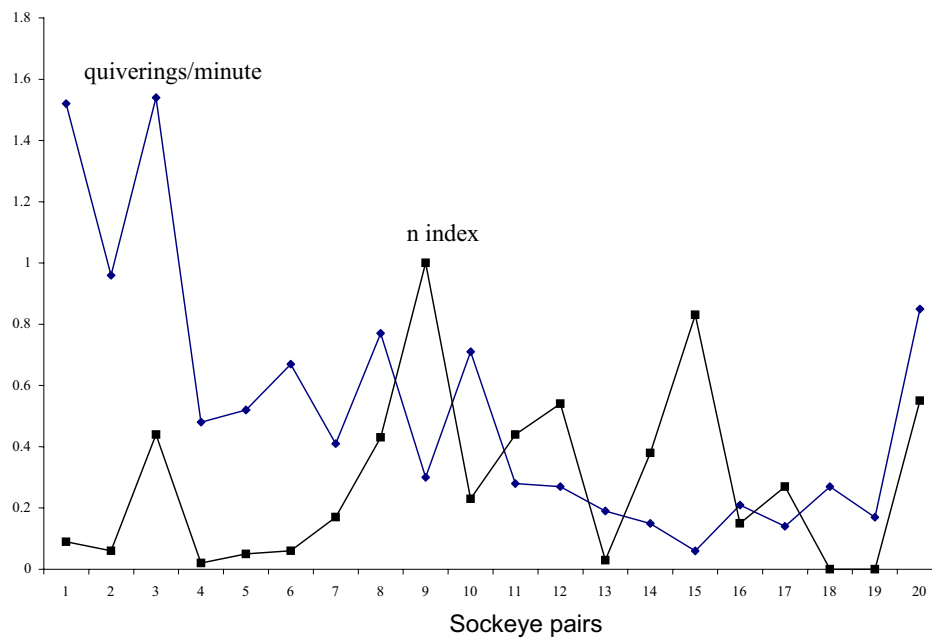


Figure 6. Relationship between the normalized index of choice of twenty sockeye females with the number of quiverings performed by their accompanied males.

The observed variation on **Figure 6** can be the result of three reasons: 1) there is a difference in the quivering quality (i.e. some males perform better quiverings than others); 2) some other male variables overcome the quiverings effect on female choice (i.e. morphology, colouration); 3) a combination of both.

A method to test differential quality in quiverings performance is suggested below. To test the second option a large number of observations identifying secondary sexual parameters is needed (see Järvi 1990 for Atlantic salmon and Petersson et al. 1999 for brown trout).

Fisher and Zahavi. A runaway selection for a handicap.

Fisherian and Zahavian models can be integrated to explain the evolution of female choice for exaggerated male traits. Theoretically, a runaway process in where the selected trait does not bear a positive correlation with quality can be interrupted and invaded by any other trait bearing a true advantage. Conversely, handicap traits, as truly quality indicators, meet the perfect conditions for the Fisherian process to run. A salmon female choosing for instance a male with a well-developed humpback (**Figure 7**) is choosing a mate that has survived despite a handicap. Only very fit, and good condition males can afford to have grown a large humpback that is, in fact, detrimental to their survival.

However, extravagant male traits cannot suddenly become available to females. The process of building a large humpback is gradual. Fisher's process solves this difficulty. A runaway selection in where males inherit a humpback larger than average and females the desire of mating with a large humpback male explains the progressive building of this and other extravagant male traits. If this mechanism were truly occurring, salmonines would make a clear example of a mating system where females are driving the males to handicap themselves in exchange for sex.



Figure 7. Pink salmon male with well-developed humpback.

Fisher and Zahavi's theories have been used to explain the selection process for morphological male traits. However, we can use them for all the other type of 'male characters' females chose (e.g. behaviours, coloration patterns).

Quiverings as quality indicators

Quiverings have the conditions of Zahavian-Fisherian selection. First, they are costly. A quivering is an action in which the muscular activity is raised to the maximum. Additionally (apart from the opportunity cost associated), during quiverings males are conspicuous and more vulnerable to possible predators. Second, females may know how to distinguish between a good and a poor quality quivering (females should be able to sense the quality of a quivering through their lateral lines). Third, quivering performance probably has a genetic basis (this idea, not tested with salmonines, assumes displays rates are heritable, see Kodric-Brown 1990).

Given these conditions, a runaway selection where the male's ability to perform quivers is linked with the female's desire of being courted by good quivering males may have naturally started.

How can we know that females prefer the males that do better quiverings?

The intensity and duration of courtship acts as an indicator of male vigor (Kodric-Brown 1990). Even to the human eye, there are noticeable differences, in terms of duration and intensity, within and between males in quivering performance (**Table 2 in Chapter 2**). Assuming females are aware of these differences we can predict that a female courted by a better quivering performer should dig at a faster rate. A suggested method to test this idea is to divide the males according to how long their quivering episodes last (in seconds). We can thus have long, medium, and short-quivering males. By comparing **I** (after controlling for size and spawning phase) between the three types of males we can test if females are most excited (dig faster) when courted by longer quivering males and thus demonstrate the possible effect of quivering quality on female choice.

A hypothesis to explain the origins and function of quiverings

Quivering most likely originated as a male fighting display. Phylogenetic inertia favours this idea. Graylings, Salmonids from the Thymallinae subfamily (considered ancestral to Salmoninae) were reported by Fabricius (1955) to perform quiverings in a male-male antagonistic context. In addition, quiverings have the characteristics of an aggressive display. By quivering, males are exhibiting their muscular power to their rivals. At the same time the trembling of their body transmitted through the water gives an accurate idea of their size. Furthermore, the logic of handicap displays (discussed above) fits perfectly into this dynamic, as quivering males give their rivals the possibility of a defenseless attack.

At some point during the evolutionary history of the Salmoninae lineage, a gradual transition between a threatening and courtship function may have occurred. This suggestion is favoured by the fact that male-male quiverings as aggressive displays are still very common in some salmonines (Legget, 1980 for dolly varden; Järvi, 1990 for Atlantic salmon; Petersson et al., 1999 for brown trout; personal observations for brown trout, Atlantic, chum, coho & pink salmons).

In a system where dominant males tend to monopolize spawnings, fighting displays could have evolved into courtship ones. A male display indicating fighting abilities would charm females if we assume inheritance (i.e. the male offspring of good fighters tends to be good fighters). Given these conditions, a runaway selection, where females experience sexual attraction for quivering males, may have naturally started.

Colouration patterns

Nuptial colouration is an interesting character to study because contrary to morphological attributes individuals are able to change their colour patterns. Salmon males can change their colours within seconds during courtship (Schroder, 1981 for chum salmon; Groot, pers. communication for pink salmon). Additionally, particular colourations have been associated to male dominance status (Schroder, 1981 for chum salmon; Fleming, 1996 for Atlantic salmon; Groot, 1996 for pink salmon, **Table 2 in Chapter 2** for sockeye salmon).

The reason why females choose males with one type of colouration versus another can be explained through Zahavian-Fisherian selection. Dominant coloration is a handicap, simply because it implies a greater number of agonistic interactions with rivals (Kodric-Brown, 1990;

Jonsson & Jonsson, 2001). Females choosing males with dominant colouration are thus choosing good quality males and a runaway process linking colouration with choice may therefore start.

Agonistic displays and the handicap principle

Instead of conferring fighting advantages, salmon aggressive displays seem to have the opposite effect. During lateral displays, the male lies in parallel to an opponent exposing his entire body with his fins erected. This has been interpreted as a manner of pretending to look bigger. However, fins are not weapons but very soft and vulnerable parts of the body that should be hidden in a fight. During a T-display two males swim in parallel until one of them progresses and positions himself in front of the other. This perpendicular position gives the opponent the possibility of an easy attack. The same argument applies to tail and flanking displays. In both the displaying male assumes a disadvantageous position before a potential fight (**Table 3**; see also **Table 3** in **Chapter 2**).

The handicap principle solves the logic of this paradox. A male giving advantages to his opponent is sending an honest signal about his power. Weaker males cannot cheat others performing T or lateral displays because many times those end in actual attacks (personal observations; see **Figure 15** in **Chapter 2**). Probably this system has been maintained because handicap signaling avoids a number of fights that will be detrimental in different degrees for both contenders.