



## General Introduction



## 1. General Introduction

### The Salmonines

The salmonines (salmon, trout, and charr) are a group of teleost fish species that are naturally distributed in the cold temperate waters of the Northern hemisphere (Groot, 1996). They, together, with Coregoninae (whitefish, cisco, inconnu, and sheefish) and Thymallinae (grayling) form the Salmonidae family (**Table 1**).

The subfamily Salmoninae contains at least five genera and as many as nine have been proposed (Oakley & Phillips, 1999). Part of this disagreement is due to the presence of some species found in Asia and Southeast Europe (commonly named archaic trouts), whose biology remains largely unknown. However, there is a consensus recognizing the following genera: *Brachymystax* (lenok), *Hucho* (huchen and taimen), *Salmo* (Atlantic salmon and brown trout), *Oncorhynchus* (Pacific trout and salmon), and *Salvelinus* (charr) (Hendry & Stearns, 2004).

Salmonines are a very interesting group of fish due to their commercial and recreational value. In addition, their particular life histories have made of them a group traditionally studied by ecologists, conservationists and evolutionary biologists, (Hendry & Stearns, 2004 and references therein).

All the salmonines reproduce in freshwater. Many of them complete their entire life cycle there, whereas others are anadromous and spend part of their growing phase in salt water. When mature, most return to their ancestral breeding grounds to spawn (Groot, 1996).

**Table 1.** Family Salmonidae (modified from Watson, 1999).

Family	Subfamily	Genus	Species	
Salmonidae	Coregoninae	<i>Stenodus</i>	(Sheefish and inconnu)	
		<i>Coregonus</i>	(Whitefish and cisco)	
		<i>Prosopium</i>	(Mountain whitefish)	
	Thymallinae	<i>Thymallus</i>	(Grayling)	
	Salmoninae	<i>Brachymystax</i>		<i>lenok</i> (Siberian lenok)
			<i>Hucho</i>	<i>hucho</i> (Huchen/taimen) <i>perryi</i>
		<i>Salmo</i>		<i>salar</i> (Atlantic salmon)
				<i>trutta</i> (Brown trout/Sea trout)
		<i>Salvelinus</i>		<i>confluentus</i> (Bull trout)
				<i>alpinus</i> (Arctic charr)
				<i>malma</i> (Dolly varden)
				<i>leucomaenis</i> (White-spotted charr)
				<i>namaycush</i> (Lake trout) <i>fontinalis</i> (Brook trout)
		<i>Oncorhynchus</i>		<i>chrysogaster</i> (Mexican golden trout)
				<i>gilae</i> (Gila/ Apache trout)
			<i>clarki</i> (Cutthroat trout)	
	<i>mykiss</i> (Rainbow trout / Steelhead)			
	<i>masou</i> (Masu salmon / yamame)			
	<i>kisutch</i> (Coho salmon)			
	<i>tschawytscha</i> (Chinook salmon)			
	<i>nerka</i> (Sockeye salmon/Kokanee) <i>keta</i> (Chum salmon) <i>gorbuscha</i> (Pink salmon)			

### Origins and evolution

The oldest salmonid fossil ever discovered (Wilson, 1977) shows that a salmonine, *Eosalmo driftwoodensis*, was living in British Columbia nearly 50 Mya (Cavender, 1980). However, based on the primitive nature of their skeletal and anatomical characters the age of the Salmonidae family is estimated as 100 Mya (Behnke, 1991). If this assumption is correct, somewhere between 100 Mya and 50 Mya a group of ancestral fishes split into the three

actual subfamilies. Salmoninae and Thymallinae subfamilies are thought to be more closely related to each other than to Coregoninae (Wilson, 1997).

The division of the three most known Salmoninae genera (*Salmo*, *Salvelinus*, and *Oncorhynchus*) probably occurred on the order of 20 million years ago (Groot, 1996). Behnke (1992) suggested that divergence of an ancient *Salmo*-type ancestor into an Atlantic Ocean group (*Salmo*) and a Pacific group (*Oncorhynchus*) may have occurred about 15 million years ago. The oldest *Salvelinus* fossil was found in northern Nevada and is at least 10 million years old (Cavender, 1986). By 6 million years ago forms similar to extant sockeye, chum, and pink (*Oncorhynchus*) appear in the fossil record (Stearley, 1992; Crespi & Teo, 2002).

Whatever the exact divergence times are, they took place millions of years before the first Quaternary ice age, and consequently the present geographic distribution of salmonines has been influenced and modified by several glacial events during the Pleistocene (Groot, 1996).

### **Spawning behaviour**

Salmonines spawn in or on gravel beds in rivers or lake shores where the eggs incubate under the protection of the gravel environment (Groot, 1996). During spawning they all share common behavioural patterns. Females excavate a series of nests in gravel in where they successively lay their eggs. Males diverge their time into competing with other male rivals and courting nesting females.

Despite the vast amount of work done with salmonines, a complete understanding of their spawning behaviour has not yet been reached. In this regard, we can identify five main problems still partially or fully unresolved.

First, there is a need of a complete and detailed comparative description of their spawning behaviour. Even though literature exists about the breeding behaviour of the main species within the three better-known genera; a study, following a homogenous methodology and including all the major species, is still lacking.

Second, there has been a discontinuity between the pioneer work of scientists in the mid years of last century (Jones & King 1949, 1950 & 1952; Jones & Ball, 1954; Fabricius, 1953; Fabricius & Gustafson, 1954) with most of the research conducted later. Jones, Fabricius and

others based their work on detailed observations in aquaria and semi-natural channels. Their analyses followed the principles of the early school of ethology, e.g. to treat behavioural traits the same as anatomical organs (Lorenz, 1937; Tinbergen, 1963) and to explain their dynamics as a feedback chain of fixed action patterns released by specific stimuli (Lorenz, 1940; Tinbergen, 1942 & 1948). Most of the later work has abandoned this approach switching to a more experimental analysis.

Third, there are many species whose spawning behaviour has been relatively less studied. Research has substantially favoured Atlantic salmon and the five Pacific salmon present in North American rivers. Furthermore, there are virtually no references about the breeding activities of some of the rare *Oncorhynchus* salmonines found in Western areas of the Southern USA and Northern Mexico (but see Rinne, 1980 for Gila trout and Knapp & Vredenburg, 1996 for golden trout).

Fourth, how two, mechanisms of sexual selection i.e. Fisherian runaway selection (Fisher, 1930) or the “good taste” model and Zahavi’s handicap principle (Zahavi, 1975) or “good genes” model may affect salmonids still remain to be discussed.

Fifth, except for a review by Stearley (1992) concentrated on the genus *Oncorhynchus* and a summary discussion by McLennan (1994), there are no studies where the behaviours among the different species are compared and discussed in an evolutionary sense. Furthermore, no studies using behaviour to infer Salmoninae phylogenies have been done.

This thesis, based on direct observations in the wild using a remote underwater video system, is an attempt to cover the first, third, fourth and fifth mentioned problems. It is separated in five chapters. This first one presents this group of fishes and introduces a theoretical overview about the Salmoninae mating system. A new approach about alternative male strategies and tactics is included. The second chapter consists in a comparative description of the Salmoninae spawning behaviour. The third one introduces the role the instincts have, and the mechanisms by which they are released. The fourth uses data from underwater observations to open a theoretical discussion about the importance of female choice. The fifth chapter is a phylogenetic study based only on behavioural and ecological traits during spawning.

**Chapters 2-4** follow a natural chronology and should be understood as a complete study of the salmonines spawning behaviour (**Chapter 2** describes what the fish do during spawning, **Chapter 3** explains how they do it and **Chapter 4** discusses why). **Chapter 5** uses the

comparative discussions in the previous chapters to open a study in which the phylogeny of the *Oncorhynchus* + *Salvelinus* species is inferred following a maximum parsimony analysis.

The discussion is limited to *Oncorhynchus*, *Salmo*, and *Salvelinus*. Other genera like *Brachymystax*, *Hucho*, and *Salmothymus* are poorly known and their reproductive biology remains a fascinating line of future research.

Despite the long tradition of using underwater video or film observations for studying spawning behaviour, this study constitutes the first long-term and systematic project based on underwater video recordings in natural conditions. It contains direct observations during spawning of twelve Salmoninae plus one Thymallinae species resulting in over three hundred hours of analyzed tapes (**Table 1** in **Chapter 2**).

## **An overview of the Salmoninae mating system**

Mating systems reflect the number of mates an individual acquires per breeding attempt, the conflict of interests of the two sexes and how they are resolved (Berglund, 1997). Anisogamy (Bateman, 1948) and 'differential parental investment' (Trivers, 1972) have determined the role of each sex during reproduction. Salmoninae males compete for access to females, which are, as in most other vertebrate species, the limiting resource (Darwin, 1859 & 1871; Anderson, 1994). Females compete for space to establish their nests. They select the nesting areas (redds) and dig a series of depressions (nests) to successively deposit their eggs (Groot, 1996; Gaudemar, 1998).

Strong male-male competition characteristic of Salmoninae results in a few males mating with several females. Females can also spawn with many males in a single spawning act or with different males in successive acts. This, results in a multiple polygamy system in which the five principal forms of competition over mates are present: termed contests, mate choice, endurance rivalry, scrambles, and sperm competition (Andersson, 1994 p.10).

Termed contests refer to fighting displays or actual fights in competition over mates. Male-male competition is probably the most studied aspect of the Salmoninae mating system. Salmonines males fight ferociously to be the sole spawning male (Keenleyside & Dupuis, 1988b). Normally size and morphology determine the outcome of fights, larger males with well developed secondary sexual characters having an advantage over smaller rivals (Schroder 1981 for chum salmon; Keenleyside & Dupuis, 1988b for pink salmon; Järvi, 1990 for Atlantic salmon; Fleming & Gross, 1993 for coho salmon; Kitano, 1996 for dolly varden; James & Sexauer, 1997 for bull trout; Foote et al., 1997 for sockeye salmon). However, eventually, even large males fail to monopolize spawnings due to competition with other large males. This simple concept has conditioned the existence of alternative male reproductive strategies and tactics (Gross 1984, 1985 & 1996; Taborsky, 1994; Healey & Prince 1998).

Mate choice refers to behavioural and morphological traits that attract and stimulate mates (Andersson, 1994 p.10). Female choice in salmonines has been thought to be overruled by male-male competition (Fleming & Gross 1994; Quinn & Foote, 1994; Petersson et al., 1999). This idea, based on the supremacy of large dominating males in the spawning grounds, only allowed females a passive role. Nevertheless, females have been reported to exhibit their choice by frequently attacking small males (Berst et al., 1981 for hybrid chars; Keenleyside & Dupuis, 1988b for pink salmon; Järvi, 1990 for Atlantic salmon; Petersson & Järvi, 1997 for



sea trout; Berejikian et al., 1997 for coho salmon; personal observations for brook trout, brown trout, Atlantic, pink, coho and sockeye salmon) and by delaying spawning when courted by non desirable males (Schroder, 1981 for chum salmon; Foote, 1988 & 1989 and Foote & Larking, 1988 for sockeye salmon; Blanchfield & Ridgway, 1999 for brook trout; Berejikian et al., 2000 for chinook salmon; Gaudemar et al., 2000b for Atlantic salmon). Delaying spawning is a form of choice by which females increase their chances of being joined by larger or better fighting males that will out-compete others. However, the opposite, accelerating spawning when being courted by a desirable male, has not yet been discussed (but see Schroder, 1981).

Endurance rivalry is the ability to remain reproductively active during a large part of the season (Andersson, 1994 p.10). Males' longer life (Fleming, 1996 for Atlantic salmon; Petersson & Järvi, 1997 for sea trout; Hamon et al., 1999 for Pacific salmon species) and protandry (Darwin, 1871 p. 220 for Atlantic salmon; Johnson, 1980 for arctic charr; Morbey, 2000 for Pacific salmon species) are two known characteristics that differentiate genders during spawning. However, no studies have determined whether differential reproductive success is associated with endurance rivalry in males. According to Andersson (1994, p. 154) larger body sizes should favor longer life spans because maximum storage capacity increases with body size more rapidly than metabolic costs. If this is the case, the better reproductive success of larger males may not only be a consequence of their fighting abilities, but also of their greater endurance.

Scramble competition describes the ability to find mates when a large number of females become available simultaneously or a large number of males must compete for them in a limited area (Alcock, 1993, p. 468). In a system where dominating males guard females and prevent other males from approaching, the ability to obtain fertilizations by means other than fighting plays a definitive role. This has even more importance as the spawning season progresses and due to differences in the time at which males and females remain sexually active (females normally remain sexually active in the spawning grounds for one week while males up to one month) the ratio between sexually active males and females increases (Quinn et al., 1996; Gaudemar, 1998).

Sperm competition can be defined as competition between the sperm of two or more males to fertilize the eggs of a single female (Mjølnerød et al., 1998). Even though, a hierarchy of males around a nesting female will generally be well established some time before gametes are released, at the end, sperm competition inevitably takes place. This occurs when several satellite males join the spawning female to emit sperm (personal observations for coho pink,

sockeye and Atlantic salmon). Paternity analyses have shown that males closest to the female at the time of the spawning fertilize most of the eggs (Mjølnerød et al., 1998 for Atlantic salmon). However, distance from female and timing of sperm release are not the only factors, sperm volume and male size are also important. Additionally, smaller males, forced by larger competitors to maintain a distance from the female, can overcome this handicap by positioning their vent closer to the female's at the spawning moment (Foote et al., 1997).

### **A new approach to alternative male reproductive strategies and tactics.**

In this thesis "strategy" is the relative age of maturation and is independent of behaviour, while "tactic" is used to describe specific behaviours performed to achieve fertilizations independent of age of maturation. This division is different from the one proposed by Gross (1996) who considered tactics as the phenotypic expression of a given genetically determined strategy. However, this notation does not contradict his view, and may be favorably used here because of: 1) the clear separation between the feeding and reproductive stages present in salmonine life histories; and 2) the impossibility of plainly separating genetic from environmental causes in the reproductive decision that each individual makes.

Basically, salmonine males can adopt three strategies; mature as old, young or precocious males. This in turn is associated with size, with the largest individuals normally being the ones staying longest in the feeding area (but see Quinn & Foote, 1994 and Healey & Prince, 1994). In addition salmonines can employ two tactics to achieve fertilizations; either they fight or they sneak.

Strategies are irreversible and conditioned to certain physiological thresholds thought to be genetically determined (Bohlin et al., 1990; Hutchings & Myers, 1994; Fleming, 1998; Healey & Prince, 1998). In contrast, tactics are reversible; males can switch back and forth between them depending on the types of rivals encountered (Foote & Larkin, 1988). The relative size between male rivals is the best predictor for the tactics that will be employed (Yamamoto & Edo, 2002 for masu salmon; Healey & Prince, 1994 for coho salmon; Foote, 1990 for sockeye salmon; Chebanov 1980 for pink salmon). However relative size is not the only factor conditioning the tactics employed, frequently newly arrived young males will fight and defeat larger males debilitated as the spawning season progresses. In addition, a male can simultaneously use two tactics with different rivals; he can, for instance act as a fighter when faced with a similar-sized male and as a sneaker when confronted with a larger

one. To better understand the dynamics of this complex system it is necessary to follow the mechanisms that elicit the escape and attack behaviours (discussed in **Chapter 3**).

The success of individuals following any combination of strategies and tactics (S-T) has been scrutinized by *theory of games* analyses (Maynard Smith, 1982). Game theory relies on the idea that the success of a player will depend on what other players are doing. Individuals expressing the same S-T compete directly among themselves; as a result their relative number at the spawning site directly affects their success. Consequently, the long-term success of a given S-T varies inversely with its frequency, penalizing abundance and favoring rarity (negative frequency dependent selection). This makes the fixation of a sole male reproductive type impossible. When the system arrives at the point that no new combinations can invade the population it is said to have reached an evolutionarily stable strategy or set of strategies (**ESS**) (Maynard Smith, 1982, see discussions in Dawkins, 1976, p. 69-86; Cronin, 1991, p.312-314; and below p. 14-16).

#### *1. The old male's strategy*

A male can delay its maturity and stay in the feeding area (ocean, lake or river depending on the species) growing for a longer period of time. Normally, the tactic employed by large males will be to fight other rivals to establish dominance around nesting females (**Figures 1 & 2**). Males losing the battles can either adopt a subdominant or *satellite* position downstream from the focal female, or look for other available females. Alternatively, males can directly adopt the tactic of satellite fish. Secondary sexually characters are fully expressed among the males that use this strategy (Darwin, 1871, p. 345).



**Figures 1 & 2.** Sockeye salmon (left) and chum salmon males fighting for total dominance in the redd.

## 2. *The young male's strategy*

A male can mature after a shorter period of growing in the feeding areas and return to the spawning grounds at an intermediate size. These fish have several options: they can search for females not defended by big males and fight other young males for absolute dominance (*alpha fighters*). Alternatively they can join big males and fight with subdominant fish to maintain the lead position among the satellites (*beta fighters*). However, young males in the presence of bigger fish will normally adopt the sneaking tactic. Sneakers wait for the moment of spawning from a strategic position away from the fighting males. At the moment of spawning they take advantage of their small size to get a position closer the female's vent (Foote et al., 1997). An alternative tactic for young males is to mimic females (Schroder 1981; **Figure 3**). By adopting female coloration and behaviours, young males can remain close to females without being attacked by other males, and thus fertilize eggs by “sneaking” (Groot, 1996).

**Table 2.** References for female mimicry in different Salmoninae species

Pink salmon	Keenleyside & Dupuis, 1988b
Chum salmon	Schroder, 1981; personal observations
Sockeye salmon	personal observations
Chinook salmon	Schroder (personal communication)
Atlantic salmon	personal observations
Arctic charr	Sigurjónsdóttir & Gunnarsson, 1989



**Figure 3.** Chum salmon male resembles a female in coloration and morphology.

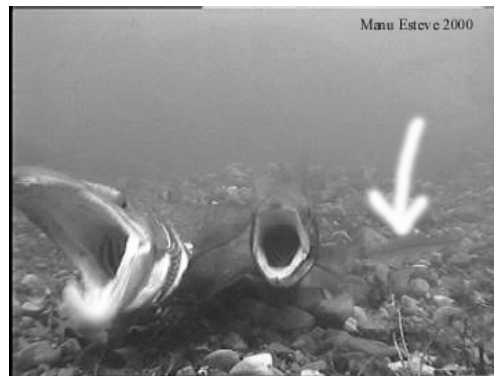
### 3. *The precocious male's strategy*

A male can mature at the parr stage before going to the feeding areas (**Table 2**). This phenomenon has been extensively studied in Atlantic salmon (Jones & King, 1952; García de Leániz, 1990; Garant et al., 2001; García-Vazquez et al., 2001; Taggart et al., 2001).

Precocious males wait for spawning events from hidden positions within the redd or in vicinity refuges (**Figure 4**, personal observations for Atlantic salmon, brown trout and brook trout). Similarly to adults, the parr fight each other to have a privileged position in the nest (normally, parr fight only when the adults are not present; personal observations for Atlantic salmon). As a result a linear dominance hierarchy is established. Generally larger parr win the contests and occupy the best positions (Myers & Hutchings, 1987 and Thomaz et al, 1997 for Atlantic salmon; Maekawa et al., 1983 for Miyabe charr; Tsiger et al., 1994 and Koseki & Maekawa, 2000 for masu salmon). However, smaller secondary precocious males are also able to release sperm at the spawning moment by darting into the nest from refuges located outside the female's nest (**Figure 5**; personal observations for Atlantic salmon). Interestingly, female precocious maturation at the parr stage has also been reported in some species, although this is considered very rare (Fleming, 1998 for Atlantic salmon; Ivankov et al., 1981 for masu salmon).



**Figure 4.** Two Atlantic salmon precocious parr wait for the return of the female to the nest. The parr in the foreground is dominant over the one in the back. The adult fish is an anadromous male.



**Figure 5.** Atlantic salmon precocious parr (pointed by the arrow) darts into the nest to release milt.

**Table 3.** Presence (yes) or absence (no) of maturation in the Salmoninae species at the parr stage.

Species	Parr maturation	References
Brown Trout	yes	L'Abe�-Lund et al., 1990; Bachman, 1991; Evans, 1994
Atlantic Salmon	yes	Fleming, 1996; Garant et al., 2001; Taggart et al., 2001
Coho salmon	no	no reports in the literature
Chinook salmon	yes	Taylor, 1989; Healey, 1991; Foote et al., 1991; Bernier et al., 1993; Unwin et al., 1999
Sockeye salmon	no	no reports in the literature
Chum salmon	no	no reports in the literature
Pink salmon	no	no reports in the literature
Masu salmon	yes	Tsiger et al., 1994; Silverstein et al. 1997; Koseki & Maekawa, 2000
Amago salmon	yes	Ueda et al. 1983
Steelhead/rainbow trout	yes	Needham & Tautz, 1934
Cutthroat trout	yes	Fleming, 1998
Brook trout	yes	Blanchfield & Ridgway, 1999; Greeley, 1932
Bull trout	yes	James & Sexauer, 1997
Dolly Varden	yes	Maekawa et al., 1983; Maekawa & Hino, 1986
Arctic Charr	yes	Jonsson & Jonsson, 2001
Lake trout	no	no reports in the literature

### Salmon and Evolutionarily Stable Strategies (ESS)

Probably, the ESS' most intuitive idea is the inverse correlation between the success of a strategy with its frequency. This concept implies the existence of a genetic link between the followers of any particular strategy. Males of the minority strategy experience a mating advantage (due to reduced competition) and consequently become more numerous in the next generation. Despite its transparency, at least three problems may tempt us to reconsider this model.

First, no such definitive genetic link has yet been found in salmonines. Even though age at maturation has shown to be partially inherited (Glebe et al., 1980; Iwamoto et al., 1984), genetics alone cannot explain fish age at maturity. For instance, several authors have found that genetic influences are weak with regard to precocious maturation (Gjerde, 1984 for

Atlantic salmon; Silverstein & Hershberger, 1992 for coho salmon; Unwin et al., 1999 for chinook salmon). Physiological thresholds are thought to determine the maturation age of the fish (Thorpe, 1994; Silverstein et al., 1997; Fleming, 1998), with age at maturity inversely related to growth rate (Thorpe, 1994; Henson & Warner, 1997; Unwin et al., 1999).

Second, generally ESS's assume an exclusive paternal inheritance link (the male offspring inherit their strategy and to a certain extent their tactics from their fathers). However, male offspring could theoretically inherit their strategies from their mothers; which could be very different from the one their fathers had (see Anderson, 1994, p. 17). A female, whose father was a sneaking precocious male could, for instance, pass the precocious maturation strategy into some of her sons, even if they were the result of a mating with an old fighting male.

Third, the role of female choice in the ESS dynamics has been virtually ignored. The discussion has only addressed the effects the number of likely competitors has in male reproductive success. However, if female choice is operating, as we shall discuss later, it well may be differentially punishing or rewarding a particular strategy independent of its relative frequency (see Henson & Warner, 2000).

Only the first problem has received sufficient attention. Bohlin et al. (1990), in his studies of precocious maturation in sea trout populations, proposed a genetic monomorphic model in which males were equipped with a mixed strategy. Age at maturity was conditioned to a threshold size that in turn was determined by environmental causes (if larger than a threshold size value, mature in the river; if not, go to the ocean). Negative frequency dependent selection was responsible for the equal fitness of the two maturation ages in this model. Hutchings & Myers (1994), in contrast, proposed the existence of two genotypes (genetic polymorphism) in Atlantic salmon that have two different thresholds of maturation depending on size. Males, in this case, could develop any of the alternative strategies depending on the inherited threshold and on the environmental influences causing it to be reached or not. Again, both strategies in this model had equal average fitness due to negative frequency dependent selection. Gross (1996) in his discussion of jack and hooknose coho salmon returned to a genetic-monomorphic model. However, he introduced a new mechanism of selection, which unlike the other two models was positively correlated with frequency. He named it status dependent selection. Status could be referred to any measure that allows ranking individuals, for instance size. Males now would follow a conditional strategy depending on their relative status. As a result the average fitness of the two forms were different and only equivalent at a switch point (deviated towards jacks according to the author).

An alternative view that encompasses some of these ideas is to consider a single multi conditional type of male (genetic monomorphism) that matures according a variable physiological threshold determined by growing velocity. The concept of a variable threshold is key to understanding this theoretical variation on ESS; it is based on the same rationale for behavioural thresholds (Tinbergen, 1948; **Chapter 3**). It assumes that accelerated growth parallels hormonal activity triggering maturation. If this were the case, the threshold for a fast growing individual would diminish with time, while the one for a slow grower would increase. This would explain why there is noticeable variation in precocious parr size (**Table 2 in Chapter 2** for Atlantic salmon), as individuals reach the switch point to maturation at different threshold-sizes. In this proposed model, the genetic link between parents and offspring would be associated with a tendency towards growth rate (e.g. the son of a fast grower tends to be a fast grower) by behaviour (ability to prey) and metabolism (ability to convert prey consumption into somatic growth). Additionally, the same argument could apply to tactics. A single multi-conditional tactics male could behave according to thresholds determining his immediate behaviours (e.g. attack or escape). These thresholds could vary depending on the individual's internal motivation and the external stimuli received, and operate always in the context of other males' (**Chapter 3**).

With regard to the second problem it is sufficient to realize that the ESS model proposed should also be genetically determined via maternal link. Finally, we also need to recognize that the role of females (third problem) adds a new mechanism of selection (choice dependent selection) to our system. This selection is not negatively correlated with frequency. However, its relative importance, when compared with the other two types discussed (status and frequency dependent selections) remains unknown.