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**LA THÈSE A ÉTÉ
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Development of Agonistic Behaviour in Size-Colour Classes of
Rainbow Trout (Salmo gairdneri) and
Brook Charr (Salvelinus fontinalis)

by

Graeme Lincoln Chew

A thesis submitted to
the Faculty of Graduate Studies and Research
in partial fulfilment of the
requirements for the degree of
Doctor of Philosophy

Department of Psychology

Carleton University
Ottawa, Ontario

April, 1986

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ABSTRACT

The development of patterns of agonistic activity in conspecific groups of newly free-swimming rainbow trout (Salmo gairdneri) and brook charr (Salvelinus fontinalis) was studied. In both species, high weekly levels of biting and chasing were seen initially but declined such that, by the end of the first month of free-swimming, the rates of chasing and biting attacks were low and comparable to rates of displacement.

In both species, large, light-coloured fry tended to dominate smaller, darker coloured fry. Using a four class, relative size-colour classification scheme it was found that for rainbow trout, relative dominance can be expressed in the following descending order of dominance: large, light-coloured (LL) fry > large, dark-coloured (LD) fry > small, light-coloured (SL) fry > small, dark-coloured (SD) fry.

This dominance order was similar for brook charr although the dominance relationship for the intermediate classes was reversed, namely: LL > SL > LD > SD. These dominance relationships were consistent throughout two successive years of observation (Experiment 1 through Experiment 4).

Spatial behaviour (station holding) was also correlated with dominance. Dominant fry, in both species, maintained stations in the longitudinal centre of the tanks, whereas nondominant group members maintained stations in the periphery. The depth and lateral positions of each station, however, appear to be random and independent of fry size-colour type.

Subsequent empirical tests, using different intruder scenarios, were performed to further evaluate the ontogeny of agonistic activity in fry of these two species.

Only dominant brook charr fry were able to secure positions of dominance when placed into host tanks; nondominant brook charr as well as rainbow trout (dominant and nondominant) were unable to do so. Moreover, of the intruders, only dominant brook charr fry were able to regain dominant status following return to home conditions.

Isolated dominant fry, of both species, were also able to regain dominant status after return to the home tank.

The general findings of the thesis including species differences in the intra-size-colour class agonistic activity, and in intruder scenarios, are discussed. Speculation concerning the physiological and behavioural mechanisms underlying the findings is also presented.

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MEMORIAM

This body of work is dedicated to the memory of my maternal grandmother, Mah (nee Lee) Foon Ngoh, who believed in the virtue of reason.

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CHAPTER 1: INTRODUCTION

The study of fish behaviour has long been a cornerstone of ethology. Correspondingly, the literature is large, underscoring the variety and number of piscine forms that have been studied. The salmonids constitute one group that has received much attention; primarily for two reasons. First, they contribute significantly to the economic welfare of many maritime nations either directly through the commercial fishing industry or indirectly via such ancillary revenues as those generated by recreational sport-fishing and related tourism. Second, the salmonids are adaptable to a variety of habitats within lacustrine, riverine, and marine environments. Thus, they are scientifically intriguing in terms of their behavioural and physiological flexibility.

Progressing from early taxonomic descriptions of salmonid morphological variation, later work has attempted to address systematically salmonid behaviour patterns. Such work stemmed not only from aquacultural concerns but also from awareness that, because of their natural inaccessibility throughout much of their adult life, a thorough understanding of salmonid behaviour, with the conspicuous exception of spawning behaviour, was lacking. With continued investigation however, a more complete understanding was inevitable. In particular, the behaviour of salmonids in a general social context has come under scrutiny and

so parallels similar efforts in other species, notably in avians where ethological issues of social organization, for example dominance and territoriality, has long been of interest (Gerking, 1953): .

The purpose of this thesis is two-fold. First, using two representative salmonid species--rainbow trout (Salmo gairdneri) and brook charr (Salvelinus fontinalis)--an attempt will be made to clarify the role different behaviours play in the agonistic interactions among members of small groups of salmonids during early development. Specifically, the thesis will document the ontogeny of behavioural differences in groups of same-aged individuals belonging to different size-~~co~~or classes during the first month of free-swimming.

Second, the response of stably interacting groups of newly free-swimming rainbow trout and brook charr fry will be studied. These challenges will involve systematic group perturbation through: (1) the addition and removal of key group members and (2) the addition and removal of intruders of known dominant or subordinate status.

Thus, three phases of experimental work are involved. The first phase (Experiment 1 and Experiment 2) is descriptive in nature; concerned with documenting the development of patterns of agonistic activity in newly free swimming rainbow trout and brook charr fry in the period from initial group formation to the time of establishment of stable levels of agonistic activity.

The second phase (Experiment 3 and Experiment 4) is both a replication as well as an extension of the first phase, involving the replication of the initial experiments with different groups. In addition, the relationship between spatial behaviour (station holding) with agonistic activity will also be addressed.

The third phase (Experiment 5 through Experiment 10 inclusive) will investigate the changes in established groups following the addition or removal of specific (dominant or nondominant) group members.

In addition to the presentation of these three phases of experimentation, the thesis also contains three appendices. The first appendix (Appendix A) is a glossary of terms used in the thesis and their specific meaning. The second appendix (Appendix B) provides background information on the two species studied. The third appendix (Appendix C) contains the complete data set for the first four experiments and a statistical treatment of those data.

Because these species are atypical of laboratory work in comparative psychology a treatment of the intra- and interspecific behaviour of both species is now presented.

Rainbow Trout Intraspecific Behaviour

The habitat of stream dwelling rainbow trout is variable but may be typified by shallow rivers with moderate flow and gravel bottoms. When in fresh water, steelhead (anadromous rainbow trout) are usually found in the lower reaches of large, swift, boulder-laden rivers from which they enter their spawning streams. The lake-resident Kamloops forms are usually found in the lower depths with adequate shallows and vegetation for good food production. For such lake populations to be self-sustaining there must be the appropriate gravel substrate for spawning.

Whatever the habitat, rainbow trout can interact successfully with other fish species by avoiding direct competition for food and space. In coastal streams, juvenile steelhead interact with juvenile coho and chinook salmon such that the two species select different microhabitats (Everest and Chapman, 1972; Hartman, 1965). When brown trout and rainbow trout are sympatric, brown trout tend to select well covered, deep pools with slow flowing water whereas rainbow trout prefer faster flowing water (Lewis, 1969). Rainbow trout also tend to feed more on drift organisms relative to the benthic feeding brown trout. Moreover, rainbow trout are known to feed exclusively on surface hatching insects when such are available.

Studies of rainbow trout behaviour have focussed on their territorial behaviour. Territoriality is observed as early as day 20 posthatching and coincides with yolk sac exhaustion (Dill, 1977). At this time, the repertoire of territorial behaviour is not large, comprised only of nipping and chasing.

Nipping (also called biting, see Appendix A) is defined as the rapid closing of the mouth of the initiator (aggressor) on or in the vicinity of some part of the target fish. Chasing, in contrast, is the pursuit of the target animal without involving any contact. Cessation of a chase may be simultaneous or terminated by either animal (Noakes and Leatherland, 1977). Typically, termination occurs after an intruder has been expelled from the defender's space.

From such early agonistic activity (see Appendix A) the rainbow trout social structure may develop into one of despotic rule by the time the fry are several months old (McIntyre and Healy, 1978; McIntyre, Healy, and Saari, 1979).

The behavioural repertoire also differentiates further during maturation. By the yearling stage, agonistic behaviours include, in addition to nipping and chasing: displacement (Cole and Noakes, 1980; Noakes and Leatherland, 1977), tail beating (Noakes and Leatherland, 1977), body wagging (Chiszar, Drake, and Windell, 1975; Hartman, 1965; Noakes and Leatherland, 1977, North, 1979), fin erection (particularly of the dorsal and pectoral fins) and opercular flaring (Cole and Noakes, 1980; Stringer and

Hoar, 1955).

Extended fighting involving biting has also been reported. Such occurrences were originally considered to be rare (Stringer and Hoar, 1955; Yamagishi, 1962) although work in this laboratory suggests prolonged periods of intense fighting may be more frequent than previously thought.

Nevertheless, these new behaviours may be considered as more subtle, less energetically taxing (McNicol and Noakes, 1981; Rhijn and Vodegel, 1980) forms of agonistic activity. Displacement may be defined as the supplanting of one fish from a hovering position by the defender. Tailbeating involves the rapid wagging of the tail by the aggressor, who confronts the target fish obliquely. This display is similar to the whole body wag involving the undulation of the entire body of the initiator while maintaining a stationary position, usually perpendicular to the intruder (Stringer and Hoar, 1955). Fin and opercular erection displays appear to be ritualized aspects of nonagonistic activities such as swimming and respiration although the displays serve strictly as social signals. However, the issue of the evolution of social signals in salmonids has yet to be fully addressed (North, 1979).

The size of individual rainbow trout appears correlated with position in the social group such that dominant individuals tend to be larger and lighter coloured than fish in nondominant social

positions (McIntyre, Healy, and Saari, 1979; Stringer and Hoar, 1955). However small-sized dominants in groups with large-sized nondominants have been reported in laboratory and semi-natural conditions (Jenkins, 1969; Yamagishi, 1962).

In terms of spatial behaviour, dominant fish usually patrol preferred portions of the range with subordinates relegated to the remaining areas (Jenkins, 1969; Yamagishi, 1962). However, interactions are dynamic with the ownership of poorly defended territories exchanged rapidly. Moreover, well-defended territories may interdigitate such that smaller fish tolerate the intrusion of larger fish. Conversely, smaller fish may hold small territories within the range of a larger, more dominant individual (Jenkins, 1969).

Yamagishi (1962) considers such subterritories to be partial ones since the intensity of the defense is minimal relative to the defense of full territories. Similar arguments have been advanced by Heland (1979) in the territorial behaviour of the brown trout (S. trutta). Alternately, multiple subterritories within a single large territory may represent mutual co-operation in which there is a reduction in observed aggression. Indeed, Jenkins (1969) and Moyle (1976) report small fish will aid the dominant fish in the defense of the common territory against invaders.

Territoriality is also modulated by environmental conditions (Lewis, 1969). With high food availability, agonistic activity

declines in frequency (Chapman, 1966; Everest and Chapman, 1972; Slaney and Northcote, 1974) whereas activity increases as the food resources are depleted.

Similarly, as population density increases, the incidence of territorial behaviour rises (Slaney and Northcote, 1974). Density-related territoriality asymptotes as the population size approaches the carrying capacity of the habitat. Presumably, as population size increases, continually escalating territorial defense becomes inefficient and stabilizes at some upper limit (Brown, 1975; Cole and Noakes, 1980). Indeed, certain displays such as body wagging rarely appear in densely populated streams (Chiszar, Drake, and Windell, 1975).

Rainbow Trout Interspecific Behaviour

The interaction between rainbow trout and sympatric species has also been studied; with the degree of interaction dependent on the specific species involved. For example, both the large mouth bass (Micropterus salmoides) and reidside shiners (Richardsonius balteatus) are known to be sympatric with rainbow trout with both species using rainbow trout as prey items (Johannes and Larkin, 1961; Stoeck and McCrimmon, 1965).

In the case of the large mouth bass, rainbow trout are not preferred prey however. This may be because the greater speed of the rainbow trout allows them to elude the slower bass. Segrega-

tion on the basis of water temperature and oxygen requirements may also serve to allow the two species to co-exist.

Similarly, redbase shiners prefer to feed on amphipods such as Gammarus rather than rainbow trout. Interestingly, redbase shiners are superior as foragers since they feed more systematically and at greater depth than do rainbow trout. Interspecific aggression occurs at three levels: (1) redbase shiner predation of trout fry, (2) large, adult trout predation of redbase shiners, and (3) juvenile trout and redbase shiner competition for resources. Because of the size difference between the two species, rainbow trout populations can be successful in habitats occupied previously by only redbase shiners (Johannes and Larkin, 1961).

Rainbow trout may also be sympatric with other salmonids. Rainbow trout and cutthroat trout (S. clarki) are known to co-occur in the streams of southwestern British Columbia (Hartman and Gill, 1968; see also Rohrer, 1981). Both occupy similar microhabitats: pools, gravel riffles, runs, and plunge pools. One species usually predominates in any given area with the cutthroat trout preferring small tributaries and headwaters whereas steelhead occupy the lower reaches of the mainstream. This allows both species to interact minimally and thus reduce competition for resources.

Segregation is also the mechanism by which rainbow trout and chinook salmon (O. tschawytscha) maintain sympatry (Everest and

Chapman, 1972). Unlike the rainbow trout - cutthroat trout situation, this segregation is temporal rather than spatial in that the two species have different egg emergence times: rainbow trout fry hatch in the spring whereas chinook salmon hatch in the fall in regions of sympatry. This staggered temporal demand places relatively less stress on the physical habitat than simultaneous hatching and appears to be advantageous to both species.

— Brook charr (Salvelinus fontinalis) and brown trout (Salmo trutta) also co-occur with rainbow trout in the wild (Jenkins, 1969; Newman, 1956). Unlike the other species however, both brown trout and brook charr interact dynamically with rainbow trout such that mixed species territorial mosaics may be formed. In such social organizations, sympatric individuals are treated as conspecifics with individual size and behaviour determining social position. As with pure rainbow trout social groups, the larger animals tend to be dominant (Gibson, 1981).

Brook Charr Intraspecific and Interspecific Behaviour

Although brook charr are not as aggressive or as territorial as other salmonids such as the rainbow trout or the Atlantic salmon (S. salar) (Gibson, 1981; Keenleyside and Yamamoto, 1962), they are known to hold territories (Slaney and Northcote, 1974), or partial territories (Jenkins, 1969), particularly in stream settings. In lacustrine habitats, depending on the size of the

range, territorial behaviour is absent with the brook charr tending to form aggregates under a single dominant fish (Gibson, 1981). In large lakes, it is not unusual to see solitary brook charr who school only when alarmed (Sedgwick, 1982), or basking in spring chilled waters in late summer (McIntyre, personal communication).

Territories, when observed, are generally located near rocks that disrupt current flow, permitting the brook charr to hover in the eddies (Moyle, 1969). These appear to be feeding-related territories with the holder of each territory having exclusive access to drift prey entering the territory (Moyle, 1976). The territories are cardioid in shape (Noakes and McNicol, 1982) such that the apex is downstream. Moreover, brook charr prefer deep water stations, even well illuminated ones, over shaded shallows (Gibson, 1978).

The resident of each territory is situated at the apex and directs defensive behaviour upstream (Noakes and McNicol, 1982), with the vigour of the defensive response inversely related to the distance from the apex. McNicol and Noakes (1981) also found that newly free-swimming brook charr alter their territorial behaviour from biting and chasing attacks to displacing charges. They suggest such changes are shifts toward less energetically costly, hence more efficient, behaviours.

Territorial behaviour appears to be under partial genetic control in addition to environmental influence (Ferguson and

Noakes, 1982, 1983a, 1983b). Using brook charr-lake charr (S. namaycush) hybrids, these workers found there is a maternal, rather than paternal, effect on the phenotypic expression of social behaviour.

Since brook charr are best able of all charrs to survive in alpine lake habitats, competition is not severe; although brook charr stocks have been known to be depleted when sympatric with brown trout (S. trutta) populations (Fausch and White, 1981). Generally, however, the success of brook charr populations in the alpine lake habitat results in a tendency to overpopulate in such conditions with large numbers of small-sized fish. Such is the case for streams as well (Moyle, 1976).

From the foregoing, it is clear both rainbow trout and brook charr are species in which agonistic behaviour plays a major role in their life history patterns. The settings in which conflict occurs are varied: hierarchical situations are documented as frequently as territorial situations. Intermediate variations of these settings may also occur.

The outcome of an interaction is, in part, influenced by the size of the participants. In size discrepant matchings, larger fish are more likely to prevail over smaller fish; hence larger fish tend to dominate smaller fish. Body colouration also plays a role in such interactions in that there are a number of qualitative reports that dominant individuals tend to be lighter

in colour than nondominant individuals.

Dominance has been defined behaviourally as the ratio of the number of successful initiations to the total number of initiations attempted (Barlow and Ballin 1976). Using this index, individuals with higher values are said to be dominant over those individuals with smaller values.

(It is noted that during the entire period of study only four unsuccessful initiations were observed; hence the ratio of the number of successful agonistic acts to total acts attempted approaches unity. Thus, fry initiating encounters more frequently than other group members will be considered to be dominant over those other members).

Returning to the role of size and colour, both morphological properties are known to be important in several fish species. For example, large resident bluegill sunfish (Lepomis macrochirus Rafinesque) are more aggressive to both large- and small-sized intruders than they are to small-sized conspecific neighbours (Henderson and Chiszar, 1977). Similarly Barlow and Ballin (1976) showed gold morphs of the Midas cichlid (Ciclasoma citrinellum) are dominant over same-sized, or even slightly larger, cryptically coloured (normal) morphs.

More recently, Denight and Ward (1982) found a positive correlation between the size of chin spot markings and inter-male aggression in the black-chinned mouthbrooder (Sarotherodon melanotheron). Interestingly, the size of a resident relative to that

of an intruder did not contribute significantly to the outcomes of aggressive interactions although this is not the case in other species (For example, see Frey and Miller, 1972; Symons, 1968).

Other species where size is a factor in establishing social relationships include Eupomacentrus altus (Kohda, 1981) and Tilapia mariae (Schwanck, 1980). In both these species, increasingly large size is associated with greater dominance although in E. altus it is the size of the genital papilla, rather than overall body size, that is the determinant. Hence, it is the size characteristics associated with reproductive readiness, rather than those associated with resource holding potential, as in T. mariae, that play a role in establishing dominance.

Overall size is also associated with dominance in juvenile brown bullheads (Ictalurus nebulosus) (Keen, 1982) as well as in the Arctic charr (Salvelinus alpinus) (Jobling, 1983; Jobling and Wandsvik, 1983). In both species, larger dominant fish have faster growth rates than do small subordinates suggesting that large size and social dominance are closely tied to growth potential (Jobling and Wandsvik, 1983).

In contrast, Miller (1979) has argued small size also has survival value; the most important being the greater potential for small-sized individuals to exploit spatially restricted habitats. Farr (1980) documents an example of a size-inverted dom-

inance, social organization in the poeciliid Girardinus metalli-
cus. Small males were more aggressive, exhibited greater sexual
 vigour, and were less affected by attack than larger males.
 Further, juvenile males who were subordinate matured later and
 were less sexually active than males who were dominant as juve-
 niles.

Large size is known to confer greater reproductive success
 in a number of species (see Kroll, 1981). Such species include
 the goby Coryphopterus nicholsi (Cole, 1982), the arena breeding
Cyprinodon macularis californiensis (Loiselle, 1982), and the
 chum salmon (O. keta) (Chebanov, 1979) and the humpbacked salmon
 (Oncorhynchus gorbuscha) (Chebanov, 1982).

With respect to dominance-related chromatic differences,
 further examples may be seen in: Coreoperca kawamebari (Kohda and
 Watanabe, 1982), the pencilfish (Nannostomus beckfordi) (Kuenzer,
 1982), the pomacentrid fish Chromis cyanea (de Boer, 1980),
 rainbow cichlids (Herotilapia multispinosa) (Wiley Driscoll and
 Welanko, 1981) and in certain Red Sea coral reef fishes (Pomacan-
thus imperator) (Fricke, 1979).

In all these species conspicuous colouration is found in the
 dominant group members. Kelly and Hourigan (1983) suggest such
 conspicuousness may enhance the optical signalling properties of
 the colour differences between individuals of different social
 rank.

Shapiro (1981) documents a singular example of the role of colouration in the social behaviour in the protogynous, tropical fish Anthias squamipinnis. The colouration of female A. squamipinnis is normally strongly contrasted with those of males. However, when sex reversal is induced, the females acquiring dominant male status also acquire the associated male colouration.

Not all colour differences may serve an intraspecific social function however. For example, the lateral body bar markings in the pumpkinseed sunfish (Lepomis gibbosus) are thought to serve a species identifying function in addition to any possible social signalling properties (Brown and Colgan, 1981).

In one of the rare studies on the social aspects of salmonid chromatic properties, Maeda and Hidaka (1979) have found the parr marks in the Japanese trout Oncorhynchus masou, a species which retains such marking into adulthood, play an important role in releasing intraspecific aggressive behaviour.

In contrast, the relationship of size and colour characteristics to agonistic activity remains unclear for rainbow trout and brook charr. This thesis will attempt to elucidate these relationships. The specific concerns of this thesis being: (1) the form and frequency of agonistic interactions between conspecifics belonging to different size-colour classes toward other group members, (2) the relationship of spatial behaviour to

the agonistic behaviour patterns, (3) the temporal nature of intragroup agonistic behaviour from initial group formation to the establishment of stable rates of interaction, (4) the nature of species differences in the relationship of agonistic activity, spatial behaviour, and size-colour characteristics of group members, and (5) the response of established groups to intruders.

Reiterating then, the experimental protocol involves an initial descriptive series concerned with documenting the early development of agonistic behaviour in S. gairdneri and S. fontinalis (Experiment 1 and Experiment 2). This series is then repeated in the following hatching season during which time the relationship between spatial behaviour and agonistic behaviour will also be studied (Experiment 3 and Experiment 4). Following these descriptive experiments, manipulations will be conducted with stable, established groups to assess the nature of the shifts in agonistic activity when the groups are disturbed through the addition or removal of group members (Experiment 5 to Experiment 10).

In this manner, aspects of the ontogeny of social behaviour in newly hatched rainbow trout and brook charr fry will be studied so that a fuller understanding of the behaviour of these species may be obtained.

CHAPTER 2: Experiment 1 and Experiment 2

The purpose of these initial studies was to investigate how different sized, different coloured rainbow trout and brook charr interact intraspecifically in early life. Since group interactions are well-formed by the mid parr stage (age 6 months) (Chiszar, Drake & Windell, 1975), fish were studied from the onset of free-swimming for one month.

Experiment 1: Rainbow Trout

Method

Rainbow trout were raised from eggs stripped and fertilized from fall spawning parental stock previously described (McIntyre, Healy & Saari, 1979). The embryos were incubated in running water at $10 \pm 0.5^{\circ}\text{C}$ in darkness. After hatching, the sac-fry were acclimatized to a 12h/12h light dark cycle (lights on at 0800 hr) and held in a 145 x 30 x 20 cm deep stream tank with water temperature at $14 \pm 2^{\circ}\text{C}$. Starter size fish food (Martins Feed Mills, Elmira, Ontario) was introduced as the fry became free swimming.

On day 1, when 80% of the fry were free swimming, 30 fry were randomly selected and housed in groups of 6 in five 31 x 24 x 31 cm deep glass aquaria. The mean length of the fry was 1.8 ± 0.5 cm (mean $\pm$ standard error of the mean, $n = 30$). Sex determination of the subjects was not made.

The floor, rear, and side walls of each aquarium were externally opaqued with black plastic. Continuously aerated fresh water entered each tank at one end and drained through a bottom draining, plexiglass standpipe at the other end. The water was maintained to a depth of 21 cm at 13 ± 1 °C by replacement at 30 litres/hr. Fish were fed twice daily during the light period throughout the course of the experiment. The tanks were cleaned daily of free floating matter using a fine mesh dip net.

All observations were made between 1000 and 2000 hrs, one half hour after feeding. No diel variation in agonistic activity was found during these hours in pilot work. Each group was observed daily in two, non-successive 10 min periods for 28 days. An all occurrence procedure of behavioural recording was used throughout.

Three classes of agonistic activity were recorded: (1) displacement, (2) chasing, and (3) biting. These behaviours have been described elsewhere (Jenkins, 1969; Newman, 1956; Noakes & Leatherland, 1977; Stringer & Hoar, 1955; Yamagishi, 1962). Briefly, displacement is the supplanting of one fish by another from a stationary position. It is comparable to the charge behaviour described by McNicol & Noakes (1981) for brook charr, although the latter term connotes a vigour of interaction not observed in these studies. Chasing is the pursuit of one fish by another through a space greater than two body lengths and is

comparable to the pursuit behaviour described by Cole & Noakes (1980). Biting, also termed nipping (Stringer & Hoar, 1955), is the closing of the jaw of the attacker upon the body of the target fish and can be the most injurious form of direct attack behaviour (Chiszar, Drake & Windell, 1975; Jenkins, 1969). It is noted that bites do not always result in contact due to evasive behaviour by the target fish (Stringer & Hoar, 1955). In this thesis, such missed bites are still recorded as bites.

For this thesis, it is understood that these behaviours are "agonistic" or "aggressive" behaviours. Operationally, a fry who initiates more attacks (displacements, chases, or bites) upon another fry than it receives is "dominant" over that other, "subordinate", fry. These terms are summarized in Appendix A.

Morphological descriptions were based on individual size and colour relative to the smallest fry of each group. Thus, a fry was judged to be large if its overall length exceeded that of the reference fish by no less than the mid-eye orbit to snout distance. Any fry not meeting this criterion was classed as small.

In terms of colouration, a light-coloured fry had dark parr marks on a pale brown, often khaki, background whereas a dark-coloured fry the background was dark brown, sometimes indistinguishable from the parr bands themselves. Thus, individuals could fall into one of four size-colour categories: (1) large, light-coloured (LL), (2) large, dark-coloured (LD), (3) small,

light-coloured (SL), and (4) small, dark-coloured (SD). This simple taxonomy was used to describe both the initiator and recipient in all dyadic encounters.

(It is noted that aside from those changes in colouration associated with transfer to and from the host tanks in the intruder experiments, the size-colour characteristics of the subjects were stable throughout the duration of each experiment.)

The robustness of the agonistic behaviours were such that multiple observers were not used. Rather following the original pilot study period (September, 1981 - April, 1982), during which time observations were made with both the candidate and supervisor in attendance, the majority of all subsequent observations (i.e. those reported here) were made by the candidate alone. Single observer procedures have been employed successfully in previous studies of salmonid agonistic activity including Chapman (1962), Dill (1977), Jenkins (1969), Keenleyside and Yamamoto (1962), Newman (1956), Stringer and Hoar (1955), and Yamagishi (1962).

Results: Frequency of Initiation

The observed per week frequencies for the three behaviours for each size-colour class over time are presented in Table 1 (Appendix C). Summing over time for displacement behaviour, LL individuals were the most aggressive and SD individuals were the least aggressive. The total frequency of displacement by LL fry

(that is, the total number of displacements observed for all LL fry in all groups summed over weeks) upon all size-colour classes was, in descending order: SL (87) > LD (54) > SD (32) > LL (31). That is, the total number of displacements of SL fry by LL fry, summed across groups over weeks, was 87. The total number of displacements of LD fry by LL fry was 54, and so on.

This order of displacement frequency is comparable to that for SL fry: SL (35) > LD (10) > LL (6) > SD (5); and by LD fry: SL (24) > LD (14) > SD (8) > LL (7).

LL fry also chased most often. The order of total frequency of chasing by LL fry was: LD (166) > SL (146) > SD (31) > LL (26). For LD fry the order was: LL (115) > SL (20) > SD (9) > LD (5). For SL fry the order was: SL (17) > SD (8) > LD (3) > LL (2). That is, for these three size-colour classes fry tended to chase fry of similar size. SD fry rarely chased, having a total of only 3 chases, of other SD fry, during the total time of study.

For biting, LL fry were again the most aggressive, with attacks concentrated primarily against LD fry. The overall pattern of biting initiations by this class was: LD (149) > SL (69) > LL (16) > SD (14). For LD attackers, the order of biting was the same as it was for chasing: LL (113) > SL (16) > SD (7) > LD (1). The pattern of biting, relative to chasing, was similar for SL initiators as well: SL (12) > SD (3) = LD (3) > LL (1). As

with displacement and chasing, the level of biting by LL fry was greater than that of any other class.

Figure 1 shows the changes over time in the mean weekly totals of each behaviour during the study period. Each score is the mean ($\pm$ standard error of the mean) of the total number of occurrences of the given behaviour across the four size-colour classes.

In Figure 1, there can be seen initially high levels of intragroup chasing and biting followed by a rapid decline in these activities by the third week of observation. By then, the mean weekly levels of chasing and biting are actually less than that of displacement.

(Note: the variation in the values of the standard error of the mean reflect the differences in the frequency of agonistic initiations among the classes. Hence, the large standard error of the mean for chasing in Week 2 is attributable to the greater amount of chasing by LL fry relative to the other three classes. Inspection of the data matrix (Table 1) reveals the initial, high levels of activity in Week 1 and Week 2 are due primarily to interactions initiated by LL fry against LD and SL fry as well as by LD fry against LL individuals. In contrast, SD fry exhibit only minimal interactions as initiators or recipients of these aggressive interactions).

Figure 1. Means ($\pm$ s.e.m.) of displacement (DIS), chasing (CHS), and biting (BITE), averaged across the four size-colour classes of rainbow trout, per week in the first year.

RAINBOW TROUT

YEAR 1

Experiment 2: Brook Charr

Method

Brook charr sac fry were obtained from Barbour Trout Farms, Hillsburgh, Ontario. The methods of rearing and maintenance as well as testing and data analysis were identical to those used in Experiment 1. The mean length of the fry at the outset was 2.0 ± 0.3 cm (mean $\pm$ s.e.m, $n=30$).

Results: Frequency of Initiation

As with the rainbow trout fry, brook charr fry displayed agonistic activity within the first week of free-swimming. Table 2- (Appendix C) presents the brook charr data matrix including observed frequencies of behaviour by size-colour class.

Again as with rainbow trout, LL brook charr fry most frequently initiated displacement of group members, with the overall order of total frequency of initiation being: SL (173) > LD (143) > SD (88) > LL (45). A similar pattern was established by SL fry: SL (38) > LD (17) > SD (14) > LL (7), but not by LD fry: LD (17) > SL (14) > SD (13) > LL (3). Displacements initiated by SD fry were rare; only four instances, directed at other SD class individuals, were observed.

LL fry also chased most often, with the overall order of total frequency of initiation being: SL (84) > LD (50) > LL (25) > SD (14). The chase pattern was different, with reduced overall frequency, for SL fry: SL (16) > SD (15) > LD (11) > (8). The

number of chases by LD fry was even lower, with the following order: SD (4) > LL (3) > LD (1) > SL (0). No chases by SD fry were observed.

LL fry also bit most frequently, with the order being: LD (21) > SL (20) > SD (6) > LL (5). Bites by SL fry followed a different pattern: LL (12) > LD (7) > SL (5) > SD (4). Dark coloured fry rarely bit; only two instances of biting, by LD fry, upon SD fry, were seen. The overall level of biting among the four size-colour classes of brook charr fry was low.

As with rainbow trout, initially high levels of chasing and biting activity decline over time so that by the fourth week the levels of chasing is comparable to that of displacement with the level of biting lower still. This can be seen in Figure 2.

In contrast, the frequency of displacement remains low and constant for both species over time. This can be readily seen in Figure 1 and Figure 2.

Inspection of the data matrix (Table 2, Appendix C) shows the early high level of interaction are due to LL encounters with SD fry, primarily in terms of displacement behaviour, as well as LL encounters with SL and LD fry (all three activities).

Figure 2. Means ($\pm$ s.e.m.) of displacement (DIS), chasing (CHS), and biting (BITE), averaged across the four size-colour classes of brook charr, per week in the first year.

BROOK CHARR

DISCUSSION

From these two experiments several features in the development of agonistic behaviour in rainbow trout and brook charr have been delineated. First, fry of both species engage in dyadic interactions on or about the onset of free swimming and thus coincides with the onset of other behaviours. This has also been reported by (Dill, 1977).

Second, of the behaviours studied, the mean levels of chasing and biting are higher in the initial two weeks than later. For rainbow trout, there is also an increase in chasing and biting from the first week to the second week. In contrast, the level of displacement activity remains low and constant throughout the experimental period for both species.

Third, the behaviour patterns are related to the size-colour morphology of the agonists such that members of the different classes behave differently over time. At the extremes of the size-colour scale used, LL individuals are the most prone to initiate and engage in an encounter whereas SD fry are the least prone to do so. Since the number of initiations may be thought to approximate relative dominance (McIntyre, Healy, & Saari, 1979; see also Barlow & Ballin, 1976), LL fry may be considered then as the most dominant of the four size-colour types and SD fry the least dominant. Such a view is consistent with anecdotal evidence of morphological correlates of dominance in investiga-

tions of older rainbow trout and brook charr samples (Jenkins, 1969; Newman, 1956) as well as in systematic investigations of dominance relationships in other fish species (see Introduction).

However, the relationship between size, colour and relative dominance is not straightforward when considering intermediate size-colour types. In brook charr, SL fry are dominant over LD fry in terms of chasing and biting (but not displacement). This situation is reversed for rainbow trout; LD fry displace, chase and bite SL fry more frequently than in return. Hence, SL fry are subordinate to LD fry in rainbow trout groups but exercise comparable, if not, superior status in brook charr samples.

CHAPTER 3: Experiment 3 and Experiment 4

In the following season the two initial experiments were repeated, with some modification. The purpose of the repetition was three-fold. First, as a replication, the second series would serve as a test of the reliability of the previous observations. Variation in: (1) the level of activity, (2) the temporal patterning of the agonistic interactions, and (3) interclass relationships, particularly between the intermediate size-colour classes, were issues for consideration.

The present studies differed from the preceding studies in that, following the establishment of stable patterns of agonistic activity, selected fry were removed from their home tanks and placed in either host tanks or isolation tanks. In this manner, the experiments provided a means by which group activity may be perturbed in systematic, tractable fashion. These later, intruder studies comprise the third and final section of the thesis.

Thirdly, this experimental series allowed for the investigation of the spatial behaviour of the fry as it pertains to agonistic activity. Since it is well known that, in both species, populations of older individuals can exhibit territorial behaviour in certain conditions but not in others (Chiszar, Drake, and Windell, 1975 ; Stringer and Hoar, 1955), investigation of spatial behaviour as it relates to agonistic

behaviour is indicated for the young fry studied here.

Station holding was the form of spatial behaviour studied here. A station is defined as that area within a territory where the resident fish spends most of its time (Kalleberg, 1958; Keenleyside and Yamamoto, 1962; more recently, Cole and Noakes, 1980). The station holding exhibited in the fry studied here is identical to that described by Keenleyside and Yamamoto (1962, p. 140) for Atlantic salmon fry:

Occasionally one darts from its resting position to feed, or attack and chase away an approaching fish, then quickly returning to take up its previous position. By this active, aggressive behaviour each fish keeps all other out of an area immediately around it.

The difference between a station and Noble's 1939 definition of a territory as "... any defended area..." is negligible. However, recent use of the term territory in salmonid work has implied it is more than a relatively fixed point (of rest) in space. Rather, it is a large area of particular shape that is patrolled by the resident of that territory (McNicol and Noakes, 1981, Slaney and Northcote, 1974). The term station holding will be used here as that was the activity studied; no efforts were made to observe patrolling or the shape of the entire space defended by a fry.

Of interest then, was to distinguish fry of the four size-colour types on the basis of their station holding behaviour. In particular, an attempt was made to distinguish between dominant

and subordinate group members on the basis of the physical positions of their stations. Also, as with agonistic activity, changes in station holding over time were documented.

Thus Experiment 3 and Experiment 4 pursue, using different samples in a later season, the behavioural questions posed in Experiment 1 and Experiment 2. In addition, these studies extend the types of behaviour studied to include spatial, as well as agonistic, behaviour.

Experiment 3: Rainbow Trout

Method

The experimental procedure used in Experiment 3 was similar to that of Experiment 1, with only three modifications. First, due to technical complications, eggs were not obtained from laboratory stock as in the initial experiment but rather came from a commercial supplier (Rainbow Springs Trout Farm, Thamesford, Ontario). The methods of incubating and hatching the eggs remained unaltered.

Second, the number of experimental animals was trebled due to an increased availability of observation tanks. The initial procedures of random selection of subjects, maintenance of light and water conditions, and feeding were also identical as those employed previously.

Third, masking tape was taped to the rims of each of the 15 tanks with each strip of tape was marked in 1 in (2.54 cm) sections. In this manner, the spatial position of each subject in three-dimensional Cartesian space was recorded. For example, the co-ordinates (0, 0, 0) represented the spatial position at the extreme end of the tank furthest away from the point of drainage, closest to the front observation pane, on the floor of the tank. Correspondingly, the diametrically opposite position had co-ordinates (20, 10, 8). Similarly, the centre of the tank had co-ordinates (10, 5, 4).

Spatial behaviour was evaluated in terms of time spent hovering in a particular position (station holding) rather than the range patrolled. The position a fry frequented the most was considered to be its preferred position.

Although spatial behaviour has been studied primarily in terms of territoriality in rainbow trout and brook charr (see McNicol and Noakes, 1981; Noakes and McNicol, 1982), station holding was considered a more appropriate measure for fry of the age studied as it is not as labile a phenomenon (Heland, 1980a, 1980b; but see also Heland, 1979; Srivastava, 1982). In this regard, several workers (Heland, 1979; Jenkins, 1969; Newman, 1956) have addressed the issue of so-called territorial mosaics in young salmonids. These mosaics entail the division of a given area into several adjoining territories. It is the mosaic pattern of distribution of these territories from which the term

is derived.

Such mosaics appear to be multi-purposed in that social as well as spatial factors contribute to the structure of the mosaic. This is in contrast to the simple definition of a territory as "a defended space" (Brown, 1975; Noble, 1939); a definition that has proved useful in the study of the spatial behaviour of other fish species (e.g. Bronstein, 1980, 1981, 1982; Cain and Baenninger, 1980; Hiltlen, 1981; Itzkowitz, 1979; Kohda, 1981; Moyer and Zaiser, 1981; Thompson and Jones, 1983).

To avoid possible difficulty with the concepts of territories and territorial mosaics and their relative merits as indices of spatial behaviour, station holding was adopted as the measure of choice. Moreover, station holding has been studied successfully in juveniles of other salmonids (Mutsin'sh, 1979; Rimmer, Paim, and Saunders, 1983; Srivastava, 1982). Recent work by Cole and Noakes (1980) with brook charr fry clearly illustrate the role of station holding as a form of spatial behaviour independent of territorial considerations. Station holding in rainbow trout fry appears not to have been addressed although studies have been conducted in populations of older fish in the related topic of orientation in different current conditions (Kelso and Northcote, 1981). Similar studies have been performed in brook charr (Gibson, 1978).

Results

The observed mean weekly totals of displacement, chasing, and biting (collapsed across the four size-colour classes) are presented in Figure 3. The observed levels (weekly totals) of each behaviour appear higher than corresponding observations obtained in Experiment 1. But, it must also be recalled the number of subjects is three times larger than the number used initially.

Of greater interest, is that the groups in the second year of study, exhibited behaviour patterns similar to those of the groups studied in the previous year. Namely, initially high rates of chasing and biting were observed, followed by a precipitous decline in both activities such that only low rates of all activities (including displacement) were seen by the end of the observation period. This decline occurs one week later in Experiment 3 than in Experiment 1 but is no less obvious.

Frequency of Initiation

The number of initiations by each size-colour class by behaviour per week are presented in Table 3 (Appendix C). For all three behaviours SL fry were the most active followed by LL fry: a reversal of the relationship between these size-colour classes found in Experiment 1. Dark coloured fry were the least aggressive: SD fry chased and bit least often, whereas LD fry displaced the least often. This difference between dark- and

Figure 3. Means ($\pm$ s.e.m.) of displacement (DIS), chasing (CHS), and biting (BITE), averaged across the four size-colour classes of rainbow trout, per week in the second year.

RAINBOW TROUT

light-coloured initiators is comparable to that found in Experiment 1.

Consideration of total agonistic activity without reference to the size-colour type of the targets can be misleading in terms of understanding intra-class dominance relationships. That is, upon closer inspection, although LL fry were only second most active (i.e. second highest number of total counts of all three behaviours), it is clear they are more aggressive towards the more active SL fry than the reverse. Consideration of the overall activity levels alone would suggest the converse.

The scores of LL to SL for displacing (120 to 3), chasing (408 to 62), and biting (341 to 64) demonstrate that LL fry are dominant over SL fry, as they were in Experiment 1. By comparison, the higher overall activity of SL fry can be accounted for in the very large number of intraclass (SL to SL), rather than interclass, interactions.

Similarly, LD fry are dominant over SL fry, although they are less active overall. The scores of total LD initiations to reciprocal SL initiations for: displacing (54 to 40), chasing (145 to 80), and biting (139 to 86) are convincing on this point and the findings of Experiment 1 are again corroborated. Thus, no data were found in the current study to argue against the view put forward in Experiment 1 that the order of relative dominance in these young rainbow trout samples is: $LL > LD > SL > SD$.

As in Experiment 1, comparable levels of all three behaviours observed in the final week of observation are preceded by markedly higher levels of chasing and biting relative to displacement activity. Inspection of Table 3 (Appendix C) reveals that much of the elevated levels of chasing and biting are attributable to interactions principally between SL and SD fry or among SL fry alone. Activity by larger fry, regardless of colour, is relatively lower and directed toward the small fry.

Spatial Behaviour

Spatial behaviour, in the form of station holding, was also observed. Station holding was operationally defined as a position held by a fry for a period of no less than 30 seconds during an observation period. The position had to be maintained consecutively although it was commonly observed fry would station hold for somewhat shorter periods, sortie from that position to engage in combat with another fish, and then return. This process could be repeated several times.

In addition, not all fry station held, rather some were seen to cruise continually throughout part or all of the tank during the observation period. In pilot work it was found that 80% to 90% of fry of both species observed holding a position for this length of time could be expected to return to that position after leaving to feed or to interact with other fry.

These pilot observations were made on newly free-swimming fry of an age comparable to that of the fry studied in the thesis work. The fry ($N > 1000$) were held in a Min-O-Cool tank. No record of the distribution of holding durations was made.

In the analysis of spatial behaviour, a multivariate analysis of variance (MANOVA) procedure was used. The analysis was performed on the Carleton University CP6 system, using the BMDP'81 4V statistical package. The data used in the analysis were obtained from 24 fry (6 fry per size-colour class). Each fry was individually distinguishable on the basis of parr markings.

The spatial co-ordinates of each fry was recorded daily and the mean weekly position calculated for each of the four weeks of observation. The co-ordinates consisted of triplet scores representing the longitudinal (parallel to the long axis, and water flow, of each tank), lateral (perpendicular to the long axis, and water flow, of each tank), and vertical (depth) co-ordinates of the observed station. The overall design involves one between-groups factor (Size-colour class) and one within-groups, or repeated measures, factor (Time). There were four levels of each factor, resulting in a 16 cell Size-Colour Class x Time matrix. Within each cell were 6 spatial co-ordinate triplets (one triplet per fry). The analysis was performed treating length, width, and depth as three separate dependent variates.

Prior to the MANOVA test, the equality of variance across size-colour class was examined for each dependent measure. The $F_{\max}$ -test was used (Kirk, 1968; Sokal and Rohlf, 1973). This test relies on the tabled cumulative probability distribution of a statistic that is the variance-ratio of the largest to smallest of several sample variances. This distribution is known (see, for example, Sokal and Rohlf, 1973, p. 210).

No significant departures from the assumption of homoscedasticity were found. Hence, the data were not transformed prior to analysis.

The analysis found no significant Size-Colour Class x Time interaction. The Wilk's lambda (L) score was 0.24 which corresponds to an approximate F value = 0.84 with df= 27, 35.7 ($p= 0.68$). The relationship between Wilk's L and the approximate F with appropriate degrees of freedom is discussed in Rao (1973, pp. 555-556).

Similarly, there was no statistically significant Time, i.e. within groups, main effect. Wilk's L = 0.90, which corresponds to an approximate F = 0.71 with df= 9, 141.3 ($p= 0.70$).

However, a statistically significant Size-Colour class, i.e. between groups, difference was found. Wilk's L for the multivariate test (i.e. includes all three dependent variables) was 0.27. This corresponds to an approximate F = 3.52 with df= 9, 43.9, $p= 0.02$. Inspection of the subsequent univariate tests

(i.e. analysis of each dependent variable separately) reveals a statistically significant difference between group on the basis of longitudinal position ($F_{3, 20} = 9.92, p < .001$).

There were no significant differences between groups in terms of lateral position ($F_{3, 20} = 0.92, p > .05$) or depth position ($F_{3, 20} = 1.71, p > .05$).

From these analyses an understanding of the spatial distribution of the rainbow trout fry observed is obtained. First, station holding is observed in the first week of free-swimming in all four size-colour classes. Moreover, there are no statistically significant shifts in spatial location of these stations after one month of observation.

Second, there are no distinguishable differences between fry of different size-colour classes on the bases of lateral or depth positioning. The mean lateral position for the sample was 7.4 ± 0.2 in ($n = 96$) while the mean depth position was 3.0 ± 0.3 in ($n = 96$).

However, fry of the different size-colour classes do exhibit statistically detectable differences in terms of longitudinal position. Inspection of the group means reveals that SD fry adopt longitudinal positions near one end of the tank ($x \pm \text{s.e.m.} = 4.4 \pm 0.7$ in, $n = 24$) whereas SL fry maintain stations closer to the opposite end of tank ($x \pm \text{s.e.m.} = 12.5 \pm 0.9$ in, $n = 24$).

In contrast, large fry tend to occupy the longitudinal centre of the tank. For LD fry the mean longitudinal position was 9.1 ± 1.1 in ($x \pm \text{s.e.m.}$, $n = 24$). For LL fry the mean longitudinal position was 9.2 ± 0.8 in ($x \pm \text{s.e.m.}$, $n = 24$).

Subsequent to all possible, paired multivariate comparisons, using a Bonferroni procedure, were conducted to further evaluate statistical differences in spatial position between the four Size-Colour groups. In such a procedure, the criterion alpha (α) level for each comparison is established by dividing the overall error rate ($\alpha = 0.05$) by the total number of possible paired comparisons (6). The criterion α then is set at $\alpha = 0.008$.

Significant differences in spatial positioning were found between the following classes. First, the spatial position of SD fry were significantly different from those of SL fry ($T = 35.0$, $p = 0.003$). Inspection of the univariate tests (i.e. each spatial dimension examined separately), shows a significant difference between SD fry and SL fry in terms of their longitudinal position ($F_{1, 20} = 29.3$, $p = 0.000$) but not in terms of depth or lateral position.

Second, the spatial position of SD fry were also significantly different from those of LL fry ($T = 19.4$, $p = 0.006$). Inspection of the univariate tests between these two groups shows a significant difference in terms of the longitudinal position ($F_{1, 20} = 10.1$, $p = 0.005$) but not in terms of depth or lateral position.

Experiment 4: Brook Charr

Method

Just as Experiment 3 was a replication and extension of the procedures used in Experiment 1, so Experiment 4 was a replication and extension of Experiment 2.

Paralleling the changes made in Experiment 3, the present experiment contained three minor modifications of the procedures used in Experiment 2. These were: (1) the use of brook charr fry derived from commercial rather than laboratory egg stock (Linwood Acres Trout Farm, Campbellvillecroft, Ontario), (2) trebling the number of observation tanks and subjects, and (3) recording spatial behaviour (station holding) in addition to the three forms of agonistic behaviour.

Results

Frequency of Initiation

The weekly levels of the three agonistic behaviours, collapsed across the four size-colour classes is presented in Figure 4. It can be seen that, by the fourth week of observation, the rates of the three behaviours are comparable. Indeed, except for elevated levels of chasing in Week 3 and Week 4, the rates of all behaviours are low and steady throughout.

Despite this phlegmatic pattern of interaction, behavioural differences among the four size-colour classes are discernible; the weekly total of each behaviour for the 16 possible dyad

Figure 4. Means ($\pm$ s.e.m.) of displacement (DIS), chasing, (CHS), and biting (BITE), averaged across the four size-colour classes of brook charr, per week in the second year.

BROOK CHARR

YEAR 2

combinations is presented in Table 4 (Appendix C). With respect to overall activity, SL fry are the most active, LL fry the second most, SD fry the third most, and LD the least active. This pattern holds for all three behaviours.

Thus for displacement, the total initiations by class, in descending order, are SL (196) > LL (170) > SD (31) > LD (20). For chasing the values are: SL (260) > LL (148) > SD (23) > LD (4). Finally, the pattern among the classes for biting is: SL (175) > LL (78) > SD (17) > LD (7). As in Experiment 3 then, light-coloured fry were more active than dark-coloured fry. Moreover, for both colour types, smaller individuals were more active than large fry.

Consideration of overall activity alone does not sufficiently depict the dominance relationships. For though the activity pattern (i.e. agonistic activity without consideration of the size-colour class of the receiving, or target, fish) is SL > LL > SD > LD, the dominance pattern (i.e. agonistic activity which takes into account the size-colour class of the receiver) is that of the one established for Experiment 2, namely: LL > SL > LD > SD. That is, the number of initiations by LL fry against SL fry is greater than the converse for all three behaviours: displacement (69 for, to 1 against), chasing (67 to 3), and biting (51 to 2). A similar pattern exists for SL to LD initiations: displacement (13 for, to 13 against), chasing (26 to 2), and biting (21 to 6). Moreover, LD fry appear marginally

dominant over SD fry, with the following values of initiation and counter-initiation: displacement (5 to 1), chasing (2 to 0), and biting (1 to 1).

The discrepancy between the activity and dominance relationships among the size-colour classes is resolved when considering the type of targets fry attack. SL fry interact most often with members of their own size-colour class; hence having a proportionately smaller number of initiations against larger fry, particularly LL fry. In contrast, LL fry interact minimally with other LL fry and LD fry; directing most of their attacks to SL fry.

In spite of an overall activity pattern different from that seen in Experiment 2 (Figure 4 versus Figure 2), the dominance relationships among the brook charr size-colour types were identical to those observed a year earlier in Experiment 2. Of particular note was the relationship between the intermediate size-colour types: SL fry were again seen to dominate LD fry. These findings further highlight the difference between brook charr and rainbow trout with regard to intermediate size-colour class relationships.

Additionally, as with the previous experiments, early anecdotal reports (Jenkins, 1969; Newman, 1956) that LL fry and SD fry occupy the most and least dominant classes, respectively, are supported by the quantitative observations of the current

experiment.

Brook Charr Spatial Behaviour

Brook charr spatial behaviour was studied in a manner identical to that used for the rainbow trout. The method of analysis, using the multivariate analysis of variance (MANOVA) was also identical.

Qualitatively, the two species differed in the onset of clear patterns of station holding. Though both species engaged in agonistic activity within the first week of free swimming, discernible station holding by brook charr was not observed until the second week of the baseline period. Hence the MANOVA procedure spans a three week rather than four week period as it did for the rainbow trout.

Thus, the data matrix used in the MANOVA was composed of one between groups variable (Size-Colour class) and one within-groups, or repeated measures, variable (Time in weeks). There were four levels of the first variable and three levels of the second, producing a 12 cell Size-Colour class x Time matrix, with 6 entries per cell. In turn, each entry was composed of three mean spatial (longitudinal, lateral, depth) co-ordinates of a particular fry for a given week.

Homoescadasticity was evaluated using the $F_{\max}$ test. No statistically significant departures from homogeneity of variance were observed in the sample. Thus, the data were not transformed

prior to analysis.

The Size-Colour Class x Time interaction was not found to be statistically significant. Wilk's L was 0.45. This corresponds to an approximate $F = 0.77$ ($df = 18, 42.9, p = 0.72$). Similarly, the Time (within group) main effect was not statistically significant. Wilk's L was 0.91; which corresponds to an approximate $F = 0.63$ ($df = 6, 76.0, p = 0.71$).

However, a significant Size-Colour class (between group) main effect was detected. Wilk's L = 0.13, corresponding to an approximate $F = 6.42$ ($df = 9, 43.9, p < 0.01$). Inspection of the subsequent univariate tests (i.e. one analysis for longitudinal scores only, followed by a separate analysis for lateral scores, and finally, an analysis of depth scores alone), reveals a significant difference between the size-colour classes on longitudinal positioning ($F = 16.8, df = 3, 20, p < .01$). No significant differences were found between groups with respect to lateral or depth positioning.

Thus, the spatial behaviour of those brook charr studied is similar to that seen in the rainbow trout fry. First, the positions of stations, once established, do not vary over the time of observation. It is noted that station holding in the brook charr sample occurred in the second week of free-swimming, rather than in the first week as it did in the rainbow trout case.

Second, fry of the different size-colour classes do not differ significantly in terms of the lateral or depth coordinates of their stations. The mean lateral position for the sample was 6.6 ± 0.3 in. ($x \pm \text{s.e.m.}$, $n = 72$) while the mean depth position was 2.8 ± 0.4 in. ($x \pm \text{s.e.m.}$, $n = 72$).

With respect to longitudinal position, SD fry tended to occupy the end of the tank furthest from the water inlet, maintaining a mean position of 15.8 ± 0.8 in. ($x \pm \text{s.e.m.}$, $n = 18$). SL fry tended to occupy the opposite end of the tank, maintaining a mean position of 5.7 ± 0.7 in ($x \pm \text{s.e.m.}$, $n = 18$).

In contrast to small group members, fry of both the LD and LL size-colour classes tended to occupy the middle regions of the tank. This is reflected in the mean longitudinal positions. Thus, for LD fry the mean longitudinal position was 9.4 ± 1.3 in ($x \pm \text{s.e.m.}$, $n = 18$) whereas for LL fry the mean longitudinal position was 10.1 ± 0.7 in ($x \pm \text{s.e.m.}$, $n = 18$).

Comparable station holding by fry of the four size-colour classes was also found for rainbow trout (Experiment 3).

These observed differences in the spatial behaviour of fry of the four size-colour classes were further evaluated using post hoc, All possible paired multivariate comparisons. A Bonferroni procedure was used by partitioning the overall α (alpha) level ($\alpha = 0.05$) by the total number of possible paired comparisons (6), to establish a criterion α (alpha) level for each comparison of $\alpha = 0.008$.

The results of these comparisons reveal that the mean weekly spatial behaviour of SD fry was significantly different, in paired comparison, with that of: (1) SL fry ($T = 76.3$, $p = 0.000$), (2) LD fry ($T = 23.1$, $p = 0.003$), and LL fry ($T = 36.2$, $p = 0.000$). Inspection of the univariate tests (i.e. longitudinal, depth, and lateral position examined separately), shows these differences are due to differences in longitudinal position and not to depth or lateral position. These differences in longitudinal position are reflected in the corresponding F statistics which are as follows: (1) SD fry-SL fry: $F_{1, 20} = 49.2$, $p = 0.000$, (2) SD fry-LD fry: $F_{1, 20} = 19.9$, $p = 0.000$, (3) SD fry-LL fry: $F_{1, 20} = 15.6$, $p = 0.001$.

It was further found the spatial position of SL fry was significantly different from that of LD fry ($T = 78.2$, $p = 0.008$). This difference was due to the difference in longitudinal position between fry of these two groups ($F_{1, 20} = 10.0$, $p = 0.008$). There were no differences between these two groups in terms of depth or lateral position.

Size-Colour Class Membership

In the preceding four experiments, there was at least one fry of each size-colour class present in each tank. To obtain a more precise ratio of the number of fry per size-colour class per group the following method was used. The total number of fry in

each size-colour class for each day of observation in Experiment 3 and Experiment 4 was obtained. These totals were summed over days and averaged to obtain a daily per tank ratio of the number of fry in each size-colour class. This ratio for rainbow trout was: 1.4 LL: 1 LD: 2.3 SL: 1.3 SD. For brook charr, the ratio was similar: 1.4 LL: 1 LD: 2.1 SL: 1.5 SD.

Thus, there were, on average, more small fry than large fry. Future studies on the agonistic behaviour in size-colour classes of these species should involve larger sample sizes, as a means of examining the development of agonistic behaviour in populations with size-colour class distributions potentially different from those studied here. In so doing, the generality of the findings of the present work may be assessed.

DISCUSSION

A picture of the development of agonistic behaviour in these two species now emerges. Both populations begin similarly: fry appear uniform in size and colour when initially free-swimming. Moreover when introduced into a new environment they distribute themselves randomly throughout the range.

Interactions begin very rapidly however, occurring with regularity by the end of the first week of introduction. In both species the lightest coloured and largest of the fry become the most dominant: they initiate attacks much more often than they are attacked themselves. Moreover, for rainbow trout they are

the most active; whereas in brook charr, they are the second most active of the classes.

In direct contrast, for both species, the smallest and darkest coloured fry are the least successful; initiating very few attacks and yet being attacked with regularity by the fry of other classes, particularly the SL fry.

SL fry and LD fry occupy the intermediate positions on the interclass dominance dimension. LD fry are more successful than SL fry in clashes between individuals of these two groups for rainbow trout but this situation is reversed in brook charr.

The spatial behaviour is correlated with agonistic activity, although there are species differences. For rainbow trout, interaction occurs in a central arena: the core regions of the tank. As the number of encounters increases with time and the dominance relationships between members of the size-colour classes are established, individuals of lower status are relegated to the outer borders of the volume by the dominant fry.

Hence SD fry hold fringe positions whereas LL fry occupy central positions in the tank. LD and SL fry occupy the regions between the centre and the periphery such that the mean weekly positions of SL fry are closer to the centre than those of LD fry. Since LD fry are dominant over SL fry and subordinate to LL fry, this spatial arrangement suggests that LD fry may be using the spatial behaviour of SL fry as a physical buffer between

themselves and LL fry. This has also been reported by McNicol and Noakes (1981) for juvenile brook charr.

For brook charr, there is no apparent forcing outward from a preferred position as with the rainbow trout. Rather individuals stake out an initial position and seek to retain that position. Dominance in this species is simply related to spatial position: the more dominant individuals lie upstream of the less dominant. Hence the mean weekly position is in perfect correspondence with that of presumed dominance, namely $LL > SL > LD > SD$ with fry of the LL class being furthest upcurrent and close to the centre, and SD fry are at the extreme edge. No such "buffering" behaviour, as exhibited by the rainbow trout fry, is seen in the brook charr fry and so differs from the recent findings of McNicol and Noakes (1981). Possible explanations for the difference between this work and that of McNicol and Noakes (1981) may lie in that the experimental settings, observation procedures as well as the ages and strain of subjects were different.

From these four initial experiments then an understanding of the activity of young fry of both these species has been obtained empirically for both agonistic and spatial patterns of behaviour. The remaining experiments further explore these ongoing processes by altering group membership through the addition or removal of dominant and nondominant individuals.

CHAPTER 4: Experiment 5 and Experiment 6

So far, the work has examined agonistic interactions in rainbow trout and brook charr fry from the onset of such activity up to the time of formation of stable, relatively low, levels of interaction. By perturbing this latter "steady state", further understanding of the dominance relationships established may be obtained. Systematic perturbation of the steady state here followed one of two related routes.

First, the response by group members to the introduction of a single, "intruder" fry was studied. Analyses were performed from: (1) the perspective of the group as well as from (2) the perspective of the intruder. The group from which the intruder was selected was designated the home group (tank) whereas the group into which the intruder was introduced was called the host group (tank). Observations at the group level were conducted for both the home and host tanks. Second, complementary experiments were performed documenting intragroup behaviour following the removal of fry.

These two procedures of addition and removal of fry were dovetailed: the fry removed from one group was used as the intruder in another group. That is, the two series were yoked.

These intruder scenarios were conducted for both species and involved: (1) intruders of dominant status (Experiment 5 — rainbow trout and Experiment 6 — brook charr), (2) isolated fry

of dominant status (Experiment 7 — rainbow trout and Experiment 8 — brook charr), and (3) intruders of nondominant status (Experiment 9 — rainbow trout and Experiment 10 — brook charr).

Experiment 5: Dominant Rainbow Trout as Intruder

The purpose of this experiment was to observe the behaviour of dominant fry under three conditions. Agonistic activity was studied: (1) in home conditions in the baseline period, (2) following transplantation to host conditions, and (3) in home conditions subsequent to the return of the intruders from the host conditions. Observations of ongoing intragroup agonistic behaviour in home and host tanks were performed concurrently.

Method

Following the completion of Experiment 3, five of the 15 tanks used in that experiment were designated as home tanks, another five tanks were designated as host tanks, and the remaining five tanks were designated for use in Experiment 7. The most dominant fry of each home tank was identified and introduced into one of the host tanks as an intruder. The criteria used to select these dominant status intruders were: (1) each intruder was of the LL size-colour class who (2) commanded the central region of its home tank.

Interactions between dominant fry with other home group members were observed for one week prior to transplantation to host conditions. The number of attacks (displacements, chases, and bites) initiated and received, by the dominant fry were recorded during this period. Simultaneously, agonistic activity in home and host conditions were also documented using the procedures employed in Experiment 3.

On the final day of the baseline period, a small portion of the ventral tip of the caudal fin of each dominant fry was removed by clipping. This procedure allowed for the rapid identification of the fry in the host tank and was found to be less traumatic than fin-branding as has been used with older subjects (McNicol and Noakes, 1979).

A 24 hour period was allowed for recovery, after which time the fry were introduced into the host tanks for a one week period. During this time, as in the baseline period, the number of attacks initiated and received by the intruders, as well as ongoing home and host tank activity, were recorded.

In the third and final phase, the intruders were returned to home conditions. The type and frequency of intruder-resident interactions were recorded as were intragroup interactions in home and host conditions. The snout to fork length of each fry was measured at the conclusion of the experiment.

Results: Dominant Individual as Intruder

The mean frequencies of initiation and reception by the intruder for each of the three conditions are presented in Figure 5. Each score represents the mean ($\pm$ standard error of the mean) activity, averaged across all three behaviours, with fry of a given size-colour class.

It can be seen in the baseline period (Figure 5, first panel), that the fry chosen as intruders were indeed dominant in home conditions. They were active against other group members with 88% of these attacks involving biting or chasing. In contrast, attacks by other group members upon the dominant fry were nearly nonexistent; the exception being a number of attacks by SL fry. Of these, 99% involved either chasing or biting.

This situation changes dramatically for the intruders following placement in the host tanks. It can be seen in Figure 5 (middle panel) intruder activity against SL fry and LL fry increases markedly over baseline (home tank) levels.

This increase is a direct response to the fierce reception by SL and LL host tank residents. Agonistic activity by the intruder against small-sized host tank residents is interpreted as displaced (redirected) activity with respect to the large resident fry. This is based on the observation that none of the intruders were able to secure central positions in the host tanks; any attempt to do so elicited vigorous chasing and biting attacks by dominant residents. Thus driven to the periphery of

Figure 5. Observed initiations ($\pm$ s.e.m.) by the dominant rainbow trout intruder (I), and by resident fry upon the intruder (R), during the BASELINE, INTRUDER, and RETURN phases of Experiment 5. (SD= small, dark; SL= small, light; LD= large, dark; LL= large, light).

RAINBOW TROUT (dominant)

the tanks by the large-sized defenders, the intruders interacted with the smaller residents who, as in Experiment 3, tended to occupy these regions. As a result, the number of intruder - small fry interactions rose (Figure 5, middle panel).

All five intruders also undergo colour changes in their respective host tanks, becoming noticeably darker so that they are indistinguishable from LD host tank residents.

These alterations in agonistic activity, spatial behaviour, and colouration strongly suggest a loss of dominance status by each of the five intruders.

These alterations continue to be observed following return of the intruders to their home tanks. First, the number of attacks by the LL residents with the returnees increased over baseline (pre-removal) levels. These interactions are primarily chase and bite sequences, with noticeably more of the interactions initiated by the residents than by the returnees. This is reflected in the total number of initiations against LL residents by the returnees relative to LL resident-initiated attacks. That is, following their experiences in the host tanks, the returnees are unable to demonstrate their previous superiority over other fry in home tank encounters.

Also, all returnees were seen to retain their dark body colouration and to station hold in peripheral regions of their home tanks; the central positions having been secured by the more

aggressive LL residents. In essence, fry who remained in the home tanks become dominant over those who were transplanted.

No statistical differences in length were observed between the intruders and those of the LL fry of the home and host tanks. Mean length was 3.8 cm (standard error of the mean = 0.3 cm, $n=15$).

Comparing the first and last panels of Figure 5, there can be seen a decrease in the number of interactions between the original dominant fry and SL fry following return. This decline is directly attributable to the very high number of attacks by the LL residents upon the returnees: the returnees are simply too occupied by the increased LL resident activity to engage in interactions with fry of other size-colour classes.

Group Behaviour: Home Tanks

The group behaviour in the home tanks during the three phases of Experiment 5 can be seen in Figure 6. There, it can be seen mean levels of displacement decline after removal of the dominant fry and remain low following their return.

By size-colour class, for SL fry, agonistic activity actually increases following removal of dominant fry but decreases following their return.

This is reflected in the number of interactions (all behaviours) during each phase: 44 (Baseline), 51 (Dominant Removed), and 26 (Dominant Returned). These encounters involved

Figure 6. Mean totals ($\pm$ s.e.m.) of displacement (DIS), chasing (CHS), and biting (BITE) by all classes of rainbow trout residents of the home tank during the BASELINE, REMOVE, and RETURN phases of Experiment 5.

RAINBOW TROUT REMOVAL OF DOMINANT

primarily other SL fry or LL fry. For SL-SL interactions, this activity represents: 55%, 43%, and 4% of the total activity in the Baseline, Dominant Removed, and Dominant Returned phases respectively. This is comparable for SL-LL interactions representing: 31%, 41%, and 61% of total activity in the Baseline, Dominant Removed, and Dominant Returned conditions respectively.

Activity (all behaviours) by LD fry also declines following the removal of the dominant fry. The total observations of LD activity per phase are: 17 (Baseline), 0 (Dominant Removed), 20 (Dominant Returned). Of these interactions, 76% in the Baseline condition and 85% in the Dominant Returned condition were encounters with LL residents.

The activity by LL fry is different than for SL or LD fry, such that the levels of chasing and biting increase rather than decrease following removal of the dominant fry. This is reflected in the LL fry - LL fry activity scores for these behaviours in each phase. For chasing, these scores are: 2 (Baseline), 165 (Dominant Removed), 27 (Dominant Returned). Comparable results are seen for biting: 35 (Baseline), 175 (Dominant Removed), and 29 (Dominant Returned).

These preceding scores also show a decline in activity among resident LL fry following the return of the dominant fry. This decline represents a shift in activity by the residents from other residents to the returnees.

Group Behaviour: Host Tanks

Behaviour in the host groups in the three phases of Experiment 5 are depicted in Figure 7. There, it can be seen the mean levels of all three agonistic behaviours decline following the introduction of intruders. In particular, the dramatic decline in chasing and biting activity is attributable to a decrease in interactions involving SL fry. For chasing, SL fry activity scores in each phase were: 137 (Baseline), 49 (Intruder Added), and 53 (Intruder Removed). Biting activity scores for SL fry were: 128 (Baseline), 34 (Intruder Added), 28 (Intruder Removed).

The decline in activity following the introduction of intruders (Figure 7) reflects the shift in activity by SL and LL residents to the intruders. With the removal of the intruders, there is a corresponding increase in intragroup activity as the fry once again direct their activity toward other group members.

Experiment 6: Dominant Brook Charr as Intruder

The purpose of this experiment was to observe the changes in agonistic activity produced by the transplantation of brook charr fry from home to host conditions and back again. The changes were observed at the intragroup level for both home and host conditions as well as at the individual level with respect to the transplanted fry.

Figure 7. Mean totals ($\pm$ s.e.m.) of displacement (DIS), chasing (CHS), and biting (BITE) by all classes of rainbow trout residents of the host tank during the BASELINE, ADD, and RETURN phases of Experiment 5.

RAINBOW TROUT

ADDITION OF INTRUDER (DOMINANT)

TOTALS
(MEAN ± SEM)

Method

Following the completion of Experiment 4, 10 of the groups used in that study were assigned to the present experiment. Half of the groups were designated home tanks while the other half were designated as host tanks.

The procedures used in this experiment are identical to those used in Experiment 5. The method of choosing ~~dominant fry~~ for transplantation, fin-clip identification, and data recording (including fry length measurements) are the same. In addition, the length of the intruders was also measured prior to placement in the host tanks.

Results: Dominant Individual as Intruder

The mean number of initiations and receptions by the intruders, collapsed across all three agonistic behaviours, is presented in Figure 8. The figure shows mean ($\pm$ standard error of the mean) activity by the intruders with fry of the four size-colour types for the baseline, host tank, and home tank phases of the experiment.

It can be seen in Figure 8 (first panel) the fry selected as intruders initiate attacks upon SL and LL home group members, with only the SL fry reciprocating. In the dominant-SL fry situations, 94% of all initiations by the dominant fry involved either chasing or biting. This was also true of SL fry

Figure 8. Observed initiations ($\pm$ s.e.m.) by the dominant brook charr intruder (I), and by resident fry upon the intruder (R), during the BASELINE, INTRUDER, and RETURN phases of Experiment 6. (SD= small, dark; SL= small, light; LD= large, dark; LL= large, light).

BROOK CHARR (dominant)

initiations against the dominant fry: chasing (66%) and biting (29%). In contrast, in the dominant-LL fry, 93% of all initiations by the dominant fry involved displacement or chasing, with few observations of biting.

Transfer of the dominant fry to the host tanks produced results very different than those observed for rainbow trout (Experiment 5): intruders continued to exhibit dominant behaviour over other group members. This can be seen in the middle panel of Figure 8.

Initiations by the intruders against SD, SL, and LL fry were noticeably greater than counter-attacks by fry of these classes. This can be seen readily in the middle panel of Figure 8. In contrast, interactions between intruders and LD host tank residents were infrequent as they were with LD home tank residents in the baseline (pre-removal) period.

Qualitatively, the brook charr intruders underwent no darkening of body colouration as did the rainbow trout (Experiment 5). Moreover, by the completion of the intruder phase, all intruders occupied the central regions of their host tanks. The mean co-ordinates (determined from observations of each intruder for four days) of these stations were: (8.30, 7.30, 3.95; $n=20$).

The introduction of the intruders elicited vigorous responses by host tank residents of both species. This process parallels the initial high levels of activity seen in the newly

formed groups in the the initial experiments. Hence, it appears that exposure to conspecifics, in fry at this early stage of development, results in an initial period of intense agonistic activity. This occurs in response to the addition of dominant and, as shall be seen later, nondominant intruders.

This phenomenon is seen again when the intruders are returned to their home tanks. That is, higher than baseline levels are seen in the interactions between the returnees and the residents in all but the SD size-colour class (Figure 8, third panel). This increased activity is a response to the reaction of LL residents to the return of the intruders; the number of initiations by these residents being noticeably greater baseline levels.

It is noted the mean length of intruders (4.4 cm) was slightly, but not significantly, greater than that of LL host tank residents (4.3 cm) as well as that of LL home tank residents (4.2 cm).

Activity following the return of the intruders to home conditions, then, is primarily conflict between the returnees and newly established LL dominants. The outcome of these interactions was resolved in favour of the returnees as they re-secured the central regions of their home tanks. The mean co-ordinates (determined from observations of all returnees for four days) were: (11.8, 6.6, 5.0; n=20). Interestingly, despite their

losses to the returnees, no colour changes were exhibited by the LL residents, although they did return to peripheral stations in the tanks.

So far, it is seen that dominant fry of both species must re-establish their positions in the home tanks, irrespective of their experiences in the host tanks. This re-establishment period is highlighted by high levels of agonistic activity by returnees and residents alike. The two species differ in that only the brook charr are able to regain their dominant status in the home tanks, as exhibited by their agonistic activity, light colouration and central station holding behaviour.

Group Behaviour: Home Tanks

As with the rainbow trout, removal of the dominant fry in the brook charr home tanks results in an increase in activity in the remaining residents. This can be seen in Figure 9 which presents the mean levels of displacement, chasing, and biting averaged across the four size-colour classes for each behaviour. There it can be seen there are increases for displacement and chasing but not biting.

Furthermore, these increases are primarily increases in SL fry and LL fry activity. For SL fry, this increase is reflected in the changes in total amount of chasing in each of the three phases of the experiment: 26 (Baseline), 80 (Dominant Removed), and 50 (Dominant Returned). LL fry were similarly active,

Figure 9. Mean totals ($\pm$ s.e.m.) of displacement (DIS), chasing (CHS), and biting (BITE) by all classes of brook charr residents of the home tank during the BASELINE, REMOVE, and RETURN phases of Experiment 6.

BROOK CHARR
REMOVAL OF DOMINANT

responsible for the majority of all observed displacement (65%) and chasing (71%) activity.

During the absence of the dominant fry, other LL fry were seen to occupy the core areas of each home tank. The mean coordinates (calculated from observations of each fry over four days) being: (9.6, 7.6, 3.8; $n = 20$).

The return of the dominant fry from the host tanks resulted in continued low frequency of biting attacks, a decrease in displacement activity, and continued increase over baseline in chasing activity. The majority (95%) of all chase encounters involved either SL or LL residents.

This pattern is thought to represent the disinhibition and inhibition of agonistic activity through the removal and return, respectively, of dominant fry.

In the absence of the most dominant group member, other fry come to be dominant but relinquish this dominance to the returnees following intensive interactions in the early stages of the re-introduction period.

Group Behaviour: Host Tanks

Mean levels of displacement, chasing, and biting among host-tank residents are shown in Figure 10. From very low baseline activity levels, agonistic interactions increase following the introduction of intruders. During this period, much of the intragroup interactions involved SL and LL residents. For SL

Figure 10. Mean totals ($\pm$ s.e.m.) of displacement (DIS), chasing (CHS), and biting (BITE) by all classes of brook charr residents of the host tank during the BASELINE, ADD, and RETURN phases of Experiment 6.

BROOK CHARR

ADDITION OF INTRUDER (DOMINANT)

fry, the percentage of total initiations by behaviour was: 73% (displacement), 45% (chasing), and 41% (biting). For LL fry, the percentage of total initiations by behaviour was: 28% (displacement), 55% (chasing), and 59% (biting).

This increased intragroup activity is a result of the destabilizing presence of the intruders who vie for dominance in the host tanks. A consequence of their activity is that the residents seek to reform previously established intragroup dominance relationships. This is reflected in the increased SL fry activity against LL fry.

Further evidence for the establishment of new intragroup relations is seen following the removal of the intruders to their home conditions. During that time, levels of displacement and chasing activity in the host tanks continue to increase.

DISCUSSION

From Experiment 5 and Experiment 6, it is evident that the removal of a single dominant individual results in changes in ongoing intragroup activity. The specific changes seem to be an increase in activity, primarily chasing, following the removal of the inhibiting presence of the most dominant fry of the group. During this time new dominant individuals emerge who are of the LL class.

Changes also occur in the behaviour of the individual who is removed and subsequently returned. In brook charr, the intruders

are able to establish dominance in host conditions. The subsequent return of brook charr intruders to their home conditions results in contests with (primarily) the newly dominant residents. These contests are resolved rapidly (within a week) in favour of the returnees.

In contrast, rainbow trout intruders are unable to attain dominance in host conditions. Following their return to home conditions, the rainbow trout intruders also encounter vigorous attacks by residents. Unlike the brook charr, however, these interactions are resolved in favour of the newly dominant resident fry.

These differences between the two species in terms of the success of intruders following their introduction to host conditions as well as following their return to home conditions remains unexplained.

2

1.0

1.1

1.25

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1.5
1.8
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2.2
2.5
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4.0

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3.2

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1.8

1.4

1.6

MICROCOPY RESOLUTION TEST CHART
NATIONAL BUREAU OF STANDARDS
STANDARD REFERENCE MATERIAL 1010a
(ANSI and ISO TEST CHART No. 2)

CHAPTER 5: Experiment 7 and Experiment 8

Experiment 7: Dominant Rainbow Trout as Isolate

It may be argued the loss in status by the dominant rainbow trout fry upon their return to the home tanks (Experiment 5) was not due to their experiences as intruders in the host tanks. Rather, it was the cessation of continued contact with the other group members in the home environment that was the primary contributor in their inability to accommodate successfully to the restructuring of the intragroup relationships during their absence.

The purpose of the present experiment was to study how separation from other group members, without exposure to new conspecifics, affects subsequent interactions following return home. By comparing the results obtained here with those of Experiment 5, the effects of removal alone may be distinguished from the combined effects of removal and transplantation to a new environment. This was achieved by isolating the dominant fry in solitary conditions.

Method

Following the completion of Experiment 3, 10 of the observation groups were used to study the behaviour of intruders of dominant status (Experiment 5). The remaining five groups were used concurrently to study the effects of isolation upon

dominant fry in their subsequent interactions with other group members.

The procedures used for selecting the most dominant fry of each group were the same as those used in Experiment 5. The interactions between these fry and other group members were observed daily for one week in the baseline period using the observation method employed in the preceding experiments. Following this period, the dominant LL fry were fin-clipped and individually housed in separate 30 cm x 20 cm x 20 cm tanks.

Although fresh water did not flow through these closed system tanks, continuous and generous aeration did generate a mild current. Daily cleaning of the tanks during the isolation period as well as the maintenance of suitable water temperature (14°C) allowed the isolated fish to move about without apparent ill-effect. The period of isolation was also one week, thus the time spent in isolation by the fry in the current experiment was identical to the period the intruders in Experiment 5 remained in the host tanks.

The isolation tanks were placed so that the fish were visible to one another: the fry were physically, but not visually, separated from the other isolates. Earlier pilot work revealed that total physical and visual isolation of fry at this age resulted in abnormal feeding and swimming behaviour with death often occurring. The method adopted minimized the possible isolation-related effects of nonspecific transplantation stress

(Newton, 1982) as well as possible isolation-induced trauma (Miller, 1980).

It is noted, isolation is not deleterious in all fish species. For example male African cichlids (Haplochromis burtoni) demonstrate no impairment in agonistic behaviour, or growth, following isolation (Fernald, 1980; Fraley and Fernald, 1982). More strikingly, Draeger and Chiszar (1982) found isolation actually enhances growth rate in the bluegill sunfish (Lepomis macrochirus).

In the current arrangement, no abnormal behaviour was observed nor were attempts to attack a fry in the neighbouring tanks observed as has been reported in other species, most notably Betta splendens (Meliska and Meliska, 1980; Meliska, Meliska, and Peeke, 1980; Rnic, 1978; Woodward Cain, Jessen, and Flanagan; 1980a, 1980b).

Following the isolation period, the isolated fry were returned to their home tanks and their interactions with other group members recorded. Hence, the treatment of the dominant fry in the baseline and return phases of the experiment was identical to the initial and final phases of Experiment 5. The two experimental procedures differed in that the dominant fry in the current experiment were isolated following removal from the home tanks rather than transplanted to host tanks as in Experiment 5.

Results: Dominant Individual as Isolate

No significant differences in body length were detected following return suggesting that, in one week's absence, growth was not enhanced through isolation although such has been reported for the bluegill sunfish (Lepomis macrochirus) (Draeger and Chiszar, 1982).

Figure 11 presents the mean number of initiations, averaged across all three behaviours, by the dominant fry against members of each size-colour class in each of the three phases of the experiment. The frequency of initiation by group members upon the dominant fry are presented as well.

In the baseline condition (Figure 11, first panel), the number of initiations by the dominant LL fry is noticeably greater than the number of encounters initiated against the dominant fry. Subsequent to this period, the dominant fry were isolated.

Following the return of the fry from isolation, the number of initiations by the returnees against SL and LL fry are greater than those observed in the baseline (pre-removal) levels. Also, the number of countering initiations by members of both these classes against the dominant fry are also noticeably greater than baseline levels. This can be seen in third panel of Figure 11.

These increases clearly favour the returning isolates who initiate against SL and LL fry more often than the converse.

Figure 11. Observed initiations ($\pm$ s.e.m.) by the dominant rainbow trout isolate (I), and by resident fry upon the isolate (R), during the BASELINE, ISOLATE, and RETURN phases of Experiment 7. (SD= small, dark; SL= small, light; LD= large, dark; LL= large, light).

RAINBOW TROUT (dominant)

Inspection of the data (not shown) reveals these encounters involved chasing and biting more frequently than displacement.

This increased activity reflects attempts by the returnees to re-establish their position in the home environment and the corresponding response to these efforts by the residents. In particular, isolates must deal with other LL fry who attain dominance during their absence. The greater number of attacks by the isolates relative to the newly dominant fry eventually enable a full recovery of status, although high rates of agonistic behaviour are exhibited by both the returning isolates and the residents on the first day of return (not shown).

Further evidence for the recovery of status by the isolates is offered in that the isolates undergo no darkening of body colouration as was seen during the subordination of the returning intruders following their return to home conditions in Experiment 5. Also the isolates, by the conclusion of the experiment, are seen to occupy the central regions of the tank whereas other LL contenders do not.

These findings strongly suggest that removal from the home tank alone cannot account for the inability of the returning dominant fry in Experiment 5 to successfully re-establish themselves. That is, losses sustained in agonistic encounters with conspecific strangers will also influence subsequent success when re-introduced to home conditions.

The elevated levels seen in the return condition in this experiment, as well as those seen in Experiment 5 and Experiment 6, illustrate the resistance of residents toward intrusion; even if the intruder is a familiar individual with previously established higher dominance status. The rapidity with which this process is manifested is evident in that such resistance is seen following only one week's absence by the dominant animal.

Group Behaviour: Home Tanks

Intragroup behaviour in the home tanks is depicted in Figure 12. There, it can be seen there is a decline in agonistic activity (as expressed as an average across the four size-colour classes for each behaviour) following the removal of the dominant fry. This finding is counterintuitive given that the removal may be thought to constitute a release from the inhibiting presence of the dominant animal. Such being the case, a rise, rather than a decline, in agonistic activity following removal would be predicted; as was seen for rainbow trout in Experiment 5.

It is noted, however, that an increase in displacement activity by SL fry was seen after the isolation of the dominant fry. The total scores of reception for each of the three conditions being: 21 (Baseline), 46 (Isolate), 7 (Return). This doubling from baseline levels was due to increased interaction among SL fry as well as between SL fry and LL fry. These two types of encounters accounted for 98% of the observed increase.

Figure 12. Mean Totals ($\pm$ s.e.m.) of displacement, (DIS), chasing (CHS), and biting (BITE) by all classes of rainbow trout residents of the home tank during the BASELINE, REMOVE, and RETURN phases of Experiment 7.

RAINBOW TROUT

ISOLATION OF DOMINANT

No such expected increases were observed for chasing or biting activity. A possible explanation for this lack of increased activity may be that the dominance relationships formed among the group members were more defined than in the intruder study (Experiment 5). That is, the competition for the space vacated by the isolated dominant fry was resolved more by acclamation than by overt conflict with no attempts to re-align dominance relationships in the absence of the dominant fish.

Experiment 8: Dominant Brook Charr as Isolate.

This experiment was identical to Experiment 7 with brook charr replacing rainbow trout as the subjects of study. The rationale of this experiment was to observe how dominant brook charr fry interact with group members following a period of isolation. It was a control study designed to differentiate the effects of (1) separation involving no contact with conspecifics from (2) separation involving contact with novel, i.e. host tank conspecifics (Experiment 6) upon subsequent home tank interactions.

Method

The procedure used was the same as that in Experiment 7. That is, dominant fry were chosen, observed for a one week period in home conditions, isolated for an equal time, then returned to

their home groups for a final week of observation.

Results

The results of Experiment 8 are presented in Figure 13. It shows the number of initiations (averaged across all three behaviours) by, and upon, the dominant fry by each size-colour class before and after isolation. Interpretation of Figure 13 is straightforward: isolation has no effect on the behavioural relationship between dominant fry and other group members.

No differences between the baseline and return conditions was observed save for a marked increase in initiations by the returning isolates upon other LL fry. These interactions primarily involved chasing (53.6% of total activity by returnees against LL fry).

The nearly complete lack of response by the residents to the returnees suggests the increased activity of the returnees above baseline levels was strictly the result of the continued dominance of the returnees. This is different from the rainbow trout situation (Experiment 7) where returnees encountered strong agonistic activity against them by the residents.

Although LL fry were seen to occupy the central volume of the home tank during the absence of the dominant/isolated fry, (mean co-ordinates: 12.9, 4.6, 1.1; determined from four days observations of five fry), these central positions were regained by the returnees without conflict. The mean station position

Figure_13. Observed initiations ($\pm$ s.e.m.) by the dominant brook charr isolate (I), and by resident fry upon the isolate (R), during the BASELINE, ISOLATE, and RETURN phases of Experiment 8. (SD= small, dark; SL= small, light; LD= large, dark; LL= large, light).

BROOK CHARR (dominant)

for the returnees being: 9.1, 6.9, 2.3; $n = 20$ (calculated from four days observation of each returnee).

Therefore, it is concluded that brief periods of isolation/absence of the most dominant brook charr fry from other group members has little effect upon its subsequent relationship with them. This is different from rainbow trout where the experience of the dominant animal in groups other than its own can radically alter subsequent behaviour in the home environment.

Moreover, rainbow trout isolates meet much greater levels of resistance upon their return than do brook charr isolates as can be seen by inspecting the difference in the scale of interaction in Experiment 7 with Experiment 8. Despite this resistance, isolates of both species eventually re-establish their former positions of dominance.

Group Behaviour: Home Tanks

As in the rainbow trout case, the mean weekly levels of chasing and biting decline following the removal of the dominant brook charr. This can be seen in Figure 14 which presents the mean activity for each behaviour obtained by averaging across the four size-colour classes. Only displacement behaviour increased, as might be expected of other agonistic behaviours if an overall disinhibition of agonistic behaviour hypothesis is entertained. This rise in displacement activity, and unexpected decline in other types of agonistic behaviour, may be

Figure 14. Mean totals ($\pm$ s.e.m.) of displacement, (DIS), chasing (CHS), and biting (BITE) by all classes of brook charr residents of the home tank during the BASELINE, REMOVE, and RETURN phases of Experiment 8.

BROOK CHARR
ISOLATION OF DOMINANT

because, after one month of regularly occurring agonistic activity, dominance relationships become set with displacement the most preferred of the three behaviours. This is evidenced in that displacement accounted for 68.8% of all agonistic activity observed.

One explanation for the prevalence of displacement over other behaviours may be that, in prolonged periods, chasing and biting are more fatiguing than displacement. Consequently, interactions occurring at this later stage of agonistic interaction involve the least energetically demanding behaviours among agonists in a state of fatigue. (See McNicol and Noakes, 1981).

Alternately, displacement may be used most frequently due to possible shifts in the reinforcement effect of the three behaviours from initial values. That is, it is possible initiated chases and bites fail to produce the responses originally seen during earlier periods and so become less emphasized in the agonistic repertoire of initiators.

Such explanations are speculative at this juncture and must await further clarification. The ultimate explanation accounting for the increase in the relative importance of displacement may prove to be a combination of both physiological and learning effects.

CHAPTER 6: Experiment 9 and Experiment 10

Experiment 9: Nondominant Rainbow Trout as Intruder

The purpose of this experiment was to study the behaviour of nondominant fish when placed as intruders in a new environment. Their behaviour in the home tanks prior, as well as subsequent, to removal was also documented. Thus this experiment was procedurally identical to Experiment 5 with subordinate, rather than dominant, fry in the role of intruders.

The response of residents to intruders of nondominant status may be different from that seen in the presence of dominant LL intruders: relatively less aggressive subordinate fry may not elicit strong responses by residents as do aggressive dominant fry. It may be possible then that a subordinate agonistic posture allows an intruder to be assimilated more readily into an established group situation than would a conspicuous, aggressive posture. If such were true, then, little or no response on the part of residents to a subordinate status intruder would be expected.

This experiment, then, in addition to being a control study for Experiment 5, examines the possible advantage of a relatively nonaggressive posture in securing a position in a new environment.

In addition, this experiment further addresses the response of members of the home and host environments to the removal and

addition of individuals of known dominance status. Group reactions may differ from those seen with dominant intruders (Experiment 5). That is, given that nondominant fry infrequently initiate interactions, the removal of a single nondominant individual may have no detectable effect on the agonistic activity of the remaining group members.

Similarly, the addition of a single, nonaggressive fry may produce no observable change in the ongoing agonistic activity of residents of host tanks.

It is these issues of individual and group behaviour in the presence and absence of nondominant fry that are the focus of this experiment.

Method

The subjects for this experiment were derived from eggs obtained from laboratory stock. The method of incubation, selection and observation of subjects from the time of free-swimming up to the formation of stable intragroup dominance relationships were the same as those employed in Experiment 1.

Ten tanks were used in this experiment; half were designated as home tanks while the other half were designated as host tanks. Assignment to each condition was random.

In the fourth week of free-swimming, one nondominant fry per home tank was chosen to act as an intruder. Two criteria were used in selection. First, all candidates were chosen from the LD

class, precluding the possibility the designate was the dominant animal of the group as well as minimizing the hazards the designate might face in the host tanks. It is noted that in earlier pilot work with clearly subordinate SD fry, as well as with SL fry, intruders were killed and on occasion cannibalized by large-sized host tank defenders.

Second, only those LD fry who consistently held stations in the peripheral regions of the home tank were chosen, further ensuring the nondominant, or at least the "non-most-dominant", status of the intruder.

After a one week baseline (home tank) observation period, the chosen fry were fin clipped, allowed 24 hrs for recovery then transplanted for one week into the host tanks. There was one intruder per tank. During this time intruder-resident as well as resident-resident interactions were recorded. Finally, the intruders were returned to the home tank for a third and concluding week of observation.

Results

The mean total initiations and receptions by the nondominant intruder against other fry in each of the three experimental conditions are presented in Figure 15. There it can be seen in the baseline conditions the LD fry chosen as intruders displayed no clear superiority in the number of initiations against other group members, i.e. were not the most dominant members of their

Figure 15. Observed initiations ($\pm$ s.e.m.) by the nondominant rainbow trout intruder (I), and by resident fry upon the intruder (R), during the BASELINE, INTRUDER, and RETURN phases of Experiment 9. (SD= small, dark; SL= small, light; LD= large, dark; LL= large, light).

RAINBOW TROUT (nondominant)

respective groups. Interactions with SD, SL, and other LD fry are infrequent, with the levels of initiation and reception approximately equal. (Attacks upon SL fry are seen to be slightly higher than reciprocal activity).

In baseline interactions with dominant LL fry, the LD fry are at a clear disadvantage with noticeably more initiations against them than by them (first panel, Figure 15). The attacks directed against the LD fry by the LL fry were of the following frequencies: displacement (60%), chasing (24%), and biting (65%). This result is identical with that of Experiment 1 where displacement was also the modal behaviour following the establishment of intra-group relationships.

Furthermore, placement of the LD intruders into the host tanks elicits aggressive responses by the residents (middle panel, Figure 15). There are low rates of initiation by SD, SL, and LD fry but high levels of initiation by LL residents with little reciprocation by the intruders. Inspection of the data (not shown) reveals that the LL residents were active in all three categories of aggressive behaviour.

In addition, the intruders retained their dark colouration demonstrating the absence of any change in their nondominant status. In spatial terms, agonistic activity was initiated whenever the intruders entered the central regions of the tank with the result that, by the conclusion of the intrusion period, all

intruders were seen to occupy positions only along the perimeter of their respective host tanks.

Upon return to their home tanks, little response was given by SD and LD fry to the returnees (third panel, Figure 15). SL fry response was equally low but higher than reciprocating LD activity toward them. In contrast, high levels of activity were once again observed for the dominant LL residents against the LD returnees relative to reciprocal activity.

These findings show that nondominant animals placed in a new environment are unlikely to improve their subordinate status as reflected in terms of colouration as well as agonistic or spatial behaviour. The responses by the dominant animals in both the intruder and return conditions emphasize the vigour of resistance to intruders by, at least some, members of established groups. This is so despite the nondominant behaviour of the intruders.

Moreover, SD, SL, and LD fry attacks against the intruding LD fry in the host tank suggests this subordinate behaviour is not a preferred situation on the part of the intruder, a possibility raised at the outset of this experiment, but rather is a position enforced by the defenders. Intruders must engage residents to secure their position, however lowly, in the host tanks -- irrespective of their previous status elsewhere.

It is further observed that the LD fry are unable to demonstrate even baseline levels of activity in their interactions against SL home tank residents upon return. As in

Experiment 5 for dominant rainbow trout fry, subordinate fry must fight to re-secure their previous positions, regardless of their original status, upon their return. In essence, the returnees are treated as novel intruders.

Group Behaviour: Home Tanks

Following the removal of the nondominant fry a slight increase in the mean levels of all three behaviours is seen in the home tanks (Figure 16). This increase is attributable to increased LL fry behaviour. These increases over baseline levels are, by behaviour: 165% for displacement, 134% for chasing, and 111% for biting. In contrast, there was actually a reduction in these behaviours by SL fry: 53% for displacement, 56% for chasing, and 43% for biting. Interactions initiated by SD and LD fry were even lower, with only one instance each of displacement and biting following the removal of the nondominant fry.

The majority of these interactions (91% of the displacement, 88% of the chasing, and 90% of the biting) are initiated by LL fry. Since LL fry are not subordinate to the LD fry chosen as intruders it is likely the increased activity following the removal of the LD fry is continued dominance behaviour rather than a disinhibition effect as was suggested for Experiment 5. The pre-eminence of the LL fry is further seen in the return conditions where 93% of displacement activity and 100% of both chasing and biting is initiated by LL fry. These results firmly

Figure 16. Mean totals ($\pm$ s.e.m.) of displacement (DIS), chasing (CHS), and biting (BITE) by all classes of rainbow trout residents of the home tank during the BASELINE, REMOVE, and RETURN phases of Experiment 9.

RAINBOW TROUT NONDOMINANT INTRUDER (REMOVE)

illustrate the ongoing nature of agonistic activity in these groups.

Thus, despite rapid stabilization of dominance-subordination relationships, dominant fry at this stage of development are unceasing in their attacks against other group members, even in the virtual absence of any resistance by those attacked. This persistence of LL fry activity may be related to continued growth in the fry which in turn affects competition for accessible resources in the tanks (see also Yamagishi, 1962).

Group Behaviour: Host Tanks

Following the introduction of the nondominant intruders into the host tanks there was an increase in the intragroup levels of chasing and biting but not of displacement (Figure 17). The majority of all three behaviours was initiated by LL fry with the following distribution by behaviour: 91% of the displacement, 99% of the chasing, and 98% of the biting. Further inspection shows that 82% of the chasing and 78% of the biting by LL fry was directed at other LL fry.

As with the home tank scenarios, group activity in the host tanks is principally continued conflict among the dominant LL residents with little activity by the SD, SL, or LD fry. Following the removal of the intruders, there is a corresponding decrease in the intra-LL class activity, involving reductions to 18% and 15% of chasing and biting respectively. This is

Figure 17. Mean totals ($\pm$ s.e.m.) of displacement (DIS), chasing (CHS), and biting (BITE) by all classes of rainbow trout residents of the host tank during the BASELINE, ADD, and RETURN phases of Experiment 9.

RAINBOW TROUT

NONDOMINANT INTRUDER (ADDITION)

reflected in the group means (Figure 17). It is noted displacement activity continues to remain low.

This reduction in LL fry activity is interpreted as not directly related with the removal of the intruder since LL fry-intruder interaction so heavily favoured the residents. Rather, the reduction is seen as a resolution of conflict among LL fry residents which would have occurred without the presence of the nondominant intruders. This resolution is yet another example of the ongoing nature of agonistic activity in these groups of developing fry.

Experiment 10: Nondominant Brook Charr as Intruder

This final experiment with brook charr was the parallel of the study of nondominant rainbow trout fry (Experiment 9). As in the case with rainbow trout however, pilot attempts to transplant small nondominant fry were unsuccessful. Further attempts to transplant LD fry were likewise met with complications: despite fastidious cleaning procedures, even these relatively large-sized fry were susceptible to Saprolegnia infection.

Any studies with LD fry then, even involving outwardly appearing healthy fish, could not discount the possibility that the subjects were diseased, if not moribund.

Ultimately, it was decided the nondominant intruders would,

in fact, be of the LL class, with the stipulation that the intruders be smaller than the most dominant fish of the host tank. Thus, the current experiment was a compromise; involving intruders of nondominance in one dimension (size) yet who were capable of surviving the transfer to a new environment.

In essence, this experiment tested the hypothesis that size differences alone could account for the different results between the two species, as represented in Experiment 5 and Experiment 6. Recall, in those studies, rainbow trout intruders were no larger than the LL defenders whereas, for brook charr, the intruders were slightly larger. It is possible then that had the brook charr intruders been smaller they, like the rainbow trout, might also have been unable to re-establish themselves upon their return to the home tanks as a result of their losses sustained in the host tanks.

This experiment, then, is further examination of the behaviour of individuals that have experienced loss of dominance as intruders, and of their subsequent attempts to recover from this loss when returned to the home environment.

Method

The methods used were comparable to those of Experiment 9: fry hatched from commercially purchased eggs (Linwood Acres Trout Farm, Campbellville, Ontario) were placed in 10 tanks in groups of 6 fry per tank, where they remained for their first

four weeks of free-swimming. Behavioural interactions were recorded in the final (fourth) week after which time the five smallest dominant animals (mean length: 3.4 cm) were removed from their home tanks and placed for one week into the tanks of the five largest dominant fry (mean length: 4.4 cm). Following this one week intruder phase, the intruders were removed and returned to their home tanks for a final, further week of observation.

Results

The activity of the intruders in their home tank is depicted in the first panel of Figure 18. Although the intruders rarely interact with other LL fry, they do show clear dominance over fry of the SD, SL and LD classes.

In addition to their light colouration and behaviour patterns, further evidence of their dominance is displayed in their occupation of the central regions of the tank. The mean co-ordinates of their stations were (9.1, 6.8, 2.3; $n = 20$).

In the host tanks, the intruders rarely interacted with SD fry but continued to exhibit dominance behaviour toward SL and LD fry though the levels were low. In encounters with resident LL fry, the smaller intruders are overwhelmed with approximately an 800% greater number of attacks upon them than they themselves are able to initiate. This vigorous defense resulted in colour shifts to dark pigmentation on the part of the intruders as well as the adoption of stations along the perimeter of the host tank.

Figure 18. Observed initiations ($\pm$ s.e.m.) by the nondominant brook charr intruder (I), and by resident fry upon the intruder (R), during the BASELINE, INTRUDER, and RETURN phases of Experiment 10. (SD= small, dark; SL= small, light; LD= large, dark; LL= large, light).

BROOK CHARR (nondominant)

The mean co-ordinates for the intruders were: (2.6, 7.1, 2.3, n= 20).

The experience in the host tanks affects the behaviour of the "nondominant" fry in subsequent encounters following return to the home tank (third panel, Figure 18). Total initiations against SL and LD fry continue to be noticeably greater than reciprocating behaviour. Encounters with LL fry also visibly increase relative to baseline levels although initiations by resident LL fry remains low. In contrast, there is a significant decrease in returnee interactions with SD fry relative to baseline.

Despite the response by resident LL fry, the returnees successfully re-establish themselves as the dominant group members. The lightening of pigmentation by all returnees as well as their re-adoption of central positions in the home tanks supports this view. Mean co-ordinates of the stations upon return are: (13.0, 5.7, 3.6, n= 20,). Thus, the losses suffered in the host tanks did not affect subsequent behaviour in the home tanks.

Group Behaviour: Home Tanks

Intragroup behaviour in the home tanks was low throughout the observation period (Figure 19). However, it is noted following removal of the "nondominant" fry, displacement activity doubled, with 54% of this doubling attributable to LL fry

Figure 19. Mean totals ($\pm$ s.e.m.) of displacement (DIS), chasing (CHS), and biting (BITE) by all classes of brook charr residents of the home tank during the BASELINE, REMOVE, and RETURN phases of Experiment 10.

BROOK CHARR
NONDOMINANT INTRUDER (REMOVE)

activity against SL and LD fry. This disinhibition of displacement was also seen in Experiment 7 and Experiment 8.

Also, following the return of the nondominant fry, encounters involving LL fry with either SL or LD fry continued with LL initiations accounting for 80% of the displacement, 75% of the chases and 80% of the biting attacks.

There were species differences then in terms of the frequency of home tank activity in these nondominant intruder studies. By inspection, brook charr activity is lower than that by rainbow trout. Second, continued activity among rainbow trout is primarily continued conflict among the most dominant members whereas for brook charr the observed activity, again primarily initiated by LL fry, appears to be for the purposes of policing established relations rather than the formation of new ones.

Group Behaviour: Host Tanks

As with behaviour in the home tanks, group activity in the host tanks was low with respect to all three behaviours (Figure 20). LL fry initiated the most frequently in all three conditions accounting for 63%, 78%, and 81% of all behaviour in the: (1) baseline, (2) intruder added, and (3) intruder removed conditions, respectively.

Furthermore, the behaviours initiated by LL fry were directed mainly at other classes (71% in the presence of the intruder and 65% following the removal of the intruder). That

Figure 20. Mean totals ($\pm$ s.e.m.) of displacement (DIS), chasing (CHS), and biting (BITE) by all classes of brook charr residents of the host tank during the BASELINE, ADD, and RETURN phases of Experiment 10.

BROOK CHARR

NONDOMINANT INTRUDER (ADDITION)

is, as in the home tanks, the majority of the activity among host tank group members is by J.L. fry; apparently for the purposes of maintaining established dominance relationships.

CHAPTER 7: GENERAL DISCUSSION

Considerations of Agonistic Behaviour

An understanding of the nature of the early development of agonistic behaviour in rainbow trout and brook charr emerges from these studies. These findings are:

(1) In both species, small groups of fry engage in intraspecific aggression (displacement, chasing, and biting) shortly after they become free-swimming. (2) By the end of the first week of free swimming (and group housing), the fry, originally homogeneous in appearance, are distinguishable into at least four different classes on the basis of relative size and colouration. These size-colour classes being: (a) large, light coloured (LL), (b) large, dark coloured (LD), (c) small, light coloured (SL), and (d) small, dark coloured (SD).

In each group of fry observed, there was at least one fry of each class present. The ratio of fry per size-colour class per tank, calculated at the conclusion of Experiment 3 and Experiment 4, was, for rainbow trout: 1.4 LL: 1 LD: 2.3 SL: 1.3 SD. For brook charr, the ratio was similar: 1.4 LL: 1 LD: 2.1 SL: 1.5 SD. Thus there were, on average, more small fry than large fry. Future replication of the work should involve larger sample sizes, so as to test the reliability and generality of the conclusions of the present work in groups with a greater membership per size-colour class,

(3) The patterns of agonistic activity among these size-colour classes are such that larger, lighter coloured fry have greater success than smaller, darker coloured conspecifics in agonistic encounters.

(4) In fry of intermediate size and colour, LD rainbow trout, are dominant over SL conspecifics. (5) However, this is the converse of the relationship between individuals of these two classes in brook charr: namely, SL brook charr fry are dominant over LD brook charr fry.

(6) Despite some variability between testing seasons, the establishment of intragroup relationships is characterized by initial high levels of chasing and biting which decline precipitously after approximately two weeks following initial housing. (7) Levels of displacement, in contrast, remain low and steady throughout the entire period of study.

This decline is thought to reflect the refining of intragroup relationships through the learning of the relative probabilities of success and failure of conflicting with other group members (Abbott, Dunbrack, and Orr, 1985; Kohda and Watanabe, 1982; Rhijn and Vodegel, 1980; see also Helfman and Schultz, 1982). This notion is consistent with the early thinking of Newman (1956) and Jenkins (1969) on the importance of learning in the ontogeny of agonistic activity in juvenile and adult populations of rainbow trout, brook charr, and brown trout.

Further, this ability to modulate individual behaviour with respect to differing social positions of different conspecific antagonists has also been documented in other species, including the pupfish (Cyprinodon variegatus Lacepede) (Itzkowitz, 1981) and the bluegill sunfish (Lepomis macrochirus Rafinesque) (Henry and Atchison, 1979).

Additionally, there may also be a physiological explanation for the decline over time in the levels of biting and chasing in that it may be a means by which fry shift to possibly energetically less costly behaviours (McNicol and Noakes, 1981). The implications of such a shift are: (1) later, lower frequencies of chasing and biting are just as effective in maintaining intraclass relationships as were earlier, higher levels and (2) ~~less~~ overt behaviours (i.e. displacement) eventually come to figure as prominently in the regulation of social interaction as the more overt behaviours as the fry mature.

Moreover, the differences observed between the first experimental series (Experiment 1 and Experiment 2) and the second experimental series (Experiment 3 and Experiment 4) illustrate the variability in the onset of this initial high period of activity. Specifically, this onset was found to occur earlier in the first series than in the second series. Variability in the values of the peak levels were also seen. Given that experimental procedures were constant over both

testing seasons, the observed inter-year variability may reflect the different origins of the subjects -- recall, fry studied in the first year were derived from laboratory stock whereas fry in the second year were hatched from commercially derived egg stock.

Despite this variability, it is noted that the species-characteristic dominance relationships among the four size-colour classes were the same in both years of study.

Considerations of Spatial Behaviour

Fry, of both species, are also characterizable on the basis of their spatial behaviour. That is, dominant individuals (LL fry) tend to occupy the central portion of the home volume whereas subordinate individuals station hold in peripheral locations. Discrimination may be made between dominant and nondominant fry on the basis of spatial position along the longitudinal axis of the range. This does not hold for depth and lateral positioning: station holding in these two dimensions is variable among individuals with no consistent patterns exhibited by members of any given size-colour class.

Specifically, dominance status is inversely related to longitudinal spatial position: fry of intermediate SL or LD status are further removed from the centre than dominant LL fry. SD fry are positioned furthest away, on the perimeter. In extreme cases,

subordinate fry are pressed against the corners facing away from the centre of the tank.

Comparable results* have been reported in natural stream settings for coho salmon fry (Chapman, 1962) and in artificial stream settings in brook charr fry (McNicol and Noakes, 1981).

This tendency of dominant group members to occupy the centre has also been found in the pencilfish (Nannostomus beckfordi) (Kuenzer, 1982). In that species, subordinates are confined to the exterior portions of the range and tended to be darkly coloured whereas dominant individuals were not.

For rainbow trout and brook charr, the relationship between dominance status and spatial position may exhibit variability: group members may periodically encroach upon, or even traverse, regions of the tank patrolled by other fry. Depending upon the response of the defending fry, the interloper may either adopt a new position in the vicinity of the defender, return to its previous station, or retreat to a new position away from the defender. The relative frequencies of these various behavioural options have not as yet been quantified although reports of interdigitation of territories has been anecdotally reported previously (Jenkins, 1969). (Further discussion on the spatial/territorial behaviour in these species may be found in Appendix B).

The preference of dominant fry to station hold in the longitudinal centre of each tank suggests there is some advantage

to such a position over alternative choices. This notion is reinforced by the fact other fry contest for that position following the removal of dominant fry. Two possible explanations may account for this. First, station holding may be feeding related as has been reported in other work with rainbow trout fry (Dill, 1977; Newman, 1956; Yamagishi, 1962) as well as with Atlantic salmon fry (Dill, 1977; Keenleyside and Yamamoto, 1962).

However, such is unlikely here since feed was distributed uniformly by hand over the water surface — food was no more concentrated in the centre than elsewhere along the surface. Hence, no advantage in terms of quicker access to food or greater food concentration is gained by station holding in the midlength regions.

Alternately, it is possible that dominant fry would occupy the centre in anticipation of food deposition, thereby excluding subordinates to the periphery and thus restricting access to much of the water surface. However, the deliberate uniform food placement pattern as well as the delay between feeding and observation (a technique employed specifically to avoid increased, feeding related, agonistic activity), renders such an explanation unlikely though not wholly improbable.

A second, more probable, explanation here is offered by consideration of water quality in the central regions relative to other regions of each tank. Although no quantitative

measurements were made, it is possible that water quality (aeration, temperature, pH, flow pattern, etc.) differed in different regions of the tanks, with the optimal conditions located in the midlength regions. For example, the water flow at the ends of the tanks may be disrupted by the aeration from the airstones at one end and by the drainpipe at the other end. Such minor turbulence could produce eddies suboptimal for respiration.

Unfortunately, such considerations of the microenvironment are beyond the strictly behavioural concerns of the thesis. The relationship between agonistic activity, spatial behaviour, and microenvironmental factors must await later study.

Considerations of the Intruder Studies

Aggressive interactions do not wholly disappear following the establishment of dominance relationships. This was seen in the final phases of Experiment 5 through Experiment 10. Rather they appear to continue with reduced frequency with the majority of interactions initiated by LL fry. Hence, intragroup relationships are stable in a dynamic rather than a static sense: the dominant individuals maintain their social (and spatial) position through regular interaction with subordinate fry. These other fry exert counter aggressive activity in return but the advantage remains with the larger, more frequently aggressive dominant fry.

Ongoing, low frequency activity following the stabilization of intragroup agonistic activity has also been reported for coho salmon fry (Chapman, 1962), brown trout (Heland, 1979; Jenkins, 1969), and stream populations of yearling rainbow trout (Jenkins, 1969).

Further evidence of this notion of counter pressure by subordinates in the present work is seen when dominant fry are removed. Activity among those remaining fry increases as they vie for the space resulting from the dominant fry's absence. The process occurs in groups of both species, but to a lesser degree in brook charr.

Activity in the home tanks continues during the absence of the dominant fry but, as in the initial housing period, biting and chasing, occur more frequently than displacement. Interactions are usually nonfatal although the lack of success of true nondominant intruder brook charr fry in novel, established groups is a conspicuous reminder that such is not always the case.

Given the dynamic equilibrium of the agonistic activity patterns among the size-colour classes, it is not surprising that the addition of intruders (even those originating from the home group and who were of previously established dominant status) is met by strong resistance on the part of the residents. For both brook charr and rainbow trout, the greatest response to an intruder is made by LL fry.

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This prior residence effect has been previously documented in rainbow trout and brook charr of several months age (Newman, 1956) as well as in developing Atlantic salmon fry (Keenleyside and Yamamoto, 1962) and coho salmon fry (Chapman, 1962). The term "prior residence" means that residence in an area confers upon an individual a greater probability of dominance over individuals who are newly introduced into that area. The most salient feature of this effect is that resident fish (dominant or nondominant) invariably initiate intense agonistic encounters against intruding fish (see Jenkins, 1969, p. 81).

This vigour in home defense is also seen in other piscine species. (see Brown, 1975 Chapter 4 and Chapter 7 for a general treatment). For example, Figler and Einhorn (1983) have found the territorial prior residence effect in convict cichlid (Cichlasoma nigrofasciatum Guenther). In encounters between residents and intruders, they found residents attacked first, such that initial biting was a reliable predictor of eventual dominance. They also found residents demonstrated a clear dominance advantage over conspecific intruders.

It is not surprising LL fry are the most active defenders: they typically occupy the central regions from where they sortie to engage subordinates. Hence, there is a greater probability an intruder will initially encounter a dominant fry than a subordinate, who is positioned in the periphery.

However, the defensive response is more than a simple result of propinquity because it is seen all host fry (including subordinates) will actively seek out the intruder during the initial period (first day) of introduction. Similar reports have been made on the pattern of initial intruder resident contact by other workers (Braddock, 1945; Chapman, 1962; Greenberg, 1947; Jenkins, 1969; McIntyre and Healy, 1979).

Moreover, though there is a concomitant increase in intragroup activity, the majority of interactions are directed principally at the intruder. From this, it follows the attacks upon the intruder are purposive in the sense they are not the random results of a general increased activity following the intruder's introduction. McIntyre and Healy (1979), working with rainbow trout fry several months old, also found resident fish directed a greater percentage of attacks toward the introduced fish than toward each other. They also reported a slight increase in intragroup activity occurred following introduction of an intruder, comparable to the events observed here.

The frequency of these interaction with the intruder declines once clear victors emerge following a number of encounters: the victors always being, with the notable exception of LL brook charr intruders, dominant residents. It is clear then that residents are able to differentiate the intruder from one another and modify their interactions with the intruder as dominance relationships between the intruder and the residents

are established.

The specific means by which individual recognition take place are beyond the scope of the thesis but some possibilities may be addressed. One possibility may be that defenders distinguish the intruder from other group members on the basis of visual cues. The most obvious cue in this study being the partial loss of the intruder's caudal fin through fin-clipping. Fin-clipping may also have affected the swimming pattern of the intruder such that his locomotion appears abnormal. (However, it should be recalled that fin-clipping was not seen to adversely affect the performance of intruders in the home tank prior to placement in the host tank).

Also, there may have been variations in external morphology such as the spot or parr band patterning that provided cues for the residents to recognize an intruder. At this point however, individual variation of such markings as possible cues in individual recognition in these species has yet to be studied.

At the level of behaviour, there may have been individual differences in aggressive behaviour. Fry may possess subtle, though individually distinct, eye or opercular movement patterns which, though not discernible by the experimenter, may allow fry to recognize one another. Only further analysis of the finer attributes of agonistic behaviour will resolve this issue.

Returning to the issue of the lack of success of subordinate (both species) and dominant (rainbow trout only) intruders, another contributing factor may be the physical characteristics of the host environment itself. Differences, however minor, in water temperature, water flow patterns, aeration, and other environmental aspects may also adversely affect the intruder but not the residents. This notion of a physically "conditioned" environment (Klopfer and Hailman, 1967), to which the physiological state of residents (but not that of the intruder) is tuned, may also account for the lethargy and eventual demise of transplanted nondominant fry in the pilot studies.

In light of the possible stress effects incurred by transplantation to a novel situation (Henry and Atchison, 1979; Newton, 1982; Yamagishi, 1962; see also Raab, Kojer, and Oswald, 1982; Weiss, 1968), in addition to the numerical superiority of defenders, it is little wonder that intruders were unsuccessful in gaining dominant positions in the host tanks. The notable exception being that all dominant brook charr intruders were able to secure positions in the host tanks comparable to those previously held in the home tanks.

Considerations of Observed Interspecies Differences

Further addressing the issue of species differences, the behaviour of rainbow trout and brook charr differed significantly in three aspects of the experimental series performed. These

are: (1) the dominance of LD fry over SL fry in the rainbow trout with the converse true for brook charr, (2) the ability of LL brook charr, but not rainbow trout, intruders to secure positions of dominance in the host tanks, and (3) the ability of LL brook charr, but not rainbow trout, to regain dominant status upon return to the home tanks following exposure to residents of the host tanks.

Although the mechanisms underlying these differences are beyond the descriptive purpose of this thesis, some speculation is in order and may be useful in guiding the future study of agonistic behaviour in these species. The discussion will proceed firstly from a neurophysiological perspective followed by strictly behavioural considerations of the results.

Previous work (McIntyre and Healy, 1979; McIntyre, Healy, and Saari, 1979) has shown the aggressive behaviour of rainbow trout to be modulated, in part, by catecholamine activity in the central nervous system. Working with fry several months in age, McIntyre, Healy, and Saari (1979) found that subordinate fry (those receiving at least 30% of attacks by dominant fry) had slightly but statistically significantly higher levels of norepinephrine (NE) than did dominant fry. Furthermore, these subordinates had lower levels of dopamine (DA) relative to dominants. It is noted both dominant and subordinate fry were same sized in that study.

Extrapolating from those findings, it is possible the dominance of LD rainbow trout fry over SL counterparts in the thesis experiments may be due, in part, to differing levels of central nervous system catecholamine activity in the two size-colour classes. Namely, dominant LD rainbow trout may have slightly lower NE levels, but higher DA levels, than SL subordinates.

If catecholamines are similarly involved in brook charr agonistic behaviour, one would expect the converse relationship between size-colour class and catecholamine activity. That is, SL brook charr would have slightly lower NE levels, and higher DA levels, than would LD subordinates.

Tests of these hypotheses would be to assay brain amines in groups of rainbow trout and brook charr similar to the ones studied here, using the assay procedure of McIntyre, Healy, & Saari (1979). One would expect the NE and DA levels of SL and LD rainbow trout fry (and of LD and SL brook charr fry), respectively, to parallel those of the dominant and subordinate rainbow trout fry described by McIntyre, Healy, and Saari (1979).

An additional test would be to directly manipulate brain amine concentrations with agonists and antagonists and then relate the induced monoamine changes to changes in aggressive behaviour. For example, injections of intraventricular 6-hydroxy dopamine (6-OHDA) is known to reliably deplete whole brain NE in rainbow trout. Consequently, the administration of 6-OHDA may

result in increased aggressive activity in previously subordinate SL rainbow trout fry or LD brook charr fry.

Neurophysiological differences may also account for the failure of LL rainbow trout, but not brook charr, intruders to deal successfully with the response of the resident fry in the host tanks. If there are interspecific differences in the catecholaminergic systems as was suggested for size-colour class considerations, another manifestation of such differences might be seen when individuals of the two species are stressed -- specifically, when confronted by hostile residents in a novel situation.

Under such circumstances, it is possible catecholamine functioning in dominant brook charr may be less disrupted than in dominant rainbow trout intruders. Consequently, the brook charr intruders, are able to sustain normal (i.e. home tank) levels of aggression whereas rainbow trout intruders perform less efficiently than they would in familiar conditions.

Central catecholaminergic involvement may be assessed by comparing levels of NE and DA following transfer to the host tank with those of controls. It would be predicted that NE and DA activity in brook charr would change less than those of rainbow trout. From the work of McIntyre, Healy, and Saari (1979), one would expect the altered levels of NE and DA in rainbow trout in the post-transfer (host tank) condition would be higher and

lower, respectively, than in the pre-transfer home tank condition, parallelling the shift from dominant to subordinate status. No changes would be expected for central catecholaminergic activity in brook charr, who were found in the present work to undergo no change in dominant status.

The observed species differences in LD-SL fry relationships as well as in the intruder scenarios may also be accounted for at the level of behaviour. In terms of the LD-SL relationships, it may be simply that size is not as crucial a factor in determining the outcome of brook charr interactions, as it may be in rainbow trout interactions, at this early age. Rather, relative speed and agility in avoiding attack may play equally important roles though such behaviours were not considered in the thesis.

With respect to species differences then, SL brook charr fry may be able to elude LD brook charr attacks whereas, in the complementary situation, SL rainbow trout may be unable to elude LD rainbow trout attacks. As a result, SL brook charr may be less hampered by injury and are more able to counterattack LD fry than their rainbow trout counterparts.

A similar argument may also account for the species differences in the intruder scenario experiments: dominant brook charr intruders may be able to elude or deflect the aggressive response of residents to a degree unmatched by dominant rainbow trout. For example, there may be interspecies differences in terms of latency to respond to an attack, ability to shift body

position so as to misdirect an attack to a less vulnerable area of the body, and so forth.

In this sense, the defensive behaviour of J.L. brook charr is better suited than that of rainbow trout when placed in an intruder situation. With such supposed reduced susceptibility to attack through defensive maneuvering, brook charr fry are more able to initiate counter aggressive attacks than the more defensively vulnerable rainbow trout fry.

Other behavioural factors may contribute to the species differences in size-colour class relationships and intruder-resident interactions seen in these samples. These include species differences in: (1) relative position of initiator and receiver in a confrontation, (2) the force of contact, (3) the point of body contact, and (4) ability to withstand repeated attack.

Only through methods of analysis finer than those employed here will such possible behavioural differences surrounding each agonistic event be uncovered. Such information may aid in interpreting the differences seen between rainbow trout and brook charr in SL-LD and intruder-resident interactions at a behavioural level. (Statistical findings suggestive of fine species differences in agonistic patterns is presented in Appendix C).

Similarities and differences between the species were also observed when the intruders were returned to the home tanks. As with the return of isolated individuals of both species, dominant brook charr fry (Experiment 6) and "subordinate" LL brook charr fry (Experiment 10) readily regained their pre-removal dominant status.

In contrast, LD subordinate rainbow trout fry continued to be subordinate following re-introduction to home conditions. Previously dominant LL rainbow trout fry, having failed to achieve dominant status in the host tanks, were likewise unable to alter their subordinate status upon return.

When these results of the isolation and intruder experiments are considered together, it is clear the experiences of the rainbow trout fry in the host tanks directly affect their subsequent lack of success in the home tanks. Of particular note is the inability of the LL rainbow trout fry to satisfactorily adjust to the shifts in home group relationships, (particularly, the emergence of a new dominant fry) despite their pre-eminent positions in the baseline phase of observation.

In contrast, dominant brook charr (Experiment 6) regain their dominant status despite the emergence of new dominant residents. Interestingly, the small LL brook charr (Experiment 10), clearly subordinate in the host tanks, also displayed dominant behaviour upon return to home conditions.

This difference between the samples of the two species, as with the species differences in LD - SI class interactions and intruder - host tank resident interactions, may be accounted for in terms of species differences in neurophysiology or fine behaviour. Specifically, central dopamine and norepinephrine levels may have returned to pre-removal levels for the LL brook charr fry, regardless of their experiences in the host tanks, upon reintroduction to the home tanks ; but not so for the LL rainbow trout fry.

Alternately, the returning brook charr may have been able to adjust their behaviour in some manner to accomodate the new intragroup, home tank relationships whereas the rainbow trout were not. For example, the previously suggested possibility of superior brook charr, relative to rainbow trout, defensive behaviour (i.e. dodging, impact resistance, etc.) may have allowed fry of the former but not the latter species to endure the attacks of home tank residents. By being less hampered, the brook charr were ultimately able to regain dominant status whereas the rainbow trout fry could not. Very likely, the results are due to the interaction of behavioural and physiological events.

Thus, it appears that at this early age, brook charr fry are more able than rainbow trout fry to cope with changes in agonistic patterns engendered by: (a) transfer to a novel environment, as well as, (b) shifts in established relationships.

However, the nature of the detailed physiological and behavioural events underlying this difference in coping ability remains unknown at this time.

Concluding Remarks

The findings of the thesis are consistent with observations made in older populations of rainbow trout and brook charr as well as in other salmonid species. First, in the present studies, it was found that the ontogeny of agonistic interaction, once initiated, proceeds from high to low frequencies of chasing and biting, with a concomitant, relative increase in the level of displacement. Similar results have been reported for underyearling rainbow trout (Cole and Noakes, 1980; Jenkins, 1969; Yamagishi, 1962), yearling rainbow trout (Chiszar, Drake, and Windell, 1975), as well as adult rainbow trout and brook charr (Jenkins, 1969). Other salmonids exhibiting a similar ontogenetic pattern include the Atlantic salmon (Keenleyside and Yamamoto, 1962), the brown trout (Heland, 1979; Newman, 1956), and the Arctic grayling (Kratt and Smith, 1979).

Second, the present quantitative observations are consistent with earlier qualitative observations (Chapman, 1962;; Jenkins, 1969; McIntyre, Healy, & Saari, 1979; Newman, 1956; Stringer and Hoar, 1955; Yamagishi, 1962 -- and recently by Abbott, Dunbrack, and Orr, 1985) that, in rainbow trout of a given size, dominant

fish are light in body colouration whereas submissive fish are conspicuously darker (although McIntyre, Healy, and Saari (1979) report a dominant fish without conspicuous light colouration in one of their groups). This was also found to hold true for the brook charr (Newman, 1956; present study).

The results of the intruder scenario studies bring several previously unreported findings to light. First, subordinate fry in both species, at this early stage of development, remain subordinate even when placed into a situation wherein residents have no prior experience with that subordinate fry.

Second, dominant rainbow trout fry do not retain their dominant status when placed into a situation with novel conspecifics. In contrast, brook charr fry are able to retain their status if they are of a size comparable to that of the dominant individuals of the host conditions.

Third, the status lost by LL fry in the host conditions is not recovered upon return to the home tanks in the rainbow trout (Experiment 5) but is recovered by the brook charr (Experiment 10).

Fourthly, the behavioural response by host tank residents to the intruders suggest fry of this age, in both species, are able to distinguish group members from non-group members. The recognition of specific individuals, however, cannot be conclusively demonstrated in these studies: all returnees to home conditions were initially treated similarly (i.e. as novel

intruders) in both species, irrespective of previous dominant-subordinate relationships.

In conclusion, this thesis has addressed the issue of behavioural differences in different size-colour classes of developing rainbow trout and brook charr. The findings are consistent with previous qualitative observations of dominance relationships between differently coloured conspecifics as well as with quantitative observations of the development of agonistic activity in other salmonids. The present work extends beyond previous investigations in its documentation of species differences in intermediate size-colour classes, species differences in responding to intruders, and concomitant differences in the relative success of dominant and subordinate individuals cast in the role of intruders.

Speculation about the possible mechanisms underlying these differences were posited from a neurophysiological as well as behavioural perspective but these hypotheses must await future study for clarification. Moreover, it is hoped such study will involve larger sample sizes than those studied here so as to test the reliability and generality of the present findings.

REFERENCES

- Abbott, J. C., Dunbrack, R. L., and Orr, C. D. (1985). The interaction of size and experience in dominance relationships of juvenile steelhead trout (Salmo gairdneri). Behaviour, 92(3-4), 241-253.
- Allan, J.D. (1981). Determinants of diet of brook trout (Salvelinus fontinalis) in a mountain stream. Canadian Journal of Fisheries and Aquatic Science, 38(2), 184-192.
- Allan, J.D. (1982). The effects of reduction in trout density on the invertebrate community in a mountain stream. Ecology, 63(5), 1444-1455.
- Barlow, G.W. and Ballin, P.J. (1976). Predicting and assessing dominance from size and coloration in the polychromatic Midas cichlid. Animal Behaviour, 24, 793-813.
- Behnke, R.J. (1972). The systematics of salmonid fishes in recently glaciated lakes. Journal of the Fisheries Research Board of Canada, 29(6), 639-671.
- Bentmar, G. (1979). Home range migrations and orientation mechanisms of the River Indalsälven trout, Salmo trutta L. Report of the Institute of Freshwater Research, Drottningholm, 58, 5-26.

- Berst, A.H., Emery, A.R., and Spangler, G.R. (1981). Reproductive behavior of hybrid charr (Salvelinus fontinalis x S. namaycush). Canadian Journal of Fisheries and Aquatic Science, 38(4), 432-440.
- Bonett, D.G. and Bentler, P.M. (1983). Goodness-of-fit procedures for the evaluation and selection of log-linear models. Psychological Bulletin, 93(1), 149-146.
- Box, G.E.P. (1950). Problems in the analysis of growth and wear curves. Biometrics, 6, 362-389.
- Braddock, J.C. (1945). Some aspects of the dominance-subordination relationship in the fish (Platypoecilus maculatus). Physiological Zoology, 18, 179-195.
- Bronstein, P.M. (1980). Betta splendens: a territorial note. Bulletin of the Psychonomic Society, 16(6), 484-485.
- Bronstein, P.M. (1981). Commitments to aggression and nest sites in male Betta splendens. Journal of Comparative and Physiological Psychology, 95(3), 436-449.
- Bronstein, P.M. (1982). Breeding, paternal behavior, and their interruption in Betta splendens. Animal Learning and Behavior, 10(2), 145-151.

Brown, J.A. and Colgan, P.W. (1981). The use of lateral-body bar markings in identification of young-of-year sunfish (Lepomis) in Lake Opinicon, Ontario. Canadian Journal of Zoology, 59(9), 1852-1855.

Brown, J.L. (1975). The evolution of behaviour. New York: W.W. Norton.

Brown, M.B. (1981). Two-way and multiway frequency tables - measures of association and the log-linear model (complete and incomplete tables). BMDP Statistical Software 1981. Berkeley: University of California Press, pp. 143-206.

Butler, R.L. (1981). Relationships of trout behaviour and management: Hatchery production and construction. In Proceedings of the Bio-Engineering Symposium for Fish Culture. (L.J. Allen and S.C. Kinney, eds.), pp. 29-33. American Fisheries Society: Washington, D.C.

Cain, N.W. and Baenninger, R. (1980). Social organization and the maintenance of aggressive behavior in community-housed male Siamese fighting fish (Betta splendens). Animal Learning and Behavior, 8(11), 171-176.

Carlander, K.D. (1969). Handbook of freshwater fishery biology. Volume 1. Ames, Iowa: Iowa State University Press.

Chapman, D.W. (1962). Aggressive behavior in juvenile coho salmon as a cause of emigration. Journal of the Fisheries Research Board of Canada, 19(6), 1047-1080.

Chapman, D.W. (1966). Food and space as regulators of salmonid populations in streams. American Naturalist, 100, 345-358.

Chebanov, N.A. (1979). Behavior and mate selection among chum brood stock of different sizes with a predominance of males in the spawning grounds. Soviet Journal of Ecology, 10(2), 141-146.

Chebanov, N.A. (1982). Spawning behavior of the humpbacked salmon (Oncorhynchus gorbuscha) with different ratios of sexes at the spawning ground. Ekologiya, 13(1), 57-66.

Chiszar, D., Drake, D.W., and Windell, J.T. (1975). Aggressive behavior in rainbow trout (Salmo gairdneri Richardson) of two ages. Behavioral Biology, 13, 425-431.

Cole, K.S. (1982). Male reproductive behaviour in spawning and success in a temperate zone goby, Coryphopterus nicholsi. Canadian Journal of Zoology, 60(10), 2309-2316.

Cole, K.S. and Noakes, D.L.G. (1980). Development of early social behaviour of rainbow trout, Salmo gairdneri (Pisces, Salmonidae). Behavioural Processes, 5(2), 97-112.

Cooney, R.T., Urquhart, D., and Barnard, D. (1981). The behavior, feeding biology, and growth of hatchery released pink and chum salmon fry in Prince William Sound, Alaska. Publication of the Alaska Sea Grant College Program (Fairbanks), Number 81-5, Report R81-4, pp. 114.

Cramer, D.P. (1981). Effect of smolt release location and displacement of adult on distribution of summer steelhead trout. Progressive Fish-Culturist, 43(1), 8-11.

Crapon de Crapona; M.-D. (1980). Olfactory communication in a cichlid fish, Haplochromis burtoni. Zeitschrift fur Tierpsychologie, 52(2), 113-134.

Crisp, D.T. (1981). A desk study of the relationship between temperature and hatching time for the eggs of five species of salmonid fish. Freshwater Biology, 11(4), 361-368.

de Boer, B.A. (1980). A causal analysis of the territorial and courtship behaviour of Chromis cyanea (Pomacentridae, Pistes). Behaviour, 73(1-2), 1-50.

Delucchi, K.L. (1983). The use and misuse of chi-square: Lewis and Burke revisited. Psychological Bulletin, 94(1), 166-176.

Denight, M.L. and Ward, J.A. (1982). Relationship of chin spot size to dominance in the black-chinned mouthbrooding cichlid fish

(Sarotherodon melanotheron). Animal Behaviour, 30, 1099-1104.

Dill, L.M., Ydenberg, R.C., and Fraser, A.H.G. (1981). Food abundance and territory size in juvenile coho salmon (Oncorhynchus kisutch). Canadian Journal of Zoology, 59(9), 1801-1809.

Dill, L.M. (1983). Adaptive flexibility in the foraging behavior of fishes. Canadian Journal of Fisheries and Aquatic Science, 40(4), 398-408.

Dill, P.A. (1977). Development of behaviour in alevins of Atlantic salmon, Salmo salar, and rainbow trout, S. gairdneri. Animal Behaviour, 25(1), 116-121.

Double, D.D., Gray, R., Page, T.L. (1980). Importance of insects and zooplankton in the diet of 0-age chinook salmon (Oncorhynchus tshawytscha) in the central Columbia river. Northwest Scientist, 54(4), 253-258.

Draeger, B. and Chiszar, D. (1982). Growth rate of bluegill sunfish (Lepomis macrochirus) maintained in groups and in isolation. Bulletin of the Psychonomic Society, 205, 284-286.

Elliott, G.V. and Jenkins, T.M. (1972). Winter food of trout in three high elevation Sierra Nevada lakes. Publication of the California Department of Fish and Game, 58(3), 231-237.

Ellison, J.P. (1980). Diets of mountain whitefish, Prosopium williamsoni (Girard), and brook trout, Salvelinus fontinalis (Mitchill), in the Little Walker River, Mono County, California. Bulletin of the California Department of Fish and Game, 66(2), 96-104.

Everest, F.H. and Chapman, D.W. (1972). Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. Journal of the Fisheries Research Board of Canada, 29(1), 91-100.

Farr, J.A. (1980). The effects of juvenile social interaction on growth rate, size and age at maturity, and adult social behavior in Girardinus metallicus (Pisces: Poeciliidae). Zeitschrift fur Tierpsychologie, 53(3), 247-268.

Fausch, K.D. and White, R.J. (1981). Competition between brook trout (Salvelinus fontinalis) and brown trout (Salmo trutta) for positions in a Michigan stream. Canadian Journal of Fisheries and Aquatic Science, 38(10), 1220-1227.

Ferguson, G.A. (1971). Statistical analysis in psychology and education. Third edition. New York: McGraw-Hill.

Ferguson, M.M. and Noakes, D.L.G. (1982). Genetics of social behaviour in charrs (Salvelinus Species). Animal Behaviour, 30(1), 128-134.

Ferguson, M.M. and Noakes, D.L.G. (1983a). Behavioural plasticity of the lake charr (Salvelinus namaycush) x brook charr (S. fontinalis) F₁ hybrids in response to varying social environment. Behavioural Processes, 8(2), 147-156.

Ferguson, M.M. and Noakes, D.L.G. (1983b). Movers and stayers: Genetic analysis of mobility and positioning in hybrids of lake charr, Salvelinus namaycush, and brook charr, S. fontinalis. Behavioral Genetics, 13(2), 213-222.

Fernald, R.D. (1980). Response of male cichlid fish, Haplochromis burtoni, reared in isolation to models of conspecifics. Zeitschrift fur Tierpsychologie, 54(1), 85-93.

Fienberg, S.E. (1980). The analysis of cross-classified categorical data. Second edition. Cambridge, Mass: MIT Press.

Figler, M.H. and Einhorn, D.M. (1983). The territorial prior residence effect in convict cichlids (Cichlasoma nigrofasciatum Guenther): Temporal aspects of establishment and retention, and proximate mechanisms. Behaviour, 85(1-2), 157-181.

Fraley, N.B. and Fernald, R.D. (1982). Social control of developmental rate in the African cichlid, Haplochromis burtoni. Zeitschrift fur Tierpsychologie, 60(1), 66-82.

Frey, D.F. and Miller, R.J. (1972). The establishment of dominance relationships in the blue gourami, Trichogaster trichopterus (Pallas). Behaviour, 42, 8-62.

Fricke, H.W. (1979). Juvenile-adult colour patterns and coexistence in the territorial coral reef fish Pomacanthus imperator. Marine Ecology, 1(2), 133-141.

Gerking, S.D. (1953). Evidence for the concepts of home range and territory in stream fishes. Ecology, 34(3), 347-365.

Gibson, R.J. (1978). The behavior of juvenile Atlantic salmon (Salmo salar) and brook trout (Salvelinus fontinalis) with regard to temperature and to water velocity. Transactions of the American Fisheries Society, 107(5), 703-712.

Gibson, R.J. (1981). Behavioural interactions between coho salmon (Oncorhynchus kisutch), Atlantic salmon (Salmo salar), brook trout (Salvelinus fontinalis) and steelhead trout (Salmo gairdneri) at the juvenile fluvial stages. Canadian Technical Report in Fisheries and Aquatic Science, 1029, 121 pp.

Gowing, H. and Momot, W.T. (1979). Impact of brook trout (Salvelinus fontinalis) on predation on the crayfish Oronectes virilis in three Michigan lakes. Journal of the Fisheries Research Board of Canada, 36(10), 1191-1196.

Grayton, B. and Beamish, F.W.H. (1977). Effects of feeding frequency on food intake, growth and body composition of rainbow trout (Salmo gairdneri). Aquaculture, 11, 159-172.

Greenberg, B. (1947). Some relations between territory, social hierarchy and leadership in the green sunfish (Lepomis cyanellus). Physiological Zoology, 20, 267-299.

Greenway, P. (1965). Body form and behavioral types in fish. Experientia, 21(489), 1-9.

Hale, J.G. and Hilden, D.A. (1969). Spawning and some aspects of early life history of brook trout, Salvelinus fontinalis (Mitchill), in the laboratory. Transactions of the American Fisheries Society, 98(3), 973-977.

Hartman, G.F. (1965). The role of behaviour in the ecology and interaction of underyearling coho salmon (Oncorhynchus kisutch) and steelhead trout (Salmo gairdneri). Journal of the Fisheries Research Board of Canada, 22(4), 1035-1081.

Hartman, G.F. and Gill, C.A. (1968). Distribution of juvenile steelhead and cutthroat trout (Salmo gairdneri and S. clarki clarki) within streams of southwestern British Columbia. Journal of the Fisheries Research Board of Canada, 25(1), 33-48.

Heland, M. (1979). The ontogenesis of territorial behaviour in the trout fry (Salmo trutta L.). Bulletin de Centre Etudiants pour Recherche Scientifique (Biarritz), 12(3), 564-565.

Heland, M. (1980a). The downstream migration of brown trout Salmo trutta fry. 1. Characteristics in an artificial environment. Annals of Limnology, 16(3), 233-243.

Heland, M. (1980b). The downstream migration of brown trout Salmo trutta fry. 2. Activity of downstream migrants compared with that of non-migrants. Annals of Limnology, 16(3), 247-254.

Helfman, G.S. and Schultz, E.T. (1982). Social transmission of behavioural traditions in a coral reef fish. Animal Behaviour, 32(2), 379-384.

Henderson, D.L. and Chiszar, D.A. (1977). Analysis of aggressive behaviour in the bluegill sunfish Lepomis macrochirus Rafinesque: Effects of sex and size. Animal Behaviour, 25, 122-130.

Henry, M.G. and Atchison, G.J. (1979). Influence of social rank on the behaviour of bluegill, Lepomis macrochirus Rafinesque, exposed to sublethal concentrations of cadmium and zinc. Journal of Fish Biology, 15(3), 309-315.

Hillden, N.-O. (1981). Territoriality and reproductive behaviour in the Goldsinny, Ctenolabrus rupestris L. Behavioural

Processes, 6(3), 207-221.

Hilton, J.W. and Sluger, S.J. (1981). Nutrition and feeding of rainbow trout. Canadian Special Publication in Fisheries and Aquatic Science, 55, 19 pp.

Hinde, R.A. (1982). Ethology: Its nature and relations with other sciences. New York: Oxford University Press.

Honda, H. (1980). Female sex pheromone of rainbow trout, Salmo gairdneri, involved in courtship behaviour. Bulletin of the Japan Society of Scientific Fisheries, 46(9), 1109-1112.

Irvine, J.R. and Northcote, T.G. (1982). Significance of sequential feeding patterns of juvenile rainbow trout in a large lake-fed river. Transactions of the American Fisheries Society, 111(4), 446-452.

Itzkowitz, M. (1979). Territorial tactics and habitat quality. American Naturalist, 114(4), 585-590.

Itzkowitz, M. (1981). The relationships of intrusions and attacks to territory size and quality in the pupfish, Cyprinodon variegatus Lacépède. Intrusion. Biological Behaviour, 6(3), 273-280.

Iwama, G. K. and Tautz, A.F. (1981). A simple growth model for salmonids in hatcheries. Canadian Journal of Fisheries and

Aquatic Science, 38(6), 649-656.

Jenkins, T.M., Jr. (1969). Social structure, position choice and microdistribution of two trout species (Salmo trutta and Salmo gairdneri) resident in mountain streams. Animal Behaviour Monographs, 2(2), 57-123.

Jobling, M. (1983). Effect of feeding frequency on food intake and growth of Arctic charr, Salvelinus alpinus L. Journal of Fish Biology, 23(2), 177-185.

Jobling, L.M. and Wandsvik, A. (1983). Effect of social interaction on growth rates and conversion efficiency of Arctic charr, Salvelinus alpinus L.. Journal of Fish Biology, 22(5), 577-584.

Johannes, R.E. and Larkin, P.A. (1961). Competition for food between reddsides shiners (Richardsonius balteatus) and rainbow trout (Salmo gairdneri) in two British Columbia lakes. Journal of the Fisheries Research Board of Canada, 18(2), 203-220.

Johnson, J.H. (1981a). Comparative food selection by co-existing subyearling coho salmon, chinook salmon and rainbow trout in a tributary of Lake Ontario, N.Y. New York Fish and Game Journal, 28(2), 150-161.

Johnson, J.H. (1981b). Predation on the eggs of steelhead trout by stream salmonids in a tributary of Lake Ontario. Progressive

Fish Culturist, 43(1), 36-37.

Johnson, J.H. and Johnson, E.Z. (1981). Feeding periodicity and diel variation in diet composition of subyearling coho salmon, Oncorhynchus kisutch, and steelhead, Salmo gairdneri, in a small stream during summer. Fisheries Bulletin, 79(2), 370-376.

Johnsen, P.B. and Hasler, A.D. (1980). The use of chemical cues in the upstream migration of the coho salmon, Oncorhynchus kisutch Walbaum. Journal of Fish Biology, 17(1), 67-73.

Kalleberg, H. (1958). Observations in a stream tank of territoriality and competition in juvenile salmon and trout (Salmo salar L. and S. trutta L.). Report of the Institute of Freshwater Research Drottningholm, 39, 55-98.

Keen, W.A. (1982). Behavioral interactions and body size differences in competition for food among juvenile brown bullhead (Ictalurus nebulosus). Canadian Journal of Fisheries and Aquatic Science, 39(2), 316-320.

Keenleyside, M.H. and Yamamoto, F.T. (1962). Territorial behaviour of juvenile Atlantic salmon (Salmo salar L.). Behaviour, 19(1-2), 139-169.

Kelley, C.D. and Hourigan, T.F. (1983). The function of conspicuous coloration in chaetodontid fishes: A new hypothesis. Animal Behaviour, 31(2), 615-617.

Kelso, B.W. and Northcote, T.G. (1981). Current response of young rainbow trout from inlet and spawning stocks of a British Columbia lake. Proceedings of the International Association of Theoretical and Applied Limnology. Stuttgart: Schweizerbartsche Verlagsbuchhandlung, 1214-1221.

Kirk, R. E. (1968). Experimental design: Procedures for the behavioral sciences. Belmont, California: Wadsworth Publishing Company, Inc.

Klopfer, P.H. and Hailman, J.P. (1967). An introduction to animal behavior: Ethology's first century. Englewood Cliffs, New Jersey: Prentice-Hall.

Kohda, M. (1981). Interspecific territoriality and agonistic behavior of a temperate pomacentrid fish, Eupomacentrus altus (Pisces: Pomacentridae). Zeitschrift fur Tierpsychologie, 56(3), 205-216.

Kohda, Y. and Watanabe, M. (1982). Agonistic behaviour and color pattern in a Japanese fresh water serranid fish, Coreoperca kawamebari. Zoological Magazine of the Zoological Society of Japan, 91(1), 61-69.

Kohda, Y. and Watanabe, M. (1982). Relationship of color pattern to dominance order in a freshwater serranid fish,

Coreoperca kawamebari. Zoological Magazine of the Zoological Society of Japan, 91(2), 140-145.

Kratt, L.F. and Smith, R.J.F. (1979). Agonistic behaviour of age 0 and 1 and nonbreeding adult Arctic grayling Thymallus arcticus (Pallas). Journal of Fish Biology, 15(4), 389-404.

Kroll, W. (1981). The behavior of the African killifish, Aphyosemion gardneri: Normative studies. Environmental Biology and Fisheries, 6(3-4), 277-284.

Kuenzer, P. (1982). Undecided fights, behaviour induced colour change and social organization in the pencilfish Nannostanus beckfordi (Teleostei, Lebiasinidae). Zeitschrift fur Tierpsychologie, 58(2), 89-118.

Le Martret, M.A. and Saglio, P. (1982). The role of pheromones in intraspecific communication in immature goldfish, Carassius auratus L. 1. Olfactometric demonstration. Biological Behaviour, 1982, 7(1), 41-54.

Lewis, S.L. (1969). Physical factors influencing fish populations in pools of a trout stream. Transactions of the American Fisheries Society, 98(1), 14-19.

Liley, N. R. (1982). Chemical communication in fish. Canadian Journal of Fisheries and Aquatic Science, 39(1), 22-35.

- Loiselle, P.V. (1982). Male spawning-partner preference in an arena-breeding teleost Cyprinodon macularis californiensis Girard (Atherinomorpha: Cyprinodontidae). American Naturalist, 120(6), 721-732.
- MacCrimmon, H.R. and Twongo, T.K. (1980). Ontogeny of feeding behaviour in hatchery-reared rainbow trout, Salmo gairdneri Richardson. Canadian Journal of Zoology, 58(1), 20-26.
- Maeda, N. and Hidaka, T. (1979). Ethological function of the parr marks in a Japanese trout, Oncorhynchus masou f. ishikawai. Zoological Magazine of the Zoological Society of Japan, 88(1), 34-42.
- Mazeaud, F. (1981). Morpholine, a nonspecific attractant for salmonids. Aquaculture, 26(1-2), 189-191.
- McAfee, W.B. (1966). Rainbow trout. In Inland Fisheries Management (A. Calhoun, ed.), pp. 192-215. Publication of the California Department of Fish and Game, Sacramento.
- McIntyre, D.C. and Healy, L.M. (1978). Effects of telencephalon damage on intraspecies aggression and activity in rainbow trout (Salmo gairdneri) juveniles. Behavioral and Neural Biology, 25, 490-501.
- McIntyre, D.C., Healy, L.M., and Saari, M. (1979). Intraspecies aggression and monoamine levels in rainbow trout (Salmo

gairdneri) fingerlings. Behavioral and Neural Biology, 25, 90-98.

McNicol, R.E. and Noakes, D.L. (1979). Caudal fin branding fish for individual recognition in behavior studies. Behavior Research Methods and Instrumentation, 11(1), 95-97.

McNicol, R.E. and Noakes, D.L.G. (1981) Territories and territorial defense in juvenile brook charr, Salvelinus fontinalis (Pisces: Salmonidae). Canadian Journal of Zoology, 59(1), 22-28.

McPhail, J.O. and Lindsey, C.C. (1970). Freshwater fishes of northwestern Canada, and Alaska. Fisheries Research Board of Canada Bulletin.

Meliska, C.J. and Meliska, J.A. (1980). The relationship of mirror-elicited display to combat behaviors in Betta splendens. Behavioral and Neural Biology, 30(2), 207-217.

Meliska, C.J., Meliska, J.A., and Peeke, H.V.S. (1980). Threat displays and combat aggression in Betta splendens following visual exposure to conspecifics and one-way mirrors. Behavioral and Neural Biology, 28(4), 473-486.

Miller, P.J. (1979). Adaptiveness and implications of small size in teleosts. Symposium of the Zoological Society (London).

44, 263-306.

Miller, R.G. (1981). Simultaneous statistical inference. Second edition. New York: Springer-Verlag.

Moyer, J.T. and Zaiser, M.J. (1981). Social organization and spawning behavior of the pteropine fish Dendrochirus zebra at Miyaka-Jima, Japan. Japanese Journal of Ichthyology, 28(1), 52-69.

Moyle, P.B. (1969). Comparative behavior of young brook trout of domestic and wild origin. Progressive Fish Culturist, 1969, 31(1), 51-56.

Moyle, P.B. (1976). Inland fishes of California. Berkeley: University of California Press.

Mutsin'sh, A.N. (1979). Current velocities and the behavior of young fish. Journal of Ichthyology, 19(5), 171-173.

Needham, P.R. and Gard, R. (1959). Rainbow trout in Mexico and California, with notes on the cutthroat series. University of California Publications in Zoology, 67(1), 1-123.

Newcombe, C.P. and Hartman, G.F. (1980). Visual signals in the spawning behaviour of rainbow trout. Canadian Journal of Zoology, 58(10), 1751-1757.

Newman, M.A. (1956). Social behaviour and interspecific competition in two trout species. Physiological Zoology, 29, 64-81.

Newton, B.J. (1982). Early stress effects on growth and adult behavior in Poecilia reticulata. Developmental Psychobiology, 15(3), 211-220.

Nilsson, N.A. and Northcote, T.G. (1981). Rainbow trout (Salmo gairdneri) and cutthroat trout (S.clarki) interactions in coastal British Columbia lakes. Canadian Journal of Fisheries and Aquatic Science, 38(10), 1228-1246.

Noakes, D.L.G. and Leatherland, J.F. (1977). Social dominance and interrenal cell activity in rainbow trout, Salmo gairdneri (Pisces, Salmonidae). Environmental Biology and Fisheries, 2(2), 131-136.

Noakes, D.L.G. and McNicol, R.E. (1982). Geometry for the eccentric territory. Canadian Journal of Zoology, 6(7), 1776-1779.

Noble, G.K. (1939). The role of dominance in the social life of birds. Auk, 56, 263-273.

North, E. (1979). Aggressive behavior of juvenile brown trout Salmo trutta, L.: An analysis of the wigwag display. Journal of

Fisheries Biology, 15(5), 571-577.

Northcote, T.G. (1981). Juvenile current response, growth and maturity of above and below waterfall stocks of rainbow trout, Salmo gairdneri. Journal of Fisheries Biology, 18(6), 741-751.

Northcote, T.G. and Kelso, B.W. (1981). Differential response to water current by two homozygous LDH phenotypes of young rainbow trout (Salmo gairdneri). Canadian Journal of Fisheries and Aquatic Science, 38(3), 348-352.

Olson, C.L. (1974). Comparative robustness of six tests in multivariate analysis of variance. Journal of the American Statistical Association, 69, 894-908.

Ottaway, E.M. and Clarke, A. (1981). A preliminary investigation into the vulnerability of young trout (Salmo trutta L.) and Atlantic salmon (S. salar L.) to downstream displacement by high water velocities. Journal of Fish Biology, 19(2), 135-145.

Raab, A., Kojer, G., and Oswald, R. (1982). Social status and coping with conflict. Features of the mesolimbic dopaminergic system. Aggressive Behavior, 8, 212-216.

Rao, C. R. (1973) Linear statistical inference and its applications (Second edition). New York: Wiley.

Refstie, T. (1980). Genetic and environmental sources of variation in body weight and length of rainbow trout fingerlings. Aquaculture, 19(4), 351-357.

Reimers, P.E. (1958). Conditions of existence, growth and longevity of brook trout in a small, high-altitude lake of the eastern Sierra Nevada. California Department of Fish and Game Bulletin, 44(4), 319-333.

Rhein, L.D., Cagan, R.H., Orkand, P.M., and Dolack, M.K. (1981). Surface specialization of the olfactory epithelium of rainbow trout, Salmo gairdneri. Tissue and Cell, 13(3), 577-587.

Rhijn, J.G. and Vodegel, R. (1980). Being honest about one's intentions. An evolutionary stable strategy for animal conflicts. Journal of Theoretical Biology, 85(4), 623-641.

Rimmer, D.M., Paim, U., and Saunders, R.L. (1983). Autumnal habitat shift of juvenile Atlantic salmon (Salmo salar) in a small river. Canadian Journal of Fisheries and Aquatic Science, 40(6), 671-680.

Roitblatt, H.L. Tham, W., and Golub, L. (1982). Performance of Betta splendens in a radial arm maze. Animal Learning and Behavior, 10(1), 108-114.

Rnic, A. (1978). The effects of defeat and victory on aggression in the Siamese fighting fish (Betta splendens): Behaviour and neurochemistry. Doctoral dissertation. Ottawa, Carleton University.

Rohrer, R.L. (1981). Lake and reservoir investigations - Henry's Lake Fisheries Investigations. Evaluations of Henry's Lake Management Program. Job Performance Report for the Idaho Department of Fish and Game, 50 pp.

Rojas-Ayala, H. (1980). The rainbow trout from Langui-Layo lagoon (Cuzco) Peru. Documenta, 8, 72-73.

Saglio, P. and Le Martret, M.A. (1982). The role of pheromones in intraspecific communication in immature goldfish, Carassius auratus L. Olfactometric study of the behavioral activity of epidermic extracts. Biological Behaviour, 7(3), 221-234.

Schwanck, E. (1980). The effect of size and hormonal state on the establishment of dominance in young males of Tilapia mariae (Pisces: Cichlidae). Behavioural Processes, 5(1), 45-53.

Sedgwick, S.D. (1982). The salmon handbook. London: Andre Deutsch.

Scott, J.P. and Fredericson, E. (1951). The causes of fighting in mice and rats. Physiological Zoology, 24, 273-309.

Shapiro, D.Y. (1981). Sequence of coloration changes during sex reversal in the tropical marine fish Anthias squamipinnis. Bulletin of Marine Science, 31(2), 383-398.

Slaney, P.A. and Northcote, T.G. (1974). Effects of prey abundance on density and territorial behavior of young rainbow trout (Salmo gairdneri) in laboratory stream channels. Journal of the Fisheries Research Board of Canada, 31, 1201-1209.

Sokal, R. E. and Rohlf, F.J. (1972). Introduction to biostatistics. San Francisco: W. H. Freeman.

Srivastava, V.M. (1982). Behavior of Atlantic salmon (Salmo salar) during suspended migration in an estuary, Sheet Harbour, Nova Scotia, observed visually and by ultrasonic tracking. Canadian Journal of Fisheries and Aquatic Science, 39(2); 248-256.

Stevens, D.G., Nebeker, A.V., and Baker, R.J. (1980). Avoidance responses of salmon and trout to air-supersaturated water. Transactions of the American Fisheries Society, 109(6), 751-754.

Stocek, R.F. and McCrimmon, H.R. (1965). The co-existence of rainbow trout (Salmo gairdneri Richardson) and largemouth bass (Micropterus salmoides Lacepede) in a small Ontario lake. Canadian Fish Culturist, 35, 37-58.

Stringer, G.E. and Hoar, W.S. (1955). Aggressive behaviour in underyearling Kamloops trout. Canadian Journal of Zoology, 33, 148-160.

Symons, P.E.K. (1968). Increase in aggression and in strength of the social hierarchy among juvenile Atlantic salmon deprived of food. Journal of the Fisheries Research Board of Canada, 25, 2387-2401.

Thomas, D.R. (1983). Univariate repeated measures techniques applied to multivariate data. Psychometrika, 48(3), 451-464.

Thomas, D.R. and Rao, J.N.K. (1984). A Monte Carlo study of exact levels of goodness-of-fit statistics under cluster sampling. Section on Survey Research Methods Proceedings of the American Statistical Association, 208-211.

Thompson, S.M. and Jones, G.P. (1983). Interspecific territoriality and competition for food between the reef fishes Forsterygian varium and Pseudolabrus celidotus. Marine Biology, 76(1), 95-104.

Thorpe, J.E., Morgan, R.I.G., Ottaway, E.M., and Miles, M.S. (1980). Time of divergence of growth groups between potential 1+ and 2+ smolts among sibling Atlantic salmon. Journal of Fish Biology, 17(1), 13-21.

Wankowski, J.W.J. (1981). Behavioral aspects of predation by juvenile Atlantic salmon (Salmo salar L.) on particulate, drifting prey. Animal Behaviour, 29(2), 557-571.

Wiley Driscoll, J. and Welanko, P.R. (1981). Dominance relationships in female Herotilapia multispinosa (Pisces: Cichlidae). Animal Learning and Behavior, 9(2), 164-168.

Woodard Cain, N., Jessen, C., and Flanagan, M. (1980a). Effects of prior social experience on agonistic responding by Siamese fighting fish (Betta splendens). Animal Learning and Behaviour, 8(3), 491-496.

Woodard Cain, N., Jessen, C., and Flanagan, M. (1980b). Social responsiveness and physical space as determinants of agonistic behavior in Betta splendens. Animal Learning and Behavior, 8(3), 497-501.

Yamagishi, H. (1962). Growth relations in some small experimental populations of rainbow trout fry, Salmo gairdneri Richardson with special reference to social relations among individuals. Japanese Journal of Ecology, 12, 43-53.

Weiss, J.M. (1968). Effects of coping responses on stress. Journal of Comparative and Physiological Psychology, 65, 251-260.

Appendix A: Terminology

The terminology used in the description of fish agonistic behaviour is variable: descriptors used for one species may have only partial applicability in another species. Also, workers studying a common group, such as the salmonids, may use different terms to describe similar behaviours as well as employ seemingly synonymous terms to describe very different behaviours.

Such inconsistency is unavoidable during the growth phases of a behavioural science (Hinde, 1982). Nevertheless, to avoid ambiguity the terms adopted in this work are those which are the most straightforward in current use. Some of the more potentially troublesome terms are presented below with accompanying definitions. Wherever possible the terms are accompanied by citations for further clarification.

Agonistic behaviour: Aggressive or conflict behaviour, including acts of attack, escape, threat, defense, and appeasement. A form of social behaviour (Brown, 1975; Scott and Fredericson, 1951).

Bite: a form of aggressive behaviour. A nip; may not necessarily involve body contact (Chiszar, Drake, and Windell, 1975; Jenkins, 1969; Stringer and Hoar, 1955).

Chase: a form of aggressive behaviour involving the pursuit of one fish by another through a distance greater than two body

lengths (Stringer and Hoar, 1955).

) Displacement: a form of aggressive behaviour involving the supplanting of one fish by another from a stationary position (Jenkins, 1969; Stringer and Hoar; 1955; Yamagishi, 1962).

Dominant fry: In a dyadic encounter, the fry who is the most aggressive (initiates the most successful attacks). (Barlow and Ballin, 1976).

Subordinate fry: In a dyadic encounter, the fry who initiates the lowest number of successful attacks (Barlow and Ballin, 1976).

Nondominant fry: a subordinate fry.

Appendix B: Rainbow Trout and Brook Charr Behavioural
Biology

Salmonids are not common subjects of study in comparative psychology. Hence, additional information concerning the behavioural biology of the two species studied in this thesis (Salmo gairdneri and Salvelinus fontinalis), pertinent to an appreciation of these species, is in order. The topics considered in this appendix include aspects of the taxonomy, systematics, morphology, and the behavioural ecology of S. gairdneri and S. fontinalis.

A consideration of the agonistic behaviour of these species, from intraspecific as well as interspecific viewpoints, may be found in the introduction.

BACKGROUND INFORMATION

The salmonid group includes not only salmon, trout, and charr (subfamily Salmoninae), but also whitefish (subfamily Coregoninae) and grayling (subfamily Thymallinae). All members of the family are native to the cooler waters of the northern hemisphere. The salmonid body type is characterized by the presence of an adipose fin and an axillary scale, usually visible as a distinct process at the base of the pelvic fin. Salmon and trout are further characterized by strong mandibular teeth, small scales, and short dorsal fins.

The salmonid form is well adapted for living in cold, nutrient poor waters of recently glaciated areas (Behnke, 1972). The advances and retreats of continental glaciers have meant transient existence in these waters with different demes likely to be geographically isolated from one another for extended periods of geological time. Hence it has been suggested that salmonids have been selected to be opportunistic foragers, adaptable in behaviour as well as overall life history (Elliott and Jenkins, 1972; Moyle, 1976). The ability of some salmonids to move freely from fresh water to salt water and back again is perhaps the most well-known example of this behavioural and physiological plasticity.

This behavioural flexibility has allowed these species to inhabit coastal and headwater streams as well as many coldwater lakes of the northern hemisphere. Since anadromous (river spawning, sea migrating) salmonids have strong homing behaviour and since many headwater streams have become isolated over geological time, salmonid populations, both resident and anadromous, tend to develop in response to local conditions. Such populations may be quite distinct from other populations but will hybridize if brought into contact. For example, in isolated mountain streams golden trout (Salmo aquabonita) have evolved independently in such areas. They are normally recognized as a distinct species yet will hybridize with rainbow trout or others of the genus if

given the opportunity (Moyle, 1976). The rainbow trout also hybridizes with cutthroat trout (Salmo clarki) (Rohrer, 1981).

The following sections first consider fundamental aspects of rainbow trout biology and behaviour. Then, similar information on brook charr is given.

RAINBOW TROUT: SYSTEMATICS

The various forms of rainbow trout have been referred to as distinct subspecies, separate species, or variants of the same species. There is also disagreement concerning the relationship of S. gairdneri to the gila trout (S. gilae), the golden trout (S. aquabonita) and the Kamchatka trout (S. mykiss) of Asia.

The taxonomic dilemma is reflected in the many changes in nomenclature. Richardson's original 1886 description of S. gairdneri was that of a steelhead. However Jordan (1892; see Moyle, 1976) preferred the term Oncorhynchus kamloops. Other taxonomic designations have been: S. kamloops whitehousei, S. irideus (Rojas-Ayala, 1980), S. rivularis, S. purpuratus, S. stellatus, and S. argentatus (Moyle, 1976). Although Needham and Gard (1959) point out the futility of employing subspecies names, some gain is achieved by allowing at least partial distinctions in nomenclature. The three common names presently used are: rainbow trout, Kamloops trout, and steelhead (trout). Although the term steelhead is reserved for the large, Pacific coast, sea-

run form, the stock originally introduced in the Great Lakes was steelhead and the later strictly freshwater stocks retain a life history pattern as that found in the sea.

The native range of the rainbow trout includes the eastern Pacific Ocean and the freshwater west of the Rocky Mountains from northwestern Mexico (including parts of Baja California) to southern Alaska. It is also thought to be native in the drainages of the Peace and Athabasca Rivers east of the Rocky Mountains (Moyle, 1976).

With regard to its Canadian range, it occurs outside British Columbia from the Avalon Peninsula, across the southern regions of the provinces from Nova Scotia to Ontario, north to central Manitoba and possibly central Saskatchewan, northern Alberta and parts of the Yukon Territories (Moyle, 1976).

The species was first introduced in the maritime provinces circa 1890 with the exception of Prince Edward Island where it was not introduced until 1925. It was introduced in the Great Lakes in 1895 and in Ontario in 1883. Dates of introduction for the other provinces are: Manitoba, 1938; Saskatchewan, 1924, and Alberta, 1958. It was introduced in the Yukon Territory in 1943 (Moyle, 1976).

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MORPHOLOGY

Rainbow trout are variable in colour, body shape, and meristic character. These variations are influenced by habitat, size, age, and sexual condition. Generally, adults are 30-46 cm long with the body somewhat vertically compressed, particularly in the larger fish. Greenway (1964) suggests such a shape is characteristic of rover-predator species: the centre of gravity of a rover-predator is close to the midpoint of the body. Such a shape allows fish to cruise more efficiently while foraging than other shapes as well as to swim or station hold-in strong stream currents with minimal effort.

Stream dwelling rainbow trout tend to be darker coloured than the silvery lacustrine Kamloops trout or the larger steel-head. Dorsal colouration, including the head and upper side of the body varies from steel blue, blue-green, yellow-green to almost brown. The sides may be silver, white, or pale yellow-green to grey. They may also be marked with a vague, pink blush. Ventral colouration may be silver, white, grey, or yellow. The cheeks and operculae are pink as well. However it is the multi-hued colouration of the lateral band from which the species derives its common name.

Spotting is mostly restricted above the lateral line but may be scattered over the entire side. The dorsal and caudal fins have regular, radiating rows of black spots. The adipose fin is

similarly lightly spotted and is lined with a black border. The other fins may also be spotted but a complete absence of spotting is not unusual. This is also seen in the Japanese trout (Oncorhynchus masou) (Maeda and Hidaka, 1979).

In some populations, the skin folds of the lower jaw have faint red lines, with the result that these rainbow trout are confused with cutthroat trout (S. clarki) in areas where the two species are sympatric. Spawning and post-spawning rainbow trout are very dark with pronounced red lateral bands. Stream residents may also retain vertical parr mark banding in adulthood and can differ in appearance from lake residents of comparable age and size.

The mouth of the rainbow trout is large with the maxillary usually extending behind the eye. The teeth are well developed on the upper and lower jaws as well as on the vomer, palatines, and the tongue. Basibranchial teeth are absent however.

The dorsal fin has 10 to 12 principal rays; the anal fin, 8 to 12 principal rays; the pelvic fins, 9 or 10 rays each; and the pectoral fins, 11 to 17 each. The tail is slightly forked. There are 16 to 22 gill rakers on each arch and 9 to 13 branchiostegal rays. The scales are small with 110 to 160 pore scales along the lateral line, 18 to 25 scale rows lie above the lateral line in contrast to the 14 to 29 scale rows lying below it.

The colouration of young rainbow trout is similar to that found in adults. However, young rainbow trout also possess 8 to 13 widely spaced parr bands centred on the lateral line with the interspaces wider than the bands. In addition, there are 5 to 10 dark marks on the back between the head and dorsal fin, white to orange tips on the dorsal and anal fins and, occasionally, a small number, of black spots on the tail (McPhail and Lindsey, 1970). As previously stated, adults from small streams may retain much of the colour pattern they exhibited as parr.

BEHAVIOURAL ECOLOGY

The life history patterns of rainbow trout vary from that of the migratory, sea-going pattern of steelhead populations to that of populations in small streams, where an individual may complete its entire life cycle in a few hundred meters of water. When in freshwater, most rainbow trout dwell in cool, clear, fast flowing permanent streams and rivers, where riffles are prevalent. They are also known to inhabit mountain lakes and reservoirs (Moyle, 1976).

Individuals with different life history characteristics may co-occur. For example, a river system could contain: (1) river resident rainbow trout, (2) early migrating (winter run) steelhead, (3) late migrating (summer run) steelhead, as well as (4) lake resident Kamloops trout (Moyle, 1976).

1. Water Conditions

Rainbow trout will survive water temperatures ranging from 0 to 28 °C. Tolerance of the temperatures at the upper extremes of this range, however, are only possible following gradual acclimation and saturation of the water with oxygen. Optimal temperature for growth varies between 13 to 21 °C. At low temperature, rainbow trout can withstand oxygen concentrations as low as 1.5 to 2 ppm but normally concentrations close to saturation are required for growth; although exposure to super-saturation conditions is lethal (Stevens, Nebeker, and Baker, 1980).

Rainbow trout also pass through a period where they are vulnerable to current velocity fluctuations (Ottaway and Clarke, 1981). The nature of the susceptibility appears to be related to the particular strain and environmental conditions involved (Butler, 1981; Northcote, 1981; Northcote and Kelso, 1981).

Their tolerance of water acidity is also broad. Rainbow trout can live in water ranging from pH 5.8 to pH 9.6 with best growth in slightly alkaline waters (pH ~ 8) (Carlander, 1969).

2. Diet

Rainbow trout begin feeding with the final absorption of the visible yolk-sac (Dill, 1977). Even at this early stage, differences in feeding behaviour may be observed (MacCrimmon and Twongo, 1980). Later trout feed on a variety of invertebrates including plankton, crustaceans, insects as well as snails and

leeches. The choice of prey depends, in part, upon the age of the fry: older fry feed on larger prey than do younger fry. This shift in prey selection is thought to increase the efficiency of energy intake as well as optimize energy expenditure (Irvine and Northcote, 1982).

Rainbow trout are equally adept at feeding both on the bottom (Moyle, 1976) and on the surface (Hilton and Sluger, 1981) although they are best known as drift feeders (Irvine and Northcote, 1982; Nilsson and Northcote, 1981). In this respect they are similar to other salmonids. For example, the Atlantic salmon (Salmo salar) also feeds on drifting, particulate prey (Wankowski, 1981) as does the chinook salmon (Oncorhynchus tshawytscha) (Double, Grey, and Page, 1980). In overall diet selection, the rainbow trout is perhaps most like the chinook salmon (O. tshawytscha) and the coho salmon (Oncorhynchus kisutch) (Johnson, 1981a).

However, despite similar flexibility in foraging strategy (or prey acceptance) -- such flexibility being useful when confronted with shifting pressures in competition (Roitblatt, Tham, and Golub, 1982) -- the rainbow trout does not appear to be as plastic as the coho salmon (O. kisutch) (Dill, 1983; Johnson and Johnson, 1981).

Nevertheless, the rainbow trout is sufficiently flexible to adjust foraging patterns to local conditions. For example, when rainbow trout and cutthroat trout (Salmo clarki) are sympatric, the two species exploit different parts of the habitat (Nilsson and Northcote, 1981). The rainbow trout become mainly limnetic surface and mid-depth feeders whereas cutthroat trout utilize more littoral prey and tend to be more piscivorous.

This partitioning of resources by sympatric salmonid species is common. For example, a similar situation exists in certain areas where pink (Oncorhynchus gorbuscha) and chum (Oncorhynchus keta) salmon are found together (Cooney, Urquhart, and Barnard, 1981). Such a strategy of concurrent feeding is particularly beneficial when population, hence territorial, constraints are operative (Dill, 1983; Dill, Ydenberg, and Fraser, 1981; Grayton and Beamish, 1977; Jobling, 1983) and habitat exploitation is at a premium.

The availability of other fishes as food is often considered necessary for the attainment of large size in rainbow trout (as well as the time of onset of feeding (Refstie, 1980)). Hence, large sized rainbow trout are typically found in large western lakes as well as in the Great Lakes. Rainbow trout are also successful in smaller lakes where invertebrates may constitute much of the diet. Such lakes are able to maintain rainbow trout averaging 2 to 3 kg. In lakes with high numbers of Gammarus, individual trout may attain sizes of 7 kg in just three years

following introduction (Moyle, 1976).

3. Competition

Rainbow trout are subject to predation in streams by other trout and charr as well as by coho salmon (O. kisutch) smolts (Johnson, 1981b). This is not so in the Great Lakes where most of the native predatory fish are not found in the streams inhabited by rainbow trout sub-adults. Diving birds, raptors and mammals remain potential predators in all areas.

Also, the Pacific lamprey parasitizes the steelhead in the Pacific Ocean to a minor extent whereas the sea lamprey is a major threat to survival in Great Lakes populations.

Interspecies interactions of rainbow trout in lakes is less well understood. Trout tend to school and roam within lakes such that aggressive behaviour is thought to play a minor role (Moyle, 1976). The decrease in individual growth rate and population size following the introduction of another species into a previously pure trout lake indicates that direct competition for limited food resources takes place upon initial meeting. Eventually, the trout and the new species will segregate by habitat and feeding strategies, with the rainbow trout preying occasionally on the other species (Johannes and Larkin, 1961).

4. Spawning

Most rainbow trout are spring spawners (February to June) but low temperatures in higher, mountain altitudes may delay spawning until July or August. California steelhead also spawn in the spring, but they frequently migrate upstream in the fall several months before they actually spawn. In some north coast streams, small numbers migrate upstream in the late spring, spend the summer in deep pools, and spawn in the spring of the following year. All varieties of rainbow trout have well-developed homing abilities and usually spawn in the same stream in which they lived as fry.

Although spawners in some areas move toward the spawning stream while ice is still on the water surface, spawning typically takes place only after the ambient water temperature is between 10 to 15.5 °C. Males are aggressive on the spawning grounds and drive others away from a nest occupied by a female. They will also defend the redd against other females (Newcombe and Hartman, 1980).

The male courts the digging female by sliding along and crossing over her body, rubbing his snout against her caudal peduncle in addition to using body undulations and body pressings. The digging female may be attended by several males with the largest, and, usually most active, courter dominant over the other males. The female excavates a redd in the gravel by turning on her side and beating her tail rapidly against the stones.

In this manner she cleans the gravel and creates a depression that is longer and deeper than her body. Nest building takes place throughout the night and day.

When ready to spawn, the female rests near the bottom of the centre of the redd. The dominant male assumes a position parallel to the female such that their bodies touch. Their mouths gape and their bodies arch and shudder resulting in the release of milt and eggs into the interstices of the redd. Often two males participate with a single female in one spawning.

Mate selection by the female involves a number of sensory modalities. Visual signalling appears to be the most important since size, in addition, to the behavioural display is known to influence which male the female selects (Chebanov, 1979).

Olfaction also plays a role in spawning. Honda (1980) has characterized a sex pheromone released in post-ovulatory female rainbow trout that is detected by males at the spawning site. The pheromone has been shown to elicit persistent courtship behaviour in sexually active males.

Although the role of pheromones is known to be important in many fish species (Liley, 1982), the nature of olfactory guided behaviour in salmonids has largely been restricted to migratory activity (Bentmar, 1979; Cramer, 1981; Johnsen and Hasler, 1980). This is so despite implications that the chemical cues involved in migration may have a broader purpose (Mazeaud, 1981). For

example, pheromones may serve an important, and as yet uncharacterized, function in salmonid social behaviour as is so for other fish species including the cichlid Haplochromis burtoni (Crapon de Craona, 1980) and the goldfish, Carassius auratus (LeMartret and Saglio, 1982; Saglio and LeMartret, 1982).

Anatomical understanding of the rainbow trout olfactory system is only a first step in understanding the role of olfaction in the behaviour of this species (Rhein, Cagan, Orkand, and Dolack, 1981).

Returning to the issue of spawning, females dig and spawn in several nests with the same or other males; the second site is usually upstream of the first such that the gravel displaced in the second excavation covers the first batch of eggs.

As many as 13,000 eggs may be deposited overall although the usual number ranges between 800 to 1,000 eggs. The eggs are 3-5 mm in diameter, demersal, and pink to orange in colour.

5. Hatching

Eggs usually hatch in 4 to 6 weeks with the newly hatched alevins requiring an additional 3-7 days to absorb the yolk-sac before becoming free swimming (Moyle, 1976). However, in this laboratory, periods of up to one month for complete yolk-sac absorption are more common. The time-course of hatching is variable, subject to the influences of habitat and temperature history of the eggs subsequent to fertilization; although

modelling procedures exist which can accurately predict hatching time by considering these variables (Crisp, 1981).

Fry begin feeding about two weeks after hatching. In the wild, emergence occurs between mid-June and mid-August when spawning is in April or May. The fry of lake-resident spawners move from the spawning river to the lake almost immediately although they may spend as long as three years in the streams. Fry of stream-resident spawners remain in the streams whereas those of steelhead migrate to the sea, usually after two years in freshwater.

Within a given population the length of time spent as young in the spawning stream, lake, or sea may vary greatly among individuals as does the time until the first spawning. Sexual maturity occurs after three years, with males often maturing a year sooner than females. Maturation has been observed as early as one year of age in males to as late as six years in females. Size at maturity is variable, ranging from 15-25 cm in some small lakes and streams, to 40 cm in steelhead and Great Lakes populations. Survival is low with the number spawning more than once less than 10% of the original population.

Maximum size also varies with habitat but, as in hatching, predicting growth rate can be accurately achieved through recent mathematical modelling procedures (Iwama and Tautz, 1981; see also Refstie, 1980). Steelhead can grow to 120 cm and 16 kg, but 4

kg is the average. Great Lakes rainbow trout grow to about 90 cm and rarely exceed 3-4 kg.

Life expectancy can be as brief as 3 or 4 years in many stream and lake populations, but that of steelhead and Great Lakes populations may be as high as 6-8 years.

BROOK CHARR

The life history of brook charr is less varied than that of the rainbow trout. Brook charr typically are inhabitants of clear, cold lakes and streams. In California for example, despite continuous and widespread stocking efforts, S. fontinalis populations have become established only in small, spring-fed headwater streams and in isolated mountain lakes. Known also as brook trout, eastern brook trout and speckled trout, the species was described initially by Mitchill in 1815 (McAfee, 1966; Moyle, 1976). They are native to the northeastern United States and eastern Canada though some populations are found as far south as Georgia in Appalachian mountain streams. Through transplantation and management, they are widely distributed throughout the western United States, South America, Asia, New Zealand, and Europe (Sedgwick, 1982).

MORPHOLOGY

Brook charr are distinguished from other trout by the olive green dorsal regions covered with whitish vermiculations. There are red spots on the flanks surrounded by blue haloes, and white trim on the pectoral, pelvic, and anal fins. The mouth is large, relative to that of rainbow trout, with an oblique tilt relative to the longitudinal body axis such that the maxillary extends past the posterior margin of the eye. Teeth are present on both jaws, tongue, palatine bones and head of the vomer but are absent from the shaft of the vomer and the basibranchial bones.

There are 110 to 132 scales in the lateral line. Also there are 10 to 14 rays in the dorsal fin, 9 to 12 in the anal fin, 11 to 14 in the pectoral fins, and 8 to 10 in the pelvic fins.

Spawning males are deep-bodied with hooked lower jaws whereas spawning females are identifiable by protrusion of the genital papilla. Both sexes may become brightly coloured at such time, with dusky to black ventral regions, reddish-orange sides, and reddish lower fins. Young fish have 8 to 12 parr marks and, in some individuals, red, yellow, or blue spots.

BEHAVIOURAL ECOLOGY

1. Water Conditions

Brook charr are among the most cold tolerant of salmonids, feeding at temperatures as low as 1°C (Elliot and Jenkins, 1972). The upper limit is about 26°C given suitable time for

acclimation although the preferred temperature range is 14-16 °C (Carlander, 1969). Temperatures above 19 °C however inhibit growth, either wholly or in part (Moyle, 1976).

2. Diet

Stream dwelling brook charr feed primarily on terrestrial insects and aquatic insect larvae. The food is taken in drift form, on or near the water surface (Ellison, 1980). They are opportunistic feeders concentrating on whatever organisms are most abundant. They can also bottom feed (Moyle, 1976) as has been observed in this laboratory in newly free swimming populations. Prey size, along with learned individual specializations, are thought to be the primary determinants of brook charr diet (Allan, 1981).

The diet of lacustrine forms is similar to the stream diets except the young charr feed heavily on zooplankton and large charr feed more on fish (Reimers, 1958) although young, laboratory-reared, fry can also be piscivorous (personal observation). Brook charr will feed whenever there is sufficient light to allow detection of prey, although the most intensive feeding, in the wild, occurs at dawn or dusk when crepuscular insects are most active. (However brook charr are known to feed preferentially during daylight in other areas (Allan, 1981)). Interestingly, similar peak periods of feeding activity have been observed in this laboratory although automated feeding occurs at regular

intervals throughout the light period.

Brook charr are efficient foragers in that they infrequently overfeed. For example, Allan (1982) found that reduction in brook charr population density had little effect on either the density of benthic vertebrates or on drift density. Gowing and Momot (1979) have similarly argued that local brook charr population size has little effect on the invertebrate community unless extremely high densities are artificially created by stocking.

3. Spawning

Brook charr can spawn either in the fall (Moyle, 1976) or winter (Sedgwick, 1984), though the specific time is dependent in part on water temperature.

Spawning sites are chosen by females, basing their choice on such factors as: (1) upwelling through the bottom, (2) a preferred colder water temperature at the redd site than in surrounding water, (3) small, pea-sized gravel, and (4) overhanging cover such as is offered by undercut stream banks or foliage. Of these factors, it is the cold, constant conditions which ensure a springtime hatching (Hale and Hilden, 1969).

Brook charr can also spawn in suboptimal habitats such as gravel riffles, sandy-bottomed springs, and gravel-bottomed lake shallows. This adaptability has allowed the species to maintain populations in lakes lacking the accessible routes other

salmonids may require.

As in rainbow trout, female brook charr excavate the redds with their tails. Excavation is not normally initiated unless males are nearby. Of the males attracted to the spawning female only one succeeds in spawning with the female; driving away other males as well as aiding the female in defense against other females.

The spawning ritual has long been known to be a complex of tactile and visually-guided behaviours. Recently, Berst, Emery, and Spangler (1981), working with hybrids of brook charr and lake charr (*S. namaycush*) have provided evidence that acoustic cues are also used. These signals appear to be for the inauguration and sequencing, hence the temporal modulation, of the courtship behaviour.

The fertilized eggs are covered by the female, thus clearing a new redd upstream from the first. Only 15 to 60 eggs are laid at a time from an average fecundity of 200 to 600 eggs (McAfee, 1966). A number of repeated excavations are thus required. Males may spawn repeatedly as well, with different mates. Spawning can occur throughout the day but peak periods centre around early morning and dusk (Sedgwick, 1984).

Egg development is slow, taking usually 100 to 144 days in water temperatures of 2 to 5 °C. McAfee (1966) reports egg development within 35 days at higher (13 °C) temperatures.

Similar results have been found in this laboratory.

In the first three to four weeks following hatching, the alevins remain in gravel, becoming more active as the yolk sac is absorbed and ambient water temperature rises. Stream dwelling fry move into the shallows, among emerging plants, or into backwaters, to feed on small crustaceans. Lacustrine forms move into shallow water also, congregating in areas shielded from wave action.

Growth is dependent on a number of factors. These include: (1) duration of the season, (2) water temperature, (3) water chemistry, (4) population density, (5) food availability, (6) competition with sympatric species, (7) predation, and (8) fishing pressure. The most rapid growth occurs in lakes and streams of moderate elevation in which large populations of fish are absent. Maximum length seldom exceeds 30 cm. Maximum weights greater than 0.5 kg and lifespans longer than 4 or 5 years are also rare.

Early maturity is characteristic of the species. Males may spawn at the end of their first summer whereas females may mature one year later. However, sexual maturity of males in their second or third year and in females in their third or fourth year is more common. At such later times the size range of the males and females is 12-15 cm and 15-20 cm respectively.

Commercial interest in the species has recently revived because of the hybridization potential in brook charr. For

example, brook charr will hybridize to produce sterile hybrids of market quality higher than that of either parent species. Brook charr will also hybridize with brown trout to produce tiger trout; so-called because of the striped colouration and voracious feeding habits of the hybrid.

Brook charr can also be crossed with lake trout (S. namaycush) to produce splake trout. These are fertile hybrids used to restock trout depleted lakes in Canada and the eastern United States.

Appendix C: Statistical Considerations

The complete data sets for the first four experiments are presented here (Table 1 to Table 4). In a previous draft of the thesis, these data sets were the bases for the mathematical-statistical modelling of behavioural interactions between fry of the four size-colour types. Although the modelling has not been included in the current form of the thesis, the data sets have been provided in the hopes they may be of use in future efforts to mathematically describe rainbow trout and brook charr behaviour.

Less ambitious treatments of the data sets are possible. Namely, using log-linear (X^2) analysis, one may search for significant interactions within each data set. Such a procedure involves the systematic deletion of interaction effects from an all-factors-interacting, "saturated", design. In each data set here, the saturated design would contain the four way interaction of Time x Initiator x Receiver x Behaviour, plus all possible three- and two-way interactions. The most parsimonious combination of interactions which still accounts for most (95%) of the data is typically chosen for interpretation.

For each experiment, there are: four levels of the Time variate (Week 1 to Week 4), four levels each of the Initiator and

Receiver variates (representing the four size-colour classes), and three levels of the Behaviour variate (displacement, chasing, and biting). Thus each saturated design would contain $4 \times 4 \times 4 \times 3$, or 192, cells.

Inspection of the tables show there are many cells with low, and even zero, values. The presence of zero values is troublesome in the log-linear analysis of categorical data although it is not necessarily catastrophic (Thomas, personal communication). The problem of low and zero values has advanced in recent years and a treatment of the topic is beyond the scope of this thesis. Further information may be found in: Bonett and Bentler, 1983; Brown, 1981; Delucchi, 1983; Fienberg, 1980; Thomas and Rao, 1984.

An accepted practical solution in dealing with zero values is to add a small, non-zero constant to each cell in the data set (Brown, 1981). Alternatively, one may consolidate across cells to reduce the number of zero cells and to increase the size of each cell (Ferguson, 1971). Both methods were used on the four data sets in the search for interaction effects.

Using the small constant method, a constant of 0.5 was added to each cell of each data set. Then, significant interactions at the $p < .05$ level were sought using the procedure outlined above (found in Brown, 1981). Using the notations Time = T, Initiator = I, Receiver = R, and Behaviour = B, the significant interactions uncovered were:

Experiment 1: T x I x R, T x R x B.

Experiment 2: T x I x R, T x B, I x B.

Experiment 3: T x I x R, T x I x B.

Experiment 4: T x I x R, R x B.

The collapsed cell method was also used. For each of the four data sets the results of the first and second weeks were summed together as were the results of the third and fourth weeks. Also, it was noted initiations by SD fry were rare (i.e. many zero values) and so were dropped from each analysis. Consequently the design of each data set now involved: two levels of the Time variate, three levels of the Initiator variate, four levels of the Receiver variate, and three levels of the Behaviour variate. Thus, each design had $2 \times 3 \times 4 \times 3$, or 72 cells, rather than the original 172 cells.

Using this approach, the significant interactions ($p < .05$) were:

Experiment 1: T x I x R, T x R x B, I x B.

Experiment 2: T x I x R, T x B, I x B.

Experiment 3: T x I x R, T x B, R x B, I x B.

Experiment 4: T x I x R, T x B, R x B.

By inspection, it can be seen the two statistical approaches yield comparable results. The interpretation of these results is straightforward. With the small constant method we find:

(1) Both species, in both years of study, show statistically significant changes in dyadic encounters over time ($T \times I \times R$ effect).

(2) These changes are reflected in changes in behaviour over time ($T \times R \times B$ -- Experiment 1; $T \times B$ -- Experiment 2; $T \times I \times B$ -- Experiment 3). These shifts represent the rise of LL fry to dominance and the decline in the relative frequency of chasing and biting with time.

(3) Differences are observed between the two samples of rainbow trout. In the first year, fry of different size-colour type were distinguishable on the basis of their behaviour as receivers in interactions ($T \times R \times B$ -- Experiment 1). Conversely, for the second year, rainbow trout fry of different size-colour were distinguishable in terms of their behaviour as initiators ($I \times B$ effect -- Experiment 3).

(4) Similarly, brook charr fry of different size-colour type, in the first year, behaved differently as initiators ($T \times I \times B$ -- Experiment 2) but not as receivers. The converse is true in the second year where the different size-colour classes behaved differently when they were defending in, but not initiating, an encounter ($R \times B$ -- Experiment 4).

Inspection of the results of the collapsed designs analyses yields similar and, in some cases, identical interpretations. Thus, one finds:

- (1) Both species, in both years, show changes in dyadic interactions over time ($T \times I \times R$ -- all experiments).
- (2) These changes are reflected in behavioural shifts over time ($T \times R \times B$ -- Experiment 1; $T \times B$ -- all other experiments).
- (3) For rainbow trout, in both years, fry of different size-colour type are distinguishable on the basis of activity from the perspective of initiator or receiver ($T \times R \times B$; $I \times B$ -- Experiment 1; $R \times B$; $I \times B$ -- Experiment 3).
- (4) For brook charr studied in the first year, fry of different size-colour type are statistically distinguishable on the basis of initiator activity ($I \times B$ -- Experiment 2). Conversely, in the second year, with a different sample, only receivers show behavioural differences among the four size-colour types ($R \times B$ -- Experiment 4).

Thus, the statistical analyses corroborate the descriptive reports contained within the main body of the thesis. It must be borne in mind these analyses were performed on data obtained from designs which were not strictly multinomial in nature and must be interpreted accordingly. This pertains particularly to the behavioural variability of fry of different size-colour type when cast in the roles of initiators or receivers.

Thus, the spirit of these analyses is exploratory in nature. The question of differences in terms of offensive (initiator) and defensive (receiver) behaviour between the species, or at least these samples, remains an intriguing question.

Table 1. Observed Frequencies (per week) of Displacement,
Chasing, and Biting in Rainbow Trout (Salmo gairdneri).
Year 1.

		I. Displacement			
		Week 1	Week 2	Week 3	Week 4
Recr	Init	Obs	Obs	Obs	Obs
LL	LL	15	6	7	3
	LD	5	2	0	0
	SL	2	3	1	0
	SD	2	1	0	0
LD	LL	19	17	15	13
	LD	6	0	2	6
	SL	7	0	0	3
	SD	0	0	1	0
SL	LL	35	17	16	19
	LD	14	1	2	7
	SL	17	9	7	2
	SD	1	0	0	0
SD	LL	10	11	7	4
	LD	3	0	0	5
	SL	1	2	2	0
	SD	0	0	0	0

II. Chasing

		Week 1	Week 2	Week 3	Week 4
Recr	Init	Obs	Obs	Obs	Obs
LL	LL	15	8	1	2
	LD	4	111	0	0
	SL	1	1	0	0
	SD	1	1	0	0
LD	LL	16	126	17	17
	LD	2	0	0	3
	SL	3	0	0	0
	SD	0	0	0	0
SL	LL	47	65	18	16
	LD	9	5	0	6
	SL	11	4	2	0
	SD	0	1	0	0
SD	LL	7	3	2	19
	LD	2	6	0	1
	SL	1	6	1	0
	SD	0	0	0	0

III. Biting

Recr	Init	Week 1	Week 2	Week 3	Week 4
		Obs	Obs	Obs	Obs
LL	LL	11	4	0	1
	LD	3	110	0	0
	SL	0	0	1	0
	SD	1	0	0	0
LD	LL	10	124	7	8
	LD	0	0	0	1
	SL	3	0	0	0
	SD	0	0	0	0
SL	LL	17	32	6	14
	LD	3	5	0	8
	SL	7	4	1	0
	SD	1	1	0	0
SD	LL	0	1	2	11
	LD	1	6	0	0
	SL	1	2	0	0
	SD	0	0	0	0

Abbreviations: Recr = receiver; Init = initiator; SD = small, dark class; SL = small, light class; LD = large, dark class; LL = large, light class; Obs = observed frequency.

Table 2. Observed Frequencies (per week) of Displacement,
Chasing, and Biting in Brook Charr (Salvelinus fontinalis).

Year 1.

I. Displacement

		Week 1	Week 2	Week 3	Week 4
Recr	Init	Obs	Obs	Obs	Obs
LL	LL	7	8	5	25
	LD	0	2	1	0
	SL	2	0	0	5
	SD	0	0	0	0
LD	LL	20	39	33	51
	LD	2	1	12	2
	SL	5	4	5	3
	SD	0	0	0	0
SL	LL	29	54	39	51
	LD	5	5	1	3
	SL	17	7	3	11
	SD	1	0	0	0
SD	LL	18	37	21	12
	LD	2	7	1	3
	SL	0	3	6	5
	SD	3	0	0	0

11. Chasing

		Week 1	Week 2	Week 3	Week 4
Recr	Init	Obs	Obs	Obs	Obs
LL	LL	24	4	33	25
	LD	0	4	0	3
	SL	0	2	4	8
	SD	0	0	0	0
LD	LL	89	134	107	50
	LD	16	1	4	1
	SL	72	12	6	11
	SD	0	0	0	0
SL	LL	97	188	98	84
	LD	39	5	2	0
	SL	135	43	15	16
	SD	0	3	0	0
SD	LL	53	43	45	14
	LD	18	7	1	4
	SL	18	25	5	15
	SD	21	6	3	0

III. Biting

Recr	Init	Week 1	Week 2	Week 3	Week 4
		Obs	Obs	Obs	Obs
LL	LL	22	1	4	5
	LD	0	2	0	0
	SL	0	2	3	12
	SD	0	0	0	0
LD	LL	60	67	49	21
	LD	10	1	6	0
	SL	60	8	7	7
	SD	0	0	0	0
SL	LL	58	78	57	20
	LD	23	2	1	0
	SL	108	30	8	5
	SD	0	1	0	0
SD	LL	37	22	33	6
	LD	17	6	2	2
	SL	14	16	3	4
	SD	9	4	3	0

Abbreviations: Recr = receiver; Init = initiator; SD = small, dark class; SL = small, light class; LD = large, dark class; LL = large, light class; Obs = observed frequency.

Table 3. Observed Frequencies (per week) of Displacement, Chasing, and Biting in Rainbow Trout (Salmo gairdneri).
Year 2.

		1. Displacement			
		Week 1	Week 2	Week 3	Week 4
Recr	Init	Obs	Obs	Obs	Obs
LL	LL	0	13	31	11
	LD	0	5	2	3
	SL	0	0	2	1
	SD	0	3	3	0
LD	LL	4	20	25	35
	LD	0	8	6	7
	SL	2	17	9	12
	SD	0	5	1	0
SL	LL	5	28	43	44
	LD	4	19	21	10
	SL	49	61	47	45
	SD	23	14	11	6
SD	LL	7	20	16	21
	LD	5	14	3	1
	SL	67	52	30	29
	SD	46	10	6	7

II. Chasing

		Week 1	Week 2	Week 3	Week 4
Recr	Init	Obs	Obs	Obs	Obs
LL	LL	0	46	84	20
	LD	0	13	22	4
	SL	0	11	15	36
	SD	0	6	3	2
LD	LL	6	50	77	51
	LD	0	13	22	19
	SL	3	28	20	29
	SD	0	10	1	3
SL	LL	9	78	180	141
	LD	4	45	50	46
	SL	69	109	353	103
	SD	47	32	5	18
SD	LL	5	30	25	39
	LD	3	11	5	13
	SL	134	93	60	95
	SD	58	25	10	4

III. Biting

		Week 1	Week 2	Week 3	Week 4
Recr	Init	Obs	Obs	Obs	Obs
LL	LL	0	40	76	31
	LD	0	12	22	6
	SL	0	12	17	35
	SD	0	7	4	2
LD	LL	5	49	98	52
	LD	0	17	23	22
	SL	2	31	19	34
	SD	0	12	1	3
SL	LL	10	77	121	133
	LD	3	39	50	29
	SL	76	108	334	98
	SD	48	29	5	16
SD	LL	9	31	31	39
	LD	5	12	6	14
	SL	108	92	63	94
	SD	74	25	7	8

Abbreviations: Recr = receiver; Init = initiator; SD = small, dark class; SL = small, light class; LD = large, dark class; LL = large, light class; Obs = observed frequency.

Table 4. Observed Frequencies (per week) of Displacement,
Chasing, and Biting in Brook Charr (Salvelinus fontinalis).
Year 2.

		I. Displacement			
		Week 1	Week 2	Week 3	Week 4
Recr	Init	Obs	Obs	Obs	Obs
LL	LL	1	6	12	46
	LD	0	2	0	0
	SL	1	0	0	0
	SD	0	0	0	2
LD	LL	2	6	7	3
	LD	0	0	0	0
	SL	2	0	0	11
	SD	1	0	0	0
SL	LL	7	24	14	24
	LD	7	5	0	1
	SL	46	38	17	24
	SD	7	1	0	1
SD	LL	10	1	5	2
	LD	3	2	0	0
	SL	17	8	23	9
	SD	12	2	3	2

II. Chasing

Recr	Init	Week 1	Week 2	Week 3	Week 4
		Obs	Obs	Obs	Obs
LL	LL	0	0	8	31
	LD	0	0	0	0
	SL	0	0	0	3
	SD	0	0	0	0
LD	LL	2	4	9	3
	LD	0	0	0	0
	SL	0	0	1	25
	SD	0	0	0	0
SL	LL	10	21	8	28
	LD	1	1	0	0
	SL	30	52	14	65
	SD	9	0	0	0
SD	LL	12	1	4	7
	LD	0	2	0	0
	SL	25	2	29	14
	SD	11	1	2	0

III. Biting

Recr	Init	Week 1	Week 2	Week 3	Week 4
		Obs	Obs	Obs	Obs
LL	LL	0	0	2	5
	LD	0	0	0	0
	SL	0	0	0	2
	SD	0	0	0	0
LD	LL	2	0	6	0
	LD	0	0	0	0
	SL	1	0	1	19
	SD	1	0	0	0
SL	LL	5	15	7	24
	LD	3	3	0	0
	SL	22	19	4	52
	SD	4	0	0	0
SD	LL	2	1	3	6
	LD	0	1	0	0
	SL	13	2	18	4
	SD	9	1	2	0

Abbreviations: Recr = receiver; Init = initiator; SD = small, dark class; SL = small, light class; LD = large, dark class; LL = large, light class; Obs = observed frequency.

END

13.08.87

FIN