

PAVLOVIAN CONDITIONING IN CONVICT CICHLIDS  
(Cichlasoma nigrofasciatum)

Patricia A. Whyte

A thesis  
presented to the University of Manitoba  
in partial fulfillment of the requirements for  
the Degree of Master of Arts in the  
Department of Psychology

Winnipeg, Manitoba

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(CICHLASOMA NIGROFASCIATUM)

BY

PATRICIA A. WHYTE

A thesis submitted to the Faculty of Graduate Studies of  
the University of Manitoba in partial fulfillment of the requirements  
of the degree of

MASTER OF ARTS

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## Abstract

The present experiment pursued Hollis' (1984) hypothesis that the biological function of Pavlovian conditioning is to provide anticipatory function-specific responses that convey a biological advantage to the individual. The experiment had three goals: to demonstrate Pavlovian conditioning in convict cichlids; to show a functional gain of learning; and to determine whether the conditioned response included a unique aggressive component and was therefore a function-specific conditioned aggressive behavior, or was indicative of a more general alert state. In the conditioning phase, fish in the paired group received six presentations on each of 30 consecutive days of a green light CS and a male rival US. US alone and CS alone control groups were matched to the appropriate number and pattern of stimuli. In the test phase, the experimental subjects were pitted against naive rivals in a signaled encounter. Although the levels of obtained conditioned responses were low, a significant pattern of outcomes during the test encounter was indicative of an advantage for the paired group. Finally, the occurrence of approach behavior only and not threat displays as conditioned responses was indicative of a general alert or preparatory function for Pavlovian conditioning in fish. Due to the lack of statistical confirmation, all conclusions were tentative.

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Traditionally, learning theory has focused on how learning occurs (mechanisms of learning) and not how learning is used (functions of learning) (Shettleworth, 1983). However, this focus has been challenged by demonstrations of learning phenomena which seemed to suggest a constraint on the mechanisms of learning (e.g., Bolles, 1970; Breland & Breland, 1961; Garcia & Koelling, 1966; Seligman, 1970; Shettleworth, 1972) by the biological requirements of particular organisms. The observed learning phenomena came to be known as constraints phenomena. Although specialized learning mechanisms were postulated to account for constraints phenomena (e.g., Bolles, 1970; Garcia & Koelling, 1966; Shettleworth, 1975), an appeal to numerous specialized mechanisms was subsequently challenged by research that demonstrated that many constraints phenomena could be accounted for by general mechanisms of learning (Domjan, 1983; Logue, 1979).

The constraints issue raised two important points. First, demonstrations of the influence of biological factors on learning suggested a need to examine learning within an ecological and evolutionary framework (Hollis, 1982; Johnston, 1981; Shettleworth, 1983). Second, the constraints issue illustrated that the functions of learning and the mechanisms of learning do not have a one-to-one relationship, although considerations of function do have implications for an analysis of mechanism (Shettleworth, 1983). Thus, both the functions and mechanisms of

learning should be taken into account in an examination of learning within an ecological and evolutionary framework (Shettleworth, 1983).

A first approximation to an analysis of both the functions and the mechanisms of learning was made by Hollis (1982, 1984). Hollis (1984) investigated the biological function of conditioned aggressive responses in male blue gourami fish. Hollis (1984) postulated that Pavlovian conditioning would result in a function-specific conditioned aggressive behavior. According to the prefiguring hypothesis (Hollis, 1984), the conditioned behavior would serve a preparatory function in that it would serve to optimize an animal's interaction with a rival. Hollis (1984) showed that using a male target fish as an unconditioned stimulus (US) in Pavlovian conditioning for another male resulted in superior territory defense for the conditioned male. It appears then, that evidence exists for the function-specific conditioned aggressive behavior that Hollis (1984) had postulated. Furthermore, since only males that defend a territory reproduce, Hollis asserted that Pavlovian conditioning conveyed a biological advantage to the conditioned males.

However, Hollis (1984) may have been in error in concluding that Pavlovian conditioning resulted in a function-specific conditioned aggressive behavior. Pilot research on the conditioning of food-seeking behavior in gouramis revealed the development of fin erection as a conditioned response. The

observation of fin erection in both food-seeking and aggressive behavior (Hollis, 1984) indicates an overlap in the response topography of the early components of food-seeking and territorial defense in the gourami. It may be that rather than prepare a subject for a particular US, conditioning may serve the function of alerting the subject to the impending occurrence of biologically significant events. As such, conditioned fin erection may subserve a general arousal/attention mechanism rather than constitute a function-specific conditioned aggressive behavior. Consequently, Hollis (1984) may have been premature in concluding that Pavlovian conditioning resulted in a function-specific conditioned aggressive behavior, and therefore, Hollis (1984) failed to provide unambiguous support for the prefiguring hypothesis.

The failure to provide clear support for the prefiguring hypothesis with gouramis as subjects does not preclude the possibility that Pavlovian conditioning may serve such a biological function. Therefore, the present research pursued Hollis' hypothesis of the biological function of conditioning with convict cichlids (Cichlasoma nigrofasciatum), a territorial fish whose threat displays are characterized by unique behaviors not observed during feeding. The research had three goals: to demonstrate Pavlovian conditioning of convict cichlids; to show a functional gain of learning; and to determine whether the conditioned response (CR) includes the unique aggressive

components, or indicates a more general alert state.

In the following sections, the factors leading up to the present research will be discussed. These include the challenge to general process learning theory posed by constraints phenomena; the consequences of the challenge, as exemplified by the biological boundaries approach to learning; ecological and evolutionary considerations; a discussion of the function of learning; and subsequent considerations for the analysis of learning. Hollis' (1984) approach will then be discussed, followed by a description of the present research.

#### Challenge to General Process Learning Theory

The study of learning has traditionally employed arbitrarily chosen stimuli and responses in order to derive laws that would be applicable in a wide variety of species and situations (Malone, 1973). Called 'general process learning theory' (Seligman, 1970), this approach was assumed to be based on the concept of equipotentiality, which asserted that all stimuli and responses are equally associable and that species differences are relatively insignificant (Malone, 1973). Thus, it is asserted that in classical conditioning any neutral stimulus (typically called a conditioned stimulus or a CS) and any biologically significant stimulus (labelled an unconditioned stimulus or US) can be associated, and that a set of general laws exist which describe how the associations between CSs and USs are developed



and maintained. For instrumental conditioning it was assumed that any response produced by an organism and any reinforcer (a stimulus, frequently a biologically significant stimulus, which increases the probability of a response which immediately precedes the stimulus) could be associated, and that a set of general laws which are thought to describe the development and maintenance of associations between responses and reinforcers exist (Seligman, 1970). Using only a few species (e.g., rats and pigeons) and apparatus (e.g., shuttle boxes in which avoidance behavior is acquired and operant chambers in which an animal learns to perform a task in order to obtain a reward), psychologists collected a large amount of data supporting the existence of general laws (Manning, 1967; Seligman, 1970).

However, the assumptions of general process learning theories were initially challenged by learning phenomena observed by Garcia and Koelling (1966) and Breland and Breland (1961). Garcia and Koelling (1966) asserted that rats were more readily able to associate gustatory cues than audio-visual cues with illness, whereas they were more readily able to associate audio-visual cues than gustatory cues with the aversive consequences of shock. The selectivity of the associations led Garcia and Koelling (1966) to conclude that given USs are not equally effective for all classes of discriminable stimuli. This conclusion contradicted the premise of equipotentiality, which asserts that all combinations of CSs and USs are equally

associable. Furthermore, Garcia, Ervin, and Koelling (1966) varied the interval between a taste CS and poisoning and found that conditioned taste aversion could be learned with delays up to 75 minutes between the CS (gustatory cue) and the US (poisoning). These findings contradicted the assumption that the CS and US must be temporally contiguous in order for learning to occur, again calling into question traditional associative mechanisms.

Breland and Breland (1961) described their attempts to condition pigs, chickens, and raccoons to perform operant responses. The pigs were trained to drop a token into a 'piggy bank', the chickens to pull a rubber loop sending a capsule down a slide and then peck the capsule off the slide, and the raccoons to drop coins into a container. Yet, in each instance, the behavior of the animals 'drifted' toward another behavior that resembled a consummatory behavior. The pigs repeatedly dropped and rooted the token, the chickens began to grab at the capsules and pound them up and down on the floor of the cage, and the raccoons manipulated the coins but would not drop them in the box. The development of the consummatory-like behaviors was not required to obtain reinforcement, and often the exhibition of the behavior resulted in the delay or omission of reinforcement. Breland and Breland (1961) argued that the development of the consummatory-like behaviors represented a failure of operant conditioning theory by contradicting the generality of the laws

of learning.

Research in more traditional learning paradigms also began to identify evidence that appeared to contradict general process learning theory. In avoidance learning it was observed that some animals would quickly learn one type of avoidance response, but were unable to learn or had difficulty in learning another (Bolles, 1970). For example, to avoid shock rats readily learn to jump out of a box (Maatsch, 1959), but had considerable difficulty learning to press a lever (D'Amato & Schiff, 1964). The failure of animals to learn certain avoidance responses led Bolles (1970) to suggest that aversive reinforcement contingencies do not act uniformly.

Research in instrumental appetitive conditioning also revealed differential conditionability of various responses. Shettleworth (1975) found that food reinforcement increased the amount of time golden hamsters spent performing open rearing, scrabbling, and digging responses. However face washing, scratching, and scent-marking were relatively insensitive to food reinforcement. Similar differential response-consequence sensitivities have been obtained with rats (Annable & Wearden, 1979; Pearce, Colwill, and Hall, 1978).

The numerous exceptions to general process learning theory that were accumulating in both classical and instrumental conditioning led researchers to suggest that animals were influenced by their evolutionary history and ecological niche in

such a way as to place a limitation or a boundary condition on learning. The term "biological constraints on learning" thus came to describe the inadequacies of general process learning theory in particular situations (Domjan, 1983). Moreover, the apparent inability of general process learning theory to account for the plethora of constraints phenomena led to the formulation of the 'biological boundaries' approach to learning.

#### Biological Boundaries Approach to Learning

Under the biological boundaries approach, learning was hypothesized to involve multiple species-specific processes that evolved to meet the demands of particular environments (Domjan, 1983; Johnston, 1981). In its most extreme form, the biological boundaries approach advocated the abandonment of general process learning theory in favor of a search for specialized learning mechanisms (Bitterman, 1975). For instance, Shettleworth (1972) argued for an approach which accepts a multiplicity of principles, and suggested that learning ability may be as species-characteristic as any feature of morphology or physiology.

Less extreme approaches rejected only portions of general process theory, or sought to modify, or add to the general laws (e.g., Bolles, 1970; Seligman, 1970). Seligman (1970) supplemented general process learning theory with the concept of preparedness. The concept of preparedness states that, as a result of evolution, an organism possesses specialized sensory-

motor and associative structures. The evolutionary-based structures will determine the speed with which an organism associates a given CS and US or a given response and outcome. Seligman (1970) defined a continuum of preparedness, on which an organism can be either prepared, unprepared, or contraprepared for learning about certain events. The rate of development of associations was assumed to be inversely related to the preparedness dimension. With these assumptions, Seligman then sought to determine whether the same laws and mechanisms that hold for the learning of prepared events also hold for unprepared and contraprepared events. Thus, Seligman did not discard general laws per se, but posited the existence of general laws across the preparedness dimension. An alternative tact taken by Rozin and Kalat (1971) argued for the treatment of learning as any other biological characteristic, subject to natural selection, with an emphasis on differences in learning mechanisms as a function of specific species and situations. Rozin and Kalat (1971) claimed that from a biological perspective there is no reason to assume that general laws of learning exist independent of the situation in which the laws are manifested. Because they doubted the existence of separate learning mechanisms for every situation, or separate laws for every species, Rozin and Kalat (1971) suggested that some general laws may exist. What these laws were, was not specified.

In addition to the postulation of addendums to general

process learning theory, specialized mechanisms were being advocated for specific behavioral phenomena. Bolles (1970) asserted that animals have innate defensive reactions, called species-specific defense reactions (SSDRs) that are specific to the circumstances that the animal experiences. Bolles (1970) identified three such behaviors: freezing, fleeing, and fighting. According to Bolles (1970) an avoidance response could only be rapidly acquired if it was similar in form to an effective SSDR in a particular situation. Bolles (1970) postulated that SSDRs had a hierarchical structure and would be evoked by aversive stimuli. Thus, in an avoidance situation the aversive stimulus would evoke the SSDR hierarchy. If the SSDR behavior resembled the experimenter-defined avoidance response, then successful avoidance behavior would rapidly emerge. If the evoked behavior did not meet the experimenter's criteria, then the aversive stimulus would follow the behavior and that behavior would be punished and therefore suppressed. Thus, Bolles viewed avoidance behavior as the outcome of the interaction of the subjects' specialized defensive behavior with traditional punishment contingencies.

Specialized associative mechanisms were postulated by Garcia and Koelling (1966) to explain the finding that rats more readily associated illness to gustatory cues than to audio-visual cues. Garcia and Koelling (1966) asserted that natural selection may have favored mechanisms which associate gustatory and olfactory

cues with internal discomfort. Under the premise of equipotentiality, it would be expected that regardless of the nature of the stimuli and the consequences, the association of a stimulus and consequence would result in conditioned responding to that stimulus. However, Garcia and Koelling (1966) asserted that when a gustatory stimulus and an audio-visual stimulus were paired with illness, the only stimulus to which an avoidance response occurred was the gustatory stimulus. Conversely, when the gustatory stimulus and the audio-visual stimulus were paired with electric shock, the only stimulus to which an avoidance response occurred was the audio-visual stimulus. Therefore, Garcia and Koelling (1966) viewed conditioned avoidance responses as the outcome of associative specificity between particular cues and particular consequences.

Specialized mechanisms were also being offered to explain findings in instrumental conditioning. Shettleworth (1975) suggested that associative specificity was responsible for the differential conditionability of action patterns in golden hamsters. Shettleworth (1975) observed that certain action patterns involving locomotion and active contact with the environment (scrabbling, digging, and open rearing) had large and immediate increases in rate and tended to increase in bout length when reinforced with food. Conversely, action patterns involving grooming and social behaviors (scent-marking, face-washing, and scratching) did not demonstrate similar effects of food

reinforcement. Instead, this second group of action patterns had small increases in rate and tended to decrease in bout length when reinforced with food. Thus, Shettleworth (1975) concluded that the differential conditionability of action patterns was due to the associative specificity between particular responses and particular reinforcers.

Problems with the biological boundaries approach. While the biological boundaries approach has been applied in a variety of situations, it has failed to generate a substantive theoretical and empirical framework within which to examine constraints issues (Domjan, 1983; Johnston, 1981). The primary focus of the approach has been to argue against the concept of equipotentiality. Yet this focus has probably precluded substantive developments. There are two apparent reasons for this failure. The first reason was the realization that the rejection of the concept of equipotentiality does not necessitate the rejection of general process learning theory. Secondly, general process learning theory has produced satisfactory accounts of the phenomena used to argue for the existence of biological constraints (e.g., Domjan, 1983).

A description of the concept of equipotentiality and its source will demonstrate that equipotentiality is not necessary to general process learning theory. The premise of equipotentiality asserts that all stimuli and responses are equally associable and that species differences are relatively insignificant (Malone,



1973). Thus, any CS and US, or response and reinforcer can be associated, and a set of general laws exist which describe the parameters for all associations (Seligman, 1970). This latter assumption will prove to be critical, as the failure of equipotentiality does not mean general laws must fail as well.

According to Seligman (1970) and Shettleworth (1972) the concept of equipotentiality is based on the work and statements of Pavlov, Thorndike, and Skinner. Seligman (1970) presents quotes from Pavlov that seem to indicate stimulus interchangeability. Yet a closer examination of Pavlov's writings reveals otherwise. Concerning the associability of different stimuli, Pavlov (1927) wrote that:

any agent in nature which acts on any adequate  
receptor apparatus of an organism can be made into a  
conditioned stimulus for that organism (p. 38).

At first reading this statement does seem to suggest stimulus interchangeability, but a close examination of the remainder of the statement reveals that Pavlov was not advocating stimulus interchangeability. The specification of an adequate receptor apparatus and the phrase 'conditioned stimulus for that organism' indicate that stimuli may be differentially associable. Pavlov went on to state:

.... a limit is set to the fineness of gradation of  
such stimuli by the degree of sensitivity and  
perfection of the peripheral receptor organs of the

organism (1927, p. 38).

When discussing conditioned inhibition, Pavlov (1927) wrote

It is obvious that any agent in nature may be used as a stimulus for the development of a conditioned inhibition, supposing of course that the organism is provided with the requisite organs for the perception of such an agent (p. 73).

Again, it initially may appear that Pavlov was arguing for stimulus interchangeability. Yet as the latter part of the quote illustrates, whether a particular stimulus is effective depends in part on the specific organism in question. Pavlov stated this a page later

The rate of development of a conditioned inhibition as well as its completeness (absolute or relative inhibition) also depends upon a number of conditions. Of first importance in this connection is the individuality of the animal, the excitable or inhibitable character of its nervous organization.... A further important factor is the intensity of the additional stimulus employed in the inhibitory combination (1927, p. 74).

Pavlov, then, recognized that not all stimuli are equally associable. In addition, Pavlov did not, as Seligman (1970) seemed to assume, ignore the adaptive aspects of learning. Pavlov (1927) wrote

The animal must respond to changes in the environment in such a manner that its responsive activity is directed towards the preservation of its existence (p. 8).

In a similar fashion, Thorndike has been misinterpreted, such that it is assumed that he suggested that the processes underlying behavior might be the same in all animals, including man (Bitterman, 1975). Yet the quote upon which this claim is based, "...so that when the situation recurs, the act will be more likely to follow than it was before...man leads, not as a demigod from another planet, but as a king from the same race " (Thorndike, 1911, p. 294) only states Thorndike's Law of Effect and a scalar approach to the continuity of species. And far from advocating equipotentiality, Thorndike expressed concern that his findings not be over-interpreted. In *Animal Intelligence* (1911) Thorndike wrote

Throughout I shall use the word animal or animals and the reader may fancy that I took it for granted that the associative processes were the same for all animals as in cats and dogs of mine. I claim for my psychology only that it is the psychology of just these particular animals. What this warrants about animals in general may be left largely to the discretion of the reader (p. 66).

In addition, Thorndike also recognized that not all stimuli will be equally associable, as evidenced by this passage,

The chick's brain is evidently prepared in a general

way to react more or less appropriately to certain stimuli and these reactions are among the most important of its instinct or inherited function (p. 167).

Statements made by Skinner have also been taken out of context, and it has been assumed that Skinner saw no place for evolutionary factors in learning. Yet an examination of Skinner's writing reveals that he was cognizant of evolutionary factors. In *Contingencies of Reinforcement* (1969) he wrote

No reputable student of animal behavior has ever taken the position that the animal comes to the laboratory as a virtual tabula rasa, that species differences are insignificant, and that all responses are about equally conditionable to all stimuli (p. 173).

And in 1983 Skinner wrote

...behavior arising from natural selection is not always effective in new environments. A means of making slight changes in behavior during the lifetime of the individual must have had survival value, and the process of respondent and operant conditioning could evolve. Along with the process of operant conditioning there must also have evolved a susceptibility to particular kinds of consequences (p. 11).

Since none of Pavlov, Thorndike, or Skinner are responsible for the concept of equipotentiality, the pervasiveness of equipotentiality must be attributed to the misinterpretations and

over-simplification by psychologists of Pavlov, Thorndike, and Skinner's work (Malone, 1973). The source of this misinterpretation can be traced to Watson (1924) who wrote, "So far as we now know (actual experimental evidence is lacking) we can take any stimulus calling out a standard reaction and substitute another stimulus for it" (1924, p. 24). This statement likely provided the foundation for future North American research which emphasized laboratory experiments and the use of only a few species of animals as experimental subjects. This narrow approach led not only to the perpetuation of the concept of equipotentiality, but also to the virtual exclusion of any consideration of evolutionary factors in learning. Subsequently, when apparent constraints challenged the concept of equipotentiality, general process learning theory was also called into question (e.g., Seligman, 1970; Shettleworth, 1972). Yet as the previous statements by Pavlov, Thorndike, and Skinner show, equipotentiality is not a necessary assumption of general process learning theory. Consequently, there is no need to discard general process learning theory on the basis of experimental findings that contradict the concept of equipotentiality.

The second reason for the failure of the biological boundaries approach is that general process learning theory has produced satisfactory accounts of many constraints phenomena. As a consequence of the narrow conceptualization of general process learning theory as a statement of equipotentiality, many

of the finer points of general process learning theory have been ignored by advocates of the biological constraints position. General process learning theory is based on the assumption that learning can be accounted for by mechanisms that are trans-species and trans-situational. While many mechanisms have been investigated, not all mechanisms have yet been identified, nor have all phenomena been fully explained. Nonetheless, general process learning theory has been able to produce satisfactory explanations of many constraints phenomena. The ability of general process learning theory to account for many constraints phenomena will be demonstrated by a description of the often ignored facets of general process learning theory and the constraints phenomena to which they apply.

One often ignored characteristic of general process learning theory is the distinction that must be drawn between learning, the formation of associations, and performance, the demonstration that the associations developed (Kimble, 1961). The occurrence of a response in a conditioning procedure provides evidence that an association was formed. However, the absence of a response does not necessarily indicate that no association was formed. Rather, an association may have been formed, but no response occurred because certain factors (e.g., response competition) prevented the occurrence of the expected response. Thus, the absence of a response may indicate a performance deficit as opposed to an associative deficit.

A consideration of the learning-performance distinction demonstrates that many constraints phenomena reflect performance deficits as opposed to associative deficits. For example, the findings of Breland and Breland (1961) in which animals performed behaviors not required for reinforcement and behaviors which delayed reinforcement (such as the pig rooting the token) were assumed to be indicative of a response-consequence associative deficit. Yet a closer examination reveals that the misbehavior of Breland and Breland's animals reflects a performance deficit which arises from response competition between behavior maintained by instrumental contingencies and behavior maintained by Pavlovian contingencies (Domjan, 1983). For instance, the rooting of the pig was the result of a Pavlovian contingency between the token and the food, which over-rode the instrumental contingency between dropping the token into the bank and the food reinforcement.

Misbehavior in rats under both Pavlovian and instrumental contingencies was examined by Timberlake, Wahl, and King (1982). Timberlake et al. (1982) observed that the Pavlovian contingency of pairing a ball bearing with food resulted in misbehavior. Since instrumental contingencies were not necessary for misbehavior to develop, Timberlake et al. (1982) suggested that misbehavior is elicited by pairing a stimulus with a reinforcer, and misbehavior is expressed in the absence of competition from behavior elicited by the delivery of food. Timberlake et al.

(1982) also observed that the instrumental contingency of requiring the rats to contact the ball bearing to obtain food resulted in misbehavior, but of a different form than that observed under the Pavlovian contingency. Timberlake et al. (1982) suggested that the finding that different forms of misbehavior occurred under both Pavlovian and instrumental contingencies indicates that different paradigms modify and measure different aspects of the expression of learning. Since the expression of learning depends upon the paradigm used and resultant response competition with other behaviors (Timberlake et al., 1982), the misbehavior of animals reflects a performance deficit as opposed to an associative deficit.

Another example of a performance deficit is the observation that certain avoidance responses are acquired more slowly than other avoidance responses (Bolles, 1970). It was postulated by Bolles (1970) that the acquisition of avoidance responses was due to the interaction between the animal's specialized defensive behaviors and traditional punishment contingencies. The emergence of an avoidance response, however, does not need to be attributed to a specialized mechanism. Instead, the emergence of an avoidance response can be seen as the result of response competition between the SSDR and the experimenter-defined behavior. In Bolles' paradigm, if the SSDR behavior resembled the experimenter-defined avoidance response, then that SSDR behavior would rapidly emerge in the situation. However, if the



evoked SSDR behavior did not meet the experimenter's criteria, then the aversive stimulus would follow the SSDR and the behavior would be punished and eventually suppressed. If one SSDR proves unsuccessful, then other SSDRs will occur until one that successfully avoids the aversive stimulus emerges. Only when all possible SSDRs have been punished and suppressed will non-SSDRs such as lever-pressing occur. Therefore, the rate of the avoidance acquisition can be seen as the result of response competition between behavior elicited by the aversive event and the type of behavior defined by the experimenter as avoidance behavior. It should be noted that Bolles' (1970) analysis of avoidance acquisitions requires that both the SSDRs and non-SSDRs be sensitive to their consequences (i.e., suppressed by punishment), and therefore Bolles assumed a continuity of mechanisms across SSDR and non-SSDR behavioral classes.

Differences in the conditionability of action patterns in golden hamsters observed by Shettleworth (1975) can also be attributed to performance variables. Shettleworth (1975) postulated that the differential conditionability of action patterns was due to the associative specificity between particular responses and particular reinforcers. However, response competition between action patterns may be the reason for the different rates of conditioning. In order to conclude that response competition is responsible for the differential conditionability of action patterns in hamsters, it would be

necessary to demonstrate that associations can be established between grooming behaviors (face-washing, scratching, and scent-marking) and food reinforcers. Most attempts to condition grooming behaviors have produced only abbreviated forms of the behaviors. One could surmise that the appearance of even an abbreviated form of grooming behavior indicates that an association was formed. Further proof of an association comes from the fact that the animals arrived at the feeder faster than animals that received equal amounts of free food, indicating they learned which action pattern is followed by food regardless of the action pattern involved (Shettleworth, 1975). In addition, Shettleworth (1975) alluded to the possibility that associations between the action patterns of face-washing, scratching, and scent-marking and food reinforcement may have been formed, but not translated into performance. Consequently, the differential conditionability of action patterns could be considered as another case of response competition. As Shettleworth (1975) wrote,

That face-washing actually decreases in bout length could mean that anticipation of food actively inhibits this AP, although its decrease in hungry animals need only be due to competition from food-anticipatory APs (p. 84).

Therefore, it seems likely that the differential conditionability

of action patterns reflects a performance deficit rather than an associative deficit.

Another aspect of general process learning theory that has often been misinterpreted concerns the temporal relationship between the CS and US. Original conceptualizations of conditioning described specific time parameters in which optimal conditioning could occur (e.g., Hull, 1943). Most subsequent research has operated under the assumption that there must be close temporal contiguity between the CS and US for conditioning to occur. Consequently, the finding that taste aversions could be learned over delays of up to 75 minutes (Garcia & Koelling, 1966) was assumed to contradict a general law of learning. However, a closer examination reveals that taste aversion learning follows the same principles as traditional instances of learning. In a traditional classical conditioning paradigm, the CS-US interval is a function of CS parameters (e.g., CS intensity, CS duration); response system parameters (e.g., CR frequency, CR topography); and training procedures (e.g., compound CSs). As such, the CS-US interval is not fixed, but reflects the conditioning environment (see Gormezano, 1972). In many conditioning preparations, the CS-US interval is short (e.g., 500-msec in conditioning of the rabbit's nictitating membrane response). In comparison, taste aversion has a relatively long CS-US interval. This long interval in taste aversion should not be unexpected given the flexibility of the

CS-US interval function. Consequently, the long CS-US interval represents a quantitative difference between taste aversion and other types of learning, and as such does not require a different set of laws (Logue, 1979). In addition, changes in the temporal relationship have the same effect on taste aversion and traditional learning. For instance, in both taste aversion and traditional learning, close temporal contiguity is more effective than very long delays, and trace conditioning is more effective than backward conditioning (Logue, 1979).

Further evidence that taste aversion learning follows the same principles as traditional learning comes from a demonstration of long-delay learning in instrumental conditioning. Lett (1973, 1975) observed that rats learned a positional response in a T-maze with delays up to 60 minutes between the response and the reward. Lett (1974) also observed that rats learned a visual discrimination between black and white chambers in a T-maze with a one minute delay of reward. Thus, long-delay learning is not particular to taste aversion.

Finally, Logue (1979) indicated that manipulations of other CS and US parameters reveal the same functional relations exist in taste aversion as in traditional learning preparations. For example, the presentation of a CS without the US (extinction) results in decreased responding in taste aversion and in traditional learning. Sensory preconditioning and second-order conditioning have been demonstrated in taste aversion as well as

in traditional learning. Increased US intensity results in better conditioning in both taste aversion and traditional learning. Generalization of the CS occurs in both taste aversion and traditional learning. And, US pre-exposures are found to retard acquisition in both taste aversion and traditional learning. Thus, the same principles can be used to describe taste aversion and traditional learning (Logue, 1979), and there is no need to consider taste aversion as specialized learning.

The taste aversion phenomenon also raised another often ignored aspect of general process learning theory, that of the qualitative relations between stimuli. Garcia and Koelling (1966) asserted that rats were more readily able to associate gustatory cues than audio-visual cues with illness, whereas they were more readily able to associate audio-visual cues than gustatory cues with the aversive consequences of shock. These observations of cue specificity were assumed to contradict general process learning theory and as such constitute a constraint on learning. The implication was that different rules of learning may exist for different sets of stimuli (Rescorla & Holland, 1982). The idea that certain CSs seem best associated with certain USs has long been recognized as a part of learning (see Schwartz, 1984). Thorndike (1935) coined the term "belongingness" to describe the idea that certain stimuli go together. However, demonstrations of cue specificity do not necessarily imply that different laws exist for different sets of

stimuli. From Garcia and Koelling's (1966) research, it was assumed that in rats gustatory cues are associated with illness and audio-visual cues are associated with aversive stimuli (shock). However, the asserted mutual exclusiveness of the cues and their respective consequences have not withstood experimental attack. It has been demonstrated that gustatory cues can be associated with shock (Krane & Wagner, 1975). Furthermore, it has been demonstrated that rats will bury the source of a novel solution (a spout) that has been paired with toxicosis (Wilkes, MacLennan, & Pinel, 1979). The latter observation could only occur if the rats made an association between visual-spatial cues and illness. Therefore, the assumption that rats cannot make an association between visual-spatial cues and illness is not supported.

In pigeons, it was assumed that visual cues are associated with food and audio cues are associated with aversive stimuli. Foree and Lolordo (1973) observed that pigeons receiving red light cues acquired a discriminative response faster with food reinforcement compared to pigeons that received auditory cues. When shock avoidance was used as reinforcement, pigeons receiving auditory cues acquired the discriminative response faster than pigeons that received visual cues. However, all subjects eventually acquired the discriminative response. The fact that all subjects eventually acquired the response suggests that associations were formed between visual cues and shock and

between auditory cues and food. When combined with the results from research with rats described above, these findings suggest that the relationship between stimuli affects the speed at which certain associations are made and translated into performance. Therefore, cue specificity is a rate parameter. Consequently, there is no need to postulate that different sets of laws exist for different sets of stimuli in order to account for cue specificity.

Taken together, the often ignored facets of performance-learning distinctions, temporal contiguity, and cue specificity demonstrate that general process learning theory can adequately account for many constraints phenomena and as such argues against the premature acceptance of a large number of specialized adaptive mechanisms in learning. However, the numerous demonstrations of performance deficits, long-delay learning, and cue specificity did suggest the need for a re-orientation of focus in the study of learning.

#### Ecological and Evolutionary Considerations

As instances of long-delay learning, cue specificity, and performance deficits aptly illustrate, the traditional approach to animal learning of employing presumed biologically irrelevant tasks in an isolated environment is unable to readily account for many instances of behavioral change (Johnston & Turvey, 1980). Given that instances of long-delay learning, cue specificity, and

performance deficits pointed to the importance of the animal's natural environment, it seemed that a consideration of learning within an ecological and evolutionary framework was necessary. Before describing the initial form this inquiry took, it is necessary to define the relevant terms and then, examine the relationship of learning to evolution.

The science of ecology has been defined as the study of the interrelationships between living organisms and their environment (Odum, 1971). As such, ecology uses a macro level of analysis that focuses on the biology of groups of organisms, functional processes of the environment, and the interrelationship of the two. In dealing with the interrelation, an evolutionary framework is adopted, and therefore a consideration of evolutionary factors is necessary. The evolutionary concepts that are of concern are natural selection, adaptation, and fitness.

In a rather broad sense, evolutionary theory deals with the development and change of life forms through the action of mechanisms of variation and mechanisms of selection. Mechanisms of variation are internal to the organism and involve random changes in heritable traits through the processes of mutation and recombination (Ridley, 1985). In comparison, mechanisms of selection are external to the organism and involve non-random establishment of traits through the process of differential reproduction (Ridley, 1985). Mechanisms of variation produce the



range of traits available for selection, and mechanisms of selection determine which of the traits will be established. Traits that provide an advantage in terms of survival and reproductive success will be passed on to future generations, a process termed natural selection. The process of natural selection results in changes in the population distribution of traits. This change in traits is what constitutes evolution. Natural selection is examined through the study of adaptation, which attempts to show how structure and behavior help animals to survive and reproduce (Dawkins, 1986). It is important to note that the central idea of Darwinian natural selection is not the often assumed claim that all organisms are adapted to their environment. Rather, Darwinian natural selection is about organisms surviving better than their competitors (Dawkins, 1986).

Fitness can be considered the measuring stick of adaptation, or evolutionary success. There are three measures of fitness: long-term optimality, short-term optimality, and inclusive fitness. Long-term optimality refers to the reproductive success of an animal over its entire life compared to its rivals. Characteristics that increase the total number of offspring of an animal, relative to its rivals, would be viewed as adaptive. Short-term optimality refers to the optimizing of some function in an animal's day-to-day life. For example, taking the most energy efficient route to get to the most energy efficient food

would be considered optimal (Dawkins, 1986). Short-term optimality can be used as a measure of adaptation in that discovery of what an animal optimizes in the short-term can provide information about the selection pressures its ancestors faced (Dawkins, 1986). For instance, if food was difficult to obtain and predation was a minor concern, a highly efficient forager would flourish and leave more offspring than its rivals. However, short-term optimality does not always translate into long-term optimality. If both predation and availability of food are important factors in survival, an animal that forages optimally and ignores predators is more likely to be attacked and consequently leave fewer offspring than its rivals. Thus, when assessing the adaptiveness of a behavior it is important to consider the relationship between short-term and long-term optimality.

Inclusive fitness involves consideration of whether a genetic tendency to help relatives will spread through a population and thus increase the average reproductive success of that population (Dawkins, 1986). As such, inclusive fitness measures adaptation in terms of the contribution of an individual's success or failure to the average reproductive success of the population.

The evolutionary concepts described in the preceding section provide a basis from which to examine the relationship of learning to evolution. Learning connects with evolution in two

ways. First, learning is a biological phenomenon and as such must have evolved as a set of mechanisms. The question to be resolved is whether the mechanisms are general (the same for many different instances of learning) or specialized (different for each instance of learning). The ability of general process learning theory to account for many constraints phenomena appears to have ruled out the existence of numerous specialized mechanisms. However, it may be that some specialized learning mechanisms do exist. Thus, considerations of learning in an ecological and evolutionary framework must address, in part, the boundary conditions on the mechanism(s) of learning.

The second way learning connects with evolution, related to the first, is that learning is assumed to serve an adaptive function (Bitterman, 1975; Hollis, 1982; Shettleworth, 1983; Staddon, 1983). That is, learning may enable an animal to survive better and produce more offspring than its competitors. For example, being able to recognize poisonous food may allow an animal to survive, produce more offspring than its rivals, and thus increase its long-term fitness. Consequently, considerations of learning in an ecological and evolutionary framework must address, in part, the possible adaptive function(s) of learning.

One approach to learning in an ecological and evolutionary context is Johnston's (1981) ecological approach which calls for descriptions of what animals learn in natural settings followed

by examinations of how animals learn. From this information, local, or species-specific, principles of adaptation would be formed. The local principles would describe how experience enables an individual of a particular species to cope with the requirements of their particular environment (Johnston, 1981). Having formulated local principles, one would then search for principles that would apply to more than one species or one ecological niche. Identification of more general laws would then give the global principles of adaptation.

The ecological approach, however, is flawed because of its failure to provide an adequate consideration of the mechanisms of learning (Shettleworth, 1981). According to Johnston (1981) the second question of the ecological approach (how does an animal learn something?) is concerned with the ways in which experience contributes to the solution of the problems faced by an animal. Yet as Shettleworth (1981) points out, statements about how experience affects behavior are learning principles. As such, learning principles describe a consistent relationship between a learning paradigm (e.g., Pavlovian conditioning) and a learning phenomenon (e.g., a conditioned response). Learning principles are not the same as learning processes, which are the mechanisms responsible for learning phenomena or behavior change. Although function does connect with learning at the level of learning principles (Shettleworth, 1983), the key relationship is between mechanisms of learning and adaptive functions of learning. Since

the ecological approach does not adequately address mechanisms of learning, it cannot provide any information concerning the relationship between the adaptive functions of learning and the more traditional concerns of the mechanisms of learning. Thus, the ecological approach advocated by Johnston (1981) does not provide for an adequate consideration of learning in an ecological and evolutionary framework.

The ability of general process learning theory to account for various constraints phenomena led to another approach to learning in an ecological and evolutionary context. This second approach calls for a continued emphasis on the mechanisms of learning using traditional methods of investigation with a recognition of the possible influence of ecological factors. Traditional experimental methods are employed, and in certain instances, ecologically relevant variables may be introduced to determine the interaction of the ecological variables and the learning mechanism. Experimental results, however, are usually interpreted in terms of learning mechanisms with little attention paid to the role of ecological variables. While such investigations may be able to account for constraints phenomena in terms of learning mechanisms, they fail to provide an adequate consideration of the possible adaptive functions of learning. As noted in the preceding section on ecological and evolutionary factors, both function and mechanism should be considered in an examination of learning.

The shortcomings of Johnston's (1981) ecological approach (failure to adequately consider mechanisms of learning) and of the traditional approach (failure to adequately consider possible adaptive functions of learning) illustrate that a focus on one aspect or the other cannot answer questions raised by constraints phenomena. The inability of either approach to provide adequate answers indicates an inter-dependency between the mechanisms and functions of learning. The question to be answered, then, concerns the nature of the relationship. In order to understand the relationship between the mechanisms and functions of learning, it is necessary to examine the components of the traditional approach to learning. Two things will be revealed by this analysis. One is that a traditional approach cannot determine the existence of specialized learning mechanisms. The second is that there is not a one-to-one relationship between the mechanisms of learning and the functions of learning.

#### The Traditional Approach to Learning

The three main components of the traditional approach to be described are learning paradigms, learning phenomena, and learning processes. According to Shettleworth (1983) a learning paradigm is a description of an experience an environment offers an animal. There are three basic paradigms that characterize most studies of learning: the presentation of a single event (e.g., habituation); the presentation of a conditioned stimulus in relation to an unconditioned stimulus (Pavlovian

conditioning); and the occurrence of a response in relation to an unconditioned stimulus (instrumental conditioning). Research into mechanisms of learning typically select either the second or third paradigm for analysis. However, many learning phenomena do not clearly follow true separate paradigms but reflect procedures that are combinations of the paradigms (Gormezano & Kehoe, 1975; Shettleworth, 1983).

A learning phenomenon is the behavioral change that occurs as a result of an experience (Shettleworth, 1983). For example, avoiding a food that has been associated with illness is a learning phenomenon. An increase in digging behavior when digging is followed by food reinforcement is also a learning phenomenon.

A consistent relationship between a learning phenomena and a learning paradigm constitutes a learning principle. Learning principles describe how experiences affect behavior. For example, the statement that positive reinforcement leads to an increase in responding is a learning principle. Learning principles are not the same as learning processes or mechanisms. A learning process or mechanism underlies the observed learning principle, is theoretical, and is defined by a set of learning paradigms and resulting phenomena (Shettleworth, 1983).

Theoretically, learning paradigms, principles, and processes should provide a framework within which to examine the notion of specialized learning phenomena and specialized learning

mechanisms (Shettleworth, 1983). The traditional approach described by Shettleworth (1983) allows for conclusions to be drawn about the existence of specialized learning phenomena. For instance, novel learning phenomenon may be the result of interacting paradigms, as demonstrated by Breland and Breland's (1961) misbehaving pigs. Or, a learning phenomenon may be only quantitatively different from other exemplars within the same paradigm, as is the case with conditioned taste aversion (Shettleworth, 1983). Thus, the traditional approach can provide an adequate identification of specialized learning phenomena. However, due to inaccuracies in the delineation of learning paradigms, the traditional approach cannot indicate whether specialized mechanisms are responsible for the particular phenomena. Gormezano and Kehoe (1975) suggest that the distinction between classical and instrumental paradigms has become blurred, such that paradigms that do not meet all of the procedural requirements of classical conditioning are nonetheless labeled as classical conditioning paradigms. Thus, results that are attributed to a classical conditioning mechanism may in fact be due to an instrumental contingency. The problem is compounded when the empirical laws of classical conditioning are used as a source of axioms from which other behavioral laws are derived (e.g., Hull, 1943; Rescorla & Solomon, 1967). Any axioms based on incorrectly labeled paradigms, and consequently derivations based on these axioms, will be inherently flawed.



Furthermore, drawing a distinction between classical conditioning and instrumental conditioning belies the complexity of conditioning. Pavlov (1927) considered the classical conditioning paradigm to be a laboratory model for the mechanism of behavioral adaptation. As such, Pavlov recognized that a multitude of interacting factors, associative and non-associative, could be involved in conditioning (Gormezano & Kehoe, 1975). Instead of attempting to untangle these complexities, psychology simplified classical conditioning into stimulus-stimulus associations, thus allowing for an easy distinction to be made between classical and instrumental paradigms. This distinction has led to a tendency to interpret experimental results solely in terms of one paradigm or the other. For instance, the misbehavior of Breland and Breland's animals was interpreted in terms of the failure of instrumental conditioning (Breland & Breland, 1961). As a consequence, possible interactions between different types of associations have been ignored. Yet a given phenomenon is not always the product of one paradigm or the other. In the case of Breland and Breland's (1961) misbehaving animals, the misbehavior was the result of response competition between classical and instrumental contingencies. The realization that conditioning is more than either stimulus-stimulus or response-reinforcer associations returns us to Pavlov's (1927) original conceptualization of conditioning as a multitude of interacting factors that determine

the course of conditioning and provide flexibility in the expression of conditioned responses (Gormezano & Kehoe, 1975). Since the traditional approach fails to recognize the complexity of conditioning, it is unable to indicate the mechanism(s) responsible for the observed phenomena.

Not only are there problems in identifying specialized learning mechanisms, an examination of the function (outcome) of learning reveals that specialized functions need not be the result of specialized mechanisms (Bitterman, 1975; Shettleworth, 1983). Consider, for example, an animal running to food and an animal running away from a predator. In each case the mechanism to obtain the outcome (i.e., running) is the same, but the outcome is different (i.e., either to obtain food or escape danger). Similarly, an animal may run to food or it may fly to food. In this instance, the mechanisms are different, running and flying, but the outcomes are the same, obtaining food. By analogy, the same learning mechanism may have different functions. For example, a Pavlovian contingency between a signal (e.g., a sound) and a stimulus (e.g., food) may serve as a signal for a predator about nearby prey and thus facilitate food procurement. Another Pavlovian contingency, between a signal and a conspecific may enable an animal to respond faster to territorial intrusion. Or different learning mechanisms may have the same function. For example, an instrumental contingency between a behavior (e.g., turning over a rock) and a consequence

(e.g., finding food) may result in an increase in rock-turning behavior and thus facilitate food gathering. And, a Pavlovian contingency between a signal (e.g., shape of a rock) and a stimulus (e.g., food) may signal the location of food and thus facilitate food gathering. Therefore, the existence of a specialized function for learning, such as conditioned taste aversion, does not mean there exists a corresponding specialized mechanism. Indeed, it would appear that an examination of function is irrelevant to the traditional examination of mechanism (Shettleworth, 1983).

However, as noted in the section on ecological and evolutionary factors and demonstrated by the inability of the traditional approach to identify specialized mechanisms, there does appear to be a relationship between the functions and mechanisms of learning. The relationship is indirect, yet examinations of function are able to provide useful information (Shettleworth, 1983; Staddon, 1983). For instance, functional explanations can account for similar outcomes produced by different mechanisms (Staddon, 1983), and functional explanations can determine whether particular mechanisms make functional sense and whether multiple mechanisms support a particular outcome (Shettleworth, 1983). Therefore, considerations of function can make contributions to the analysis of learning mechanisms (Crawford, 1986; Shettleworth, 1983; Staddon, 1983). It follows that an examination of learning in an ecological and evolutionary

framework will benefit from an approach that takes into consideration the possible adaptive functions provided by learning and the relation of adaptive functions to learning mechanisms.

### Analysis of Function

An examination of the function of learning requires a careful consideration of what function is and how to measure it. The function of a behavior is inferred from its outcome. For example, the function of running may be to escape from a predator, to catch prey, or it may be part of territory defense. Adaptive functions are functions which provide an animal with some advantage that enables it to survive better and reproduce more offspring than its rivals. However, not all functions of behavior are adaptive. In some cases, behavior that appears to be adaptive may actually be maladaptive in terms of reproductive success. For example, a behavior such as foraging may provide an animal with a short-term advantage in terms of the amount of food gathered. But if that animal concentrates solely upon foraging and consequently falls prey to a predator, the foraging strategy becomes maladaptive in that it leads to decreased reproductive success. Therefore, it must be proven that the function of a behavior is adaptive.

There are, however, problems in the assessment of the adaptive functions of behavior. Ideally, one wants to assess the function of behavior in terms of its contribution to reproductive

success or inclusive fitness (Shettleworth, 1983). However, a particular behavior, such as foraging, is often far removed from actual reproductive gains. Further, in order to conclude that a certain behavior contributes to reproductive success or inclusive fitness, one would have to examine successive generations of offspring, an approach that is possible, but highly impractical (Dawkins, 1986; Shettleworth, 1983). Furthermore, when asking questions about adaptation, it is necessary to determine what alternatives for selection were available and, why one alternative fared better than others. Given that such selection may have taken place millions of years ago, experimental confirmation of an adaptive argument is difficult (Dawkins, 1986). Given these difficulties, a functional analysis of behavior has been discounted, because it can only tell us about the current utility of a feature and not about its evolutionary history (Jamieson, 1986), or because it has consisted of "loose speculation about adaptive significance" (Bitterman, 1975, p.708).

Yet, as Dawkins (1986) points out, there are four well-established methods for examining adaptation. The first method involves making use of existing genetic and behavioral variation. In this method, one seeks to determine whether differences in physical characteristics or behavior enable an animal to survive and reproduce better than its rivals. For example, a comparison between light and dark forms of the peppered moth showed that in

areas with dark tree trunks, bird predators ate more of the light-colored moths, indicating that the dark moths were better protected against bird predators than the light moths. In contrast, in areas where tree trunks were lighter, the bird predators ate more of the dark moths, indicating that the light moths were better protected than the dark moths (see Dawkins, 1986). However, since one variant has frequently been eliminated by natural selection, there are seldom two alternatives available for comparison. Consequently, comparisons of this form are difficult to make (Dawkins, 1986).

The second method avoids the problem of the first method through the use of artificially produced genetic or behavioral variation. In this method, artificial variations are compared to variations of real animals. Evidence of an adaptive function for the variation in the real animal would come from the observation that the real variation provides an advantage over the artificial variation. For example, Tinbergen, Broekhuysen, Feekes, Houghton, Kruuk, and Szuk (1967) compared eggshell removal by black-headed gulls with an artificial variation of nests without eggshells removed. Tinbergen et al. (1967) observed that nests with eggshells removed lost fewer eggs than nests that did not have eggshells removed. Thus, a comparison between a real and an artificially produced variation indicated an adaptive function for the real variation. However, this method is flawed in that the artificial variants may not represent what actually occurred

in nature (Dawkins, 1986).

The third method, the comparative method, involves a comparison between species in different niches. In this method, one species that is subject to a certain environmental pressure (e.g., heavy predation) is compared to a closely related species that is subject to a different environmental pressure (e.g., light predation). Differences between the behavior of the first species and the second species may reveal something about the behavior the first species has evolved as an anti-predator adaptation (Dawkins, 1986). An example of the comparative method is an analysis of the nesting behavior of gulls (Dawkins, 1986). Most gulls nest on the ground and practice eggshell removal. In comparison, kittiwake gulls nest on steep cliffs, do not remove eggshells, and have highly conspicuous nests. However, because of their location, kittiwake nests are virtually free from predation. Therefore, the difference between kittiwakes and ground-nesting gulls in eggshell removal suggests that eggshell removal is an anti-predator adaptation. Furthermore, the fact that eggshell removal occurs in close relatives of kittiwakes suggests that some kittiwakes could have removed eggshells at one time, thereby providing an alternative for natural selection. But those kittiwakes did not survive, and the non-removal of eggshells was selected for in kittiwakes (Dawkins, 1986). Thus, the comparative method can provide plausible alternatives that selection may have operated on in the past, and information about

the adaptive function of behavior. The problem with the comparative method that should be noted is that it involves correlations (e.g., between eggshell removal and predation) and therefore does not imply causation (Dawkins, 1986).

The fourth method for studying adaptation involves the use of design features. Design features are the behavioral or morphological features of an animal that may have enabled the animal to survive while its rivals died. In this method, the design feature(s) of an animal are determined. Through a comparison with a hypothetical alternative, this information is then used to infer why animals with a particular design feature were selected while their rivals died (Dawkins, 1986). An example of the design features argument is an analysis of the echolocation system of bats (Dawkins, 1986). Bats hunt insects by sending out high frequency pulses of sound and then listening to the echo that returns from the insect. In order to determine whether the bats' echolocation system is indeed designed to catch insects and thereby serve a possible adaptive function, a comparison is drawn between the bats' echolocation system and the similar sonar system constructed by humans. If there is a clear match between what the man-made system has been designed to do and what the animal's system does then it is likely that the function of the design feature has been identified. In the case of the bats' echolocation system, there is a close match between the location of objects by the man-made sonar system and the



location of insects by the bats' echolocation system. Therefore, one can conclude that the function of the bats' system is the catching of insects, as opposed to some other function such as communication. The selection pressure on the bats' ancestors was likely one of starvation. Bats without an echolocation system would not have been able to catch insects efficiently and would have died, whereas bats with an echolocation system would have been better at catching insects, and therefore survived and produced more offspring. Thus, there is evidence that the echolocation system of bats serves an adaptive function.

Of the four methods for studying adaptation proposed by Dawkins (1986), the design features method is the most useful to an examination of the adaptive functions of learning. As noted earlier, there are two basic problems associated with an examination of the adaptive functions of learning. The first problem is that it is difficult to connect the present behavior of an animal with possible past influences on behavior. However, with the design features method a discovery of what an animal optimizes in the short-term (e.g., territory defense) can be used to infer why natural selection favored a particular design feature in the past. For example, a design feature (e.g., some behavior) that enables an animal to defend its territory better than its rivals and is translated into a reproductive advantage suggests that territory defense played an important role in the survival of that animal's ancestors.

The second problem of the analysis of the adaptive functions of learning is that the current behavior of an animal is often far removed from actual reproductive gains, making it difficult to assess long-term optimality. A common strategy to overcome this problem is to measure the adaptive function of behavior in terms of some currency that is thought to be related to reproductive success. The design features method contributes to this solution in that the design feature that has been identified as important in the course of natural selection can be used to infer long-term optimality. For example, successful territory defense has been postulated as a currency in the evaluation of the long-term adaptive function of intraspecific aggressive behavior in fish (Hollis, 1984). However, there is a problem in the use of a currency to assess long-term optimality. As noted earlier, the relationship between short-term and long-term optimality is not straightforward. In many cases, it can be assumed that a feature that allows an animal to do better than its rivals in the short term is also responsible for long-term success. For example, an animal that is very successful at territory defense in an environment where territory defense is important and food is plentiful would likely enjoy greater reproductive success than a less successful territory defender. However, if food was not as plentiful, an animal that concentrates most of its energy on territory defense may fail to procure sufficient food, and therefore will have less

reproductive success than another animal that is a more efficient food-gatherer. Thus, a behavior that is optimal in the short term may actually be less than optimal in the long term. Consequently, when using a currency to measure long-term optimality, one must be aware of the possibility that the connection between a currency and reproductive success is not always straightforward. Presently, there is no solution to this problem, and until a solution is found the use of a currency to gauge reproductive success remains the best alternative.

#### Considerations for Learning

The preceding points concerning examinations of functions and mechanisms of learning provide guidelines by which to investigate learning in an ecological and evolutionary framework. An examination of learning within an ecological and evolutionary framework was deemed necessary because the traditional approach to learning failed to provide an adequate consideration of constraints phenomena. The main issue raised by constraints phenomena is whether learning consists of a multitude of specialized mechanisms or a set of general mechanisms. That issue can now be addressed.

Present evidence seems to indicate that learning is composed of a set of general mechanisms. There are five factors that lead to this conclusion. First, learning phenomena transcend species and classes (Razran, 1971). Second, many of the constraints phenomena that appeared to indicate the existence of specialized

mechanisms have been accounted for by general mechanisms. Third, the fact that many learning phenomena are the result of an interaction between paradigms suggests a common basis for learning. Fourth, the statement, "Nature selects for outcomes, not processes of development" (Lehrman, 1970, p.29) implies that natural selection operates on the behavioral outcomes of learning, not on the mechanisms of learning. Nature is concerned with how learning facilitates behavioral change, not how that learning occurs. Without any direct selection pressure for mechanisms, it is unlikely that a multitude of specialized learning mechanisms would have evolved (Tierney, 1986). And finally, Tierney (1986) surveyed recent genetic and neurophysiological observations and concluded that learned behavior is neither more complex nor a more costly adaptation than unlearned behavior. Tierney (1986) further proposed that learning may be a general process that precedes some innate forms of behavior and does not require a multitude of specialized learning mechanisms.

It should be noted that a conceptualization of learning as a general process does not mean that specialized learning mechanisms may not exist. Bird song learning is an example of learning that is not easily explained by general mechanisms of learning. The amount of involvement of learning in song acquisition appears to vary from species to species (Dawkins, 1986; Shettleworth, 1983; Staddon, 1983; Tierney, 1986). At

present, there is insufficient evidence to support either a general mechanism or specialized mechanism account of bird song learning.

Based on the five factors just described, it seems likely that learning consists of a set of general mechanisms that evolved long ago. One line of support for this hypothesis will be obtained if it can be demonstrated that a particular mechanism has the same function across behaviors. For instance, if Pavlovian conditioning can be shown to provide an adaptive advantage in feeding behavior, territory defense, and courting behavior, it would indicate that a general mechanism can serve different functions. Another line of support would be obtained if the same function in different species had the same mechanism. If two different species of fish showed improved territory defense through Pavlovian conditioning, it would indicate that the mechanism responsible for the improved territory defense is a general mechanism that operates across species. In order to pursue these lines of support for learning as a set of general mechanisms it will be necessary to first examine the adaptive function of a particular mechanism.

The prefiguring hypothesis. Hollis (1982) has adopted such a strategy and outlined a research program designed to evaluate the adaptive function of Pavlovian conditioning in foraging behavior, defensive behavior, and reproductive behavior. Hollis (1982) proposed that the biological function of Pavlovian conditioned

responses, which frequently appear to be energetically costly, is to enable an organism to optimize its interaction with a forthcoming biologically important event (the US). The biological function of optimizing the interaction with the US Hollis (1982) called 'prefiguring'. Presumably, preparing for a specific US provides an immediate advantage to an organism and the selective advantage afforded by the Pavlovian CR's would ultimately be manifested in an increase in the reproductive potential of the animal or that of its close kin (Hollis, 1982).

In a test of the prefiguring hypothesis, Hollis (1984) examined whether Pavlovian conditioning of aggressive behavior would confer an advantage to a territorial male blue gourami, enabling the gourami to better defend his territory in a signaled encounter. Since the prefiguring hypothesis maintains that the function of Pavlovian defensive conditioning is a conditioned response which optimizes the defense strategy, Hollis (1984) postulated that Pavlovian conditioning would result in a function-specific conditioned aggressive behavior. Blue gouramis were chosen as subjects because of the close relationship between their aggressive behavior and reproductive gains. Male gouramis will establish a territory, build a nest, and court females. Since females seldom mate with non-territorial males, territory defense is very important for the reproductive success of gouramis (Hollis, 1984). As such, territory defense serves as a currency by which to evaluate the biological function of

conditioning.

In Hollis' (1984) experiment, four pairs of male blue gouramis were used as subjects, with one member of each pair chosen to receive the Pavlovian conditioning treatment, and the other member receiving the explicitly unpaired control treatment. The Pavlovian conditioning consisted of a 10-sec presentation of a red light CS followed immediately by a 15-sec presentation of the US (a rival male). A glass jar containing another male gourami had been placed next to the door of the tank divider. For US presentation the divider door was raised, revealing the rival in the glass jar. Each session consisted of 15 pairings with an inter-trial interval of 60 sec-180 sec (mean = 120 sec). The unpaired control group received fifteen, 10-sec presentations of the red light CS followed an average of four hours later (range = 1hr-7hrs) by fifteen, 15-sec presentations of the US. Four antagonistic behaviors were recorded as dependent measures: 1) frontal display, defined as the unfolding and spreading of the dorsal, ventral, and caudal fins (fin erection) in the characteristic "face-to-face" posture; 2) biting, defined as contacting with open mouth, accompanied by an abrupt forward lunge; 3) tail-beating, defined as side-to-side undulations of the body, including the fins, usually carried out in a normal swimming position but occasionally at a head-upward or head-downward angle of from 30 to 80 degrees to the horizontal plane; and 4) submissive posturing, defined as assuming a body angle of

from 15 to 60 degrees with the horizontal, typically at the air-water interface, with all fins in a folded position, eventually accompanied by a blanching of color (Hollis, 1984). Of these four behaviors, frontal display was the only CR acquired by the CS. After training, the territorial defense test was conducted. Both the conditioned fish and the control fish received the CS, the door was lifted, and the fish were allowed to confront each other. A record was kept of the frequency of frontal display, biting, tail-beating, and submissive posturing. During the test, the paired males performed significantly more biting and tail-beating than their unpaired rivals. One could conclude from these results that the paired males were superior to their rivals because of the functional role played by Pavlovian conditioning. Hollis (1984) noted, however, that for the unpaired control group the red light CS may have predicted the absence of the rival male US, and as such may have resulted in the inhibition of aggressive responding. To determine whether inhibition was responsible for the differences between the paired experimental group and the unpaired control groups in the test confrontation, Hollis (1984) conducted another experiment in which the control procedure was changed. The control subjects received the same US presentations as the paired males, but never received the red light CS in training or in the test. The results of the second experiment were similar to the first, as the paired males delivered significantly more bites and tail-beating than did their control



rivals.

On the basis of these results, Hollis (1984) concluded that Pavlovian conditioning may provide a means whereby territorial males increase the likelihood of successful territory defense. The red light CS serves as a signal to which the fish approaches the site of intrusion, with all fins erect, ready to do battle. Upon confrontation, the paired male is much more aggressive than its unconditioned counterpart. The CR, then, serves a preparatory function in that it functions to optimize the paired male's interaction with a rival. Furthermore, under the assumption that any behavior that yields a defensive advantage also yields a reproductive advantage (Hollis, 1984), Pavlovian conditioning appears to convey a biological advantage to the paired males.

It appears then, that evidence exists for the function-specific conditioned aggressive behavior that Hollis (1984) had postulated. However, pilot research on the conditioning of food-seeking behavior in gouramis suggests otherwise. In the pilot research, an auto-shaping procedure was used in which subjects received pairings of a red light CS and a food US. During each conditioning session, a subject received 20, 10-sec presentations of a red light CS followed at CS offset by the delivery of one pellet of Nutrafin tropical fish food (32 mg). The food pellet was delivered by a modified Coulbourn dry food dispenser to a feeding ring (7.6 cm in diameter) that floated on the surface of

the tank. The inter-trial interval was 30-sec. The gouramis that received the red light CS and food US pairings developed fin erection as an anticipatory conditioned response.

The observation of fin erection in both food-seeking and aggressive behavior (Hollis, 1984) indicates an overlap in the response topography of the early components of food-seeking and territorial defense behavior in the gourami. As such, it is possible that conditioned fin erection may be an index of a process other than prefiguring. Rather than prepare a subject for a particular US, conditioning may serve the function of alerting the subject to the impending occurrence of biologically significant events. From this perspective, the CS activates a general arousal, alertness, or state of readiness which facilitates interactions with subsequent events (Brown, 1961; Hull, 1943). While similar to the prefiguring hypothesis in many respects, the conditioning of general arousal differs from prefiguring in that the product of conditioning is not directly related to a specific US. The observation of fin erection as a conditioned response to both feeding and territorial USs could be interpreted as support for the contention that conditioned fin erection subserves a general arousal/attention mechanism rather than being a function-specific conditioned aggressive behavior. Consequently, Hollis (1984) was premature in concluding that Pavlovian conditioning resulted in a function-specific conditioned aggressive behavior, and therefore, Hollis (1984)

failed to provide unambiguous support for the prefiguring hypothesis.

The failure to provide support for the prefiguring hypothesis with gouramis as subjects does not, however, preclude the possibility that Pavlovian conditioning may serve such a biological function. But, in order to evaluate the biological function of Pavlovian conditioning of aggressive behavior, it will be necessary to examine behaviors that appear only in aggression-related situations. While identifying behaviors which are unique to aggressive situations in gouramis may not be possible, such behaviors can be identified for convict cichlids, another territorial fish. Pilot research with convict cichlids has demonstrated that convict cichlids show two distinct threat displays in male-to-male encounters that are not observed during feeding: gill-cover extension and lateral display. Gill-cover extension is the spreading of the opercula membranes and the branchiostegal membranes. Lateral display is the dropping of the branchiostegal membranes while simultaneously extending the dorsal and anal fins and slightly tilting the body in a horizontal plane. At maximum intensity, all fins are spread, the branchiostegal and opercula membranes are spread, and the fish beats from side to side (Weber & Weber, 1976). Both of these displays are intended to make the fish look larger and therefore more threatening. In a confrontation, both gill-cover extension and lateral display may be used as threat displays. Gill-cover

extension is most common when the fish are head to head. Lateral display is most common when the fish are side by side.

Confrontations are usually limited to threat displays. However, if threat displays fail to decide a victor, tail-beating, face-to-face confrontation and finally biting may occur. The role of threat displays in a confrontation emphasizes the importance of the initial stages of a confrontation. It follows that a fish that displays first may gain an advantage and be more likely to emerge the victor. Thus, the aggressive behavior of convict cichlids allows for the investigation of function-specific conditioned aggressive behavior. Consequently, the present research pursued Hollis' (1984) hypothesis of the biological function of conditioning using convict cichlids as subjects.

In the present research a strategy similar to that employed by Hollis (1984) was used. In convict cichlids, as in gouramis, a currency closely related to reproduction is territory defense. Male cichlids establish a territory which they fiercely defend against intruders. The establishment and maintenance of a territory is critical for survival, because without a territory, the fish would not mate and reproduce (Fryer & Iles, 1972; Weber & Weber, 1976). Once a territory has been established, females are either accepted or driven away by males (Weber & Weber, 1976). When pairs are formed, they are usually monogamous and of long duration. Convict cichlids are substratum brooders. The eggs are laid on a solid surface and both the eggs and the fry

are guarded by the parents. Intruders, because they pose a risk to the survival of the fry, are quickly driven off. Since the establishment and maintenance of a territory is critical to the reproductive success of cichlids, territory defense was used as a currency to assess the biological function of Pavlovian conditioning.

The present experiment consisted of two phases. In the first phase Pavlovian conditioning sessions were given in which subjects received pairings of a green light CS and visual access to a male rival US. The second phase consisted of a test session in which the subjects were pitted against naive rivals in a signaled encounter. A US alone and a CS alone group were used to ensure that conditioned responding reflected an association between the CS and US and was not due to the presentation of the CS alone or the US alone.

Three goals were sought in the present research. First, to demonstrate Pavlovian conditioning in convict cichlids. Pavlovian conditioning would be demonstrated by the development of conditioned responding to the green light CS by the subjects that receive CS-US pairings, along with significantly less conditioned responding by the control Ss that received either the CS alone or the US alone presentations.

The second goal was to show a functional gain of learning. Dawkins (1986) proposed a comparison between a design feature and a hypothetical alternative in order to assess the similarity

between the two and thereby provide proof of adaptation. In the present research, a design feature (conditioned aggressive behavior) was compared to an alternative (unconditioned aggressive behavior) in order to assess the difference between the two. As such the present analysis deviated slightly from Dawkins' (1986) proposed methods of studying adaptation. A functional gain of learning would be demonstrated if Pavlovian conditioning enables the paired subjects, compared to the control subjects, to respond faster and with greater aggression than the naive rivals in a signaled encounter.

The third goal of the present research was to determine whether the CR includes a unique aggressive component and is therefore a function-specific conditioned aggressive behavior, or is indicative of a more general alert state. Since the CR observed by Hollis (1984) has also been observed in food-seeking behavior, it cannot be concluded that the observed CR is function-specific. This problem was avoided by the present research because convict cichlids show unique threat displays that are not observed during feeding. Evidence for a function-specific conditioned aggressive behavior would be obtained if the CR consists of either gill-cover extension, lateral display, or both displays. Conversely, a more general alert state would be indicated if the CR did not consist of threat display but consisted only of approach behavior.

## Method

Subjects

The subjects were 28 adult male convict cichlids (Cichlasoma nigrofasciatum). The subjects were selected from laboratory stock and were of similar body length.

Apparatus

The fish were housed in eight experimental tanks measuring 64 cm in length x 29 cm in width x 30 cm in height. The tanks were maintained at 27 degrees Celsius with a 12 hr light, 12 hr dark illumination schedule. Each tank was filtered by means of an undergravel filtration system with a 3 cm gravel base. The tanks were divided into three chambers by removable partitions that were painted black with Cabot's Flexiblac Protective Paint (#3230) to prevent visual contact between the fish. The area between the partitions measured 15 cm in length x 29 cm in width x 30 cm in height and was reserved for the removable stimulus panel. The two remaining areas, labeled side A and side B, measured 24.5 cm in length x 29 cm in width x 30 cm in height. Side A and B each housed a single experimental subject.

The removable stimulus panel consisted of a submersible glass box measuring 11.5 cm in length x 29 cm in width x 27 cm in height. The 29 cm x 27 cm sides of the panel had a 12 cm x 12 cm aperture in the center. On both the A and B sides of the panel, the aperture was covered by black-painted doors. Each door could be raised or lowered independently in one second by motors placed

above the panel. A wire-mesh (1.2 x 1.2 cm) cage measuring 12 cm x 12 cm x 11.5 cm could be placed between the doors and was used to house a conspecific during conditioning. Opening the doors on either side of the panel permitted access to the conspecific's wire-mesh cage. With the wire-mesh removed the conspecific compartment area of the stimulus panel formed a passage between the two side areas. Thus, when both doors were raised simultaneously the two subjects had access to each other's territory.

Each side of the stimulus panel had two light bulbs (24v) protruding 3 cm into the tank. The red lights were on the left and the green lights were on the right of each side of the panel. The lights were 6 cm down from the top and 4.5 cm in from the edge of the stimulus panel. The timing of the lights and the doors was controlled by a Coulbourn solid state logic system. Sessions were recorded by a RCA video camera (model CKC021) and recorder (model VLP 950HF). Sessions were viewed on a Panasonic color television monitor (model PC-20L13). The camera was mounted on a movable stand that was positioned 1 m in front of each tank. The video recorder and the monitor were located in an adjoining room. This avoided any possible disruptions in behavior caused by the presence of the experimenter in the experimental room.



Procedure

Twelve of the subjects were randomly assigned to one of three experimental groups ( $n = 4$ ). The groups consisted of a paired group, a CS alone group, and a US alone group. Twelve fish served as naive rivals against which the experimental fish were pitted during the test phase. The final four fish were used as USs during conditioning. The experimental subjects were housed in area A of the tanks and the naive rivals were housed in area B. Each tank contained similar sized subjects on the A and B sides. The fish were placed in their appropriate areas seven days before the experiment began to allow them to adjust to their surroundings and establish territories. Each fish was fed daily 5 ml of Tetramin dry fish food. The fish that served as USs were not used for any other experimental purposes and were housed in a separate tank. Immediately following the initial adjustment period, all subjects received exposure to the stimulus panel and door movement for five days in order to habituate reactions to both stimuli. The stimulus panel was placed in the tank and the doors were operated using the US schedule that would be employed in subsequent conditioning sessions.

Conditioning phase. Conditioning sessions began on the sixth day and were given for 30 consecutive days. Five minutes prior to each session the stimulus panel was placed in the tank; the appropriate partition was removed; and, the male conspecific that was to serve as the US was placed in the center compartment

of the panel.

During each conditioning session, subjects in the paired group received six, 10-sec presentations of the green light CS followed at CS offset by a 15-sec presentation of the US. The inter-trial interval was 600-sec. Subjects in the CS alone group received six CS presentations on the same schedule as the paired group, but did not receive any US presentations. Subjects in the US alone group received six US presentations on the same schedule as the paired group, but did not receive any CS presentations. The naive rivals did not receive any stimulus presentations.

The responses monitored during conditioning were defined as follows: 1) Approach - orientation to and movement toward the CS or the stimulus panel door; 2) Gill-cover extension - spreading of the opercula membranes and the branchiostegal membranes; 3) Lateral display - dropping of the branchiostegal membranes while simultaneously extending the dorsal and anal fins and slightly tilting the body in a horizontal plane to the CS. At maximum intensity, all fins are spread, the branchiostegal and opercula membranes are spread, and the fish beats from side to side; 4) Panel nipping - contact of the stimulus panel with an open mouth; 5) Tail-beating - the fish lies alongside its rival, head to tail. The fish uses rapid undulations of its tail to drive a stream of water against its rival's head, and may occasionally slap the rival with its tail; 6) Jaw-locking - the fish grip each other's jaws and push and pull; 7) Circling - the fish,

positioned with their heads at each other's tails, move in tight circles; 8) Biting - contacting the rival with an open mouth; and 9) Submissive posturing - tilting of body laterally with depressed dorsal and anal fins and withdrawn branchiostegal and opercula membranes. For paired subjects recording of behavior began 10 sec before CS onset and continued through the CS and US presentation periods. For CS alone subjects, recording of behavior began 10 sec before CS onset and continued through the CS presentation period. For US alone subjects, recording of behavior began 10 sec before US onset and continued through the US presentation period. If a behavior occurred before CS onset for paired or CS alone subjects or before US onset for US alone subjects, it was not counted as a response. Responses occurring in the CS-US interval were defined as CRs.

Test phase. The test phase was initiated on the day following the last conditioning session. The test phase was conducted by inserting the stimulus panel without the wire-mesh cage into the tank and removing the partitions from areas A and B. After a five minute period the green light CS was presented for 10 sec to the experimental subject only, then the doors on both sides of the panel were raised, and the experimental subject and the naive rival could access each other. The access period was 30 minutes long. During the CS presentation the same responses were monitored as during CS presentations in the conditioning phase. During the access period the following

responses were also monitored in order to determine whether the paired subjects defended their territory more successfully than the naive rivals or the control fish: 1) latency and duration of bout of approach to passage, entrance to passage, and entrance to rival's territory; 2) latency and duration of bout gill-cover extension; 3) latency and duration of bout of lateral display; 4) latency and duration of bout of tail-beating; 5) latency and duration of bout of jaw-locking; 6) latency and duration of bout of circling; 7) latency and frequency of biting; and 8) latency and duration of bout of submissive posturing.

### Results

The results were analyzed in two sections, one dealing with the conditioning phase data and the second dealing with the test phase data. Analysis of variance (ANOVAs) and orthogonal components for trend were used for the conditioning phase data. ANOVAs, Mann-Whitney U-tests, t-tests, orthogonal comparisons, and correlations were used for the test phase data.

#### Conditioning Phase

Of the nine responses monitored during the conditioning phase, only approach (orientation to and movement toward the CS or stimulus panel door) was regularly observed in all subjects. Panel nipping was observed in a few instances in paired and US alone subjects during inter-trial intervals, but was never observed as a response to the light CS. Gill-cover extension occurred on three trials in paired subjects along with approach behavior. Lateral display, tail-beating, jaw-locking, biting, and submissive posturing were not observed during the CS period. Gill-cover extension, lateral display, and tail-beating were observed during the US presentation period in the paired and US alone groups. Because of the absence or very low frequency of all behaviors except approach during the CS presentation, only approach behaviors were analyzed. A measure of inter-observer reliability was calculated as a percent agreement of identifying approach responses by independent observation. The percent

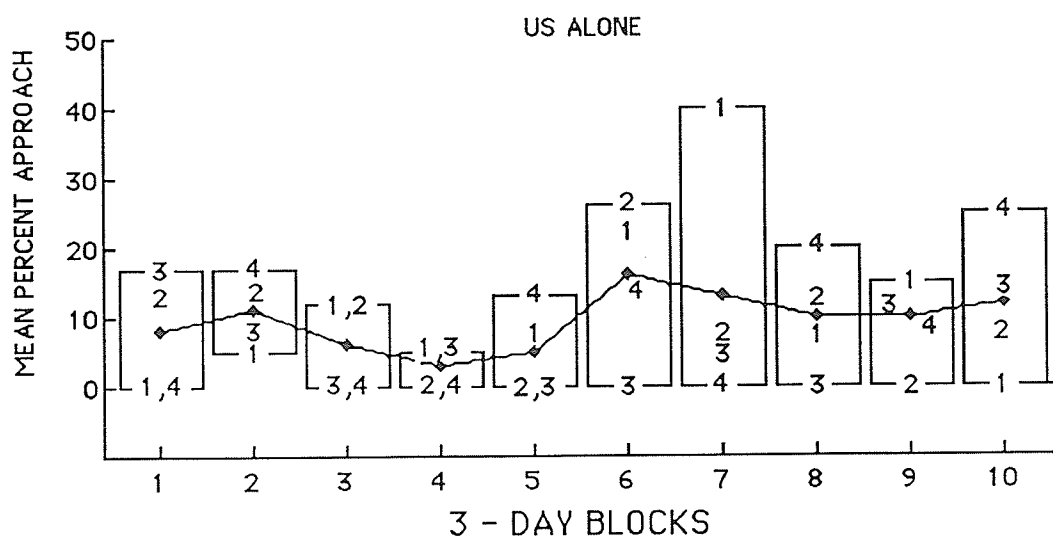
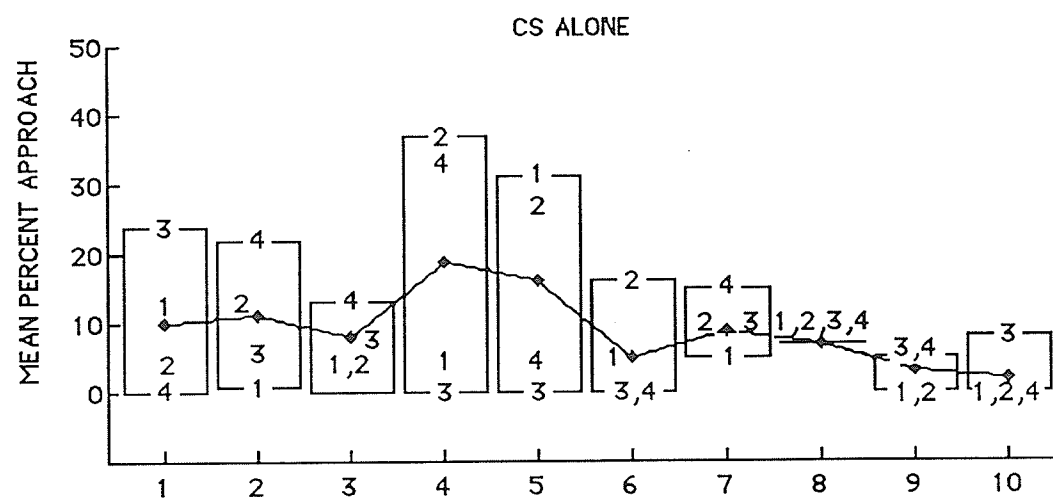
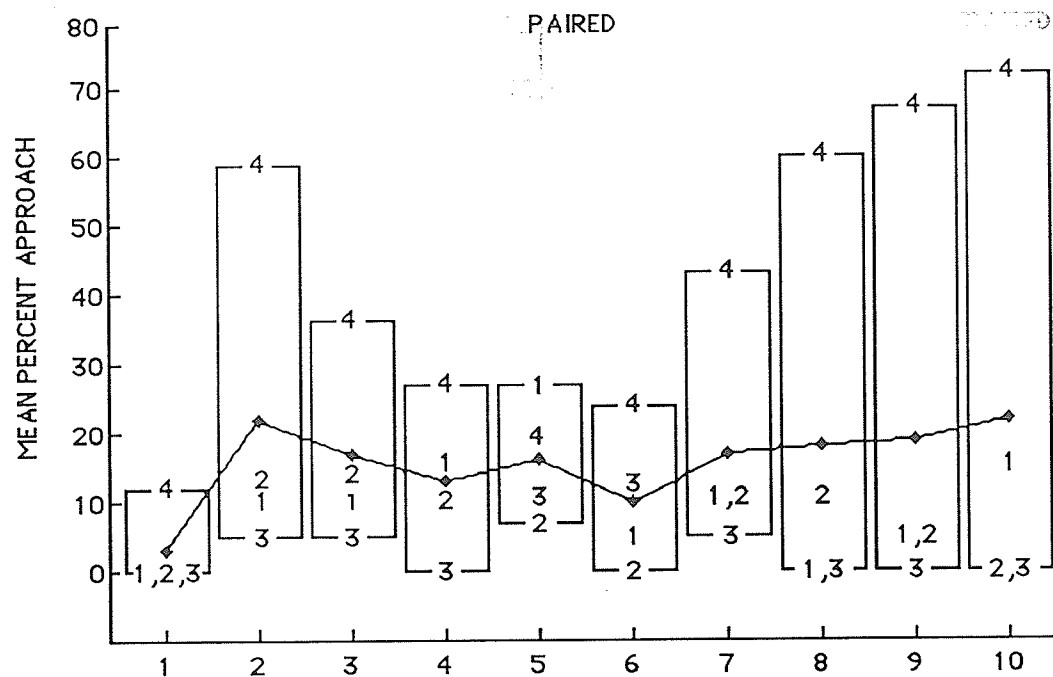
agreement was calculated to be 96 percent.

Figure 1 presents the mean percentage approach responses as a function of 10 three-day blocks for the paired, CS alone, and US alone groups. The mean percentage approach responses of each subject from each group are plotted by the subject's number. The histograms depict the range of individual subject scores in each group.

The top frame of Figure 1 presents the mean percentage approach responses for the paired group. The gradual increase in approach responses is suggestive of the acquisition of conditioned responses (CRs). However, orthogonal components for trend failed to reveal a significant increasing trend over blocks. The absence of a significant increasing trend may in part be due to the large amount of variability in approach responses in individual subjects, as revealed by the histograms. As can be seen from the frame, subject four had a gradual increase in mean percentage approach across blocks whereas the remaining subjects showed no such increase. The level of responding for subject four was considerably higher than that of subjects one, two and three on all blocks except block five. As a consequence, the variability for the group was quite high. The increasing trend and higher level of responding in subject four provided evidence that learning occurred in at least one subject.

The middle frame of Figure 1 presents the mean percentage approach responses for the CS alone group. As can be seen from

Figure 1. Mean percentage approach responses as a function of 10 three-day blocks for the paired (top frame), CS alone (middle frame), and US alone (bottom frame) groups.





the frame, the CS initially produced a low degree of approach, or alpha responses (Gormezano & Moore, 1969). Over the days of conditioning, the alpha responses decreased, thereby indicating that habituation to the CS occurred. Orthogonal components for trend identified a significant decreasing linear function  $F(1, 3) = 98.88, p < .002$ , confirming that habituation occurred. Responses of individual subjects, plotted by subject number, revealed no consistent pattern of responding as subjects reversed their relative positions from block to block. In addition, the highest level of responding of a single subject (subject two, block four) is considerably less than that of subject four in the paired group (top frame). And finally, the degree of variability revealed by the histogram is considerably less than that of the paired group (top frame).

The bottom frame of Figure 1 presents the mean percentage approach responses for the US alone group. The level of responding indicates a flat function. Because orthogonal components for trend did not reveal any significant components, there was no evidence of conditioning. The responses of individual subjects revealed no consistent pattern of responding, as subjects reversed their relative positions from block to block. The highest level of responding of an individual subject (subject one, block 17) is considerably less than that of subject four of the paired group (top frame). And finally, the degree of variability revealed by the histograms is less than that of the

paired group (top frame).

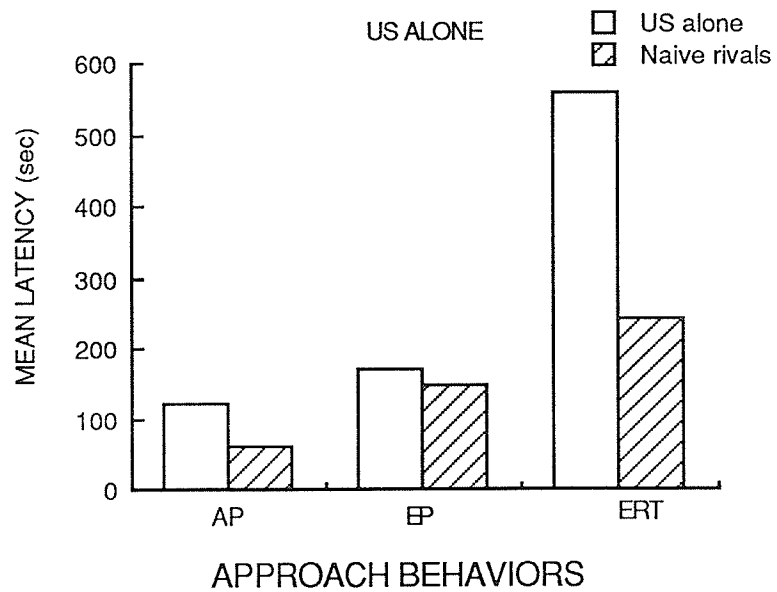
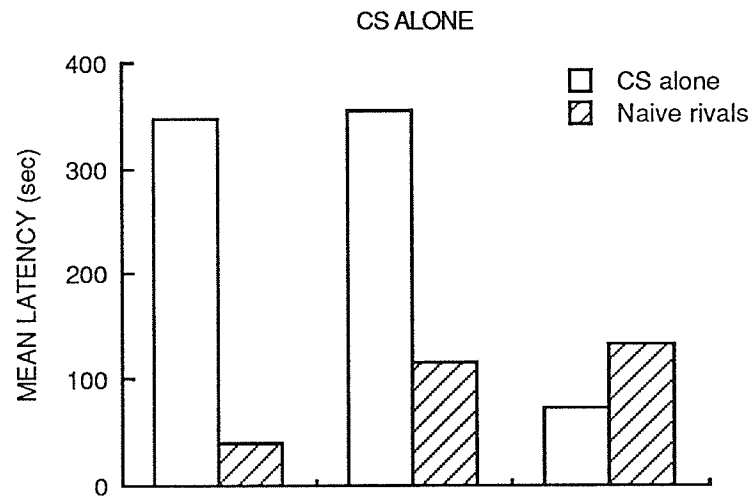
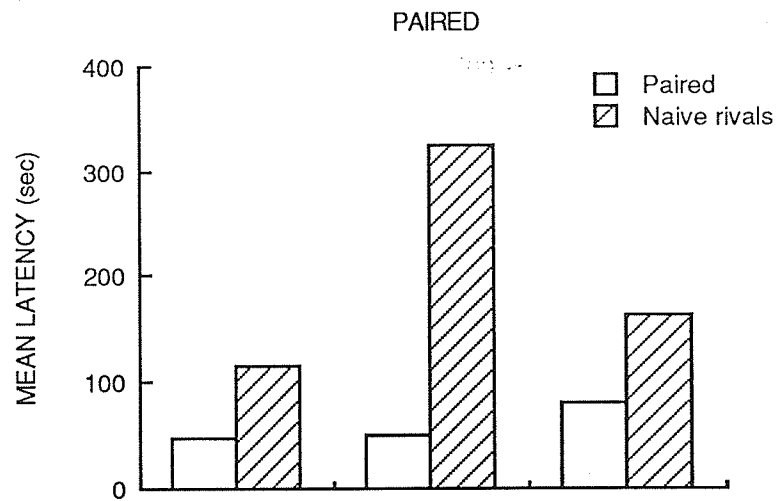
An ANOVA found no significant differences between paired, CS alone, and US alone groups. The high degree of variability between subjects, revealed by the histograms in Figure 1, may be in part responsible for the failure to find significant differences between groups. A comparison of the three frames of Figure 1 illustrates, however, that subject four of the paired group exhibited a considerably higher level of responding than subjects in the CS alone and US alone groups. Thus, for at least one paired subject, there is evidence that learning occurred.

#### Test Phase

The latency, frequency, and duration of responses monitored during the test phase were divided into two clusters, one consisting of approach behaviors (approach to passage, entrance to passage, and entrance to rival's territory), and the second consisting of aggressive behaviors (gill-cover extension, lateral display, tail-beating, jaw-locking, circling, biting, and submissive posturing). A measure of inter-observer reliability was calculated with Pearson product-moment correlation coefficients applied to independent scoring of the test sessions. The inter-observer reliability coefficients were calculated to be 98 percent.

Approach behavior. Figure 2 presents the mean latency of approach behaviors for subjects in the paired group (top frame), CS alone group (middle frame), and US alone group (bottom frame)

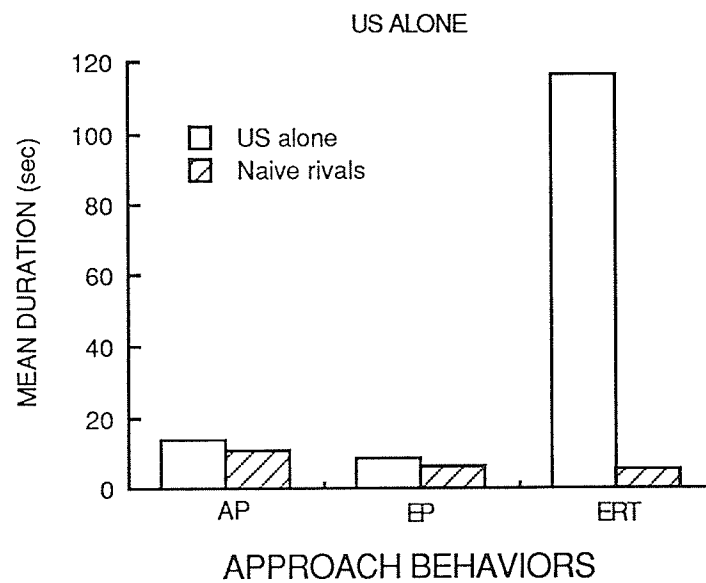
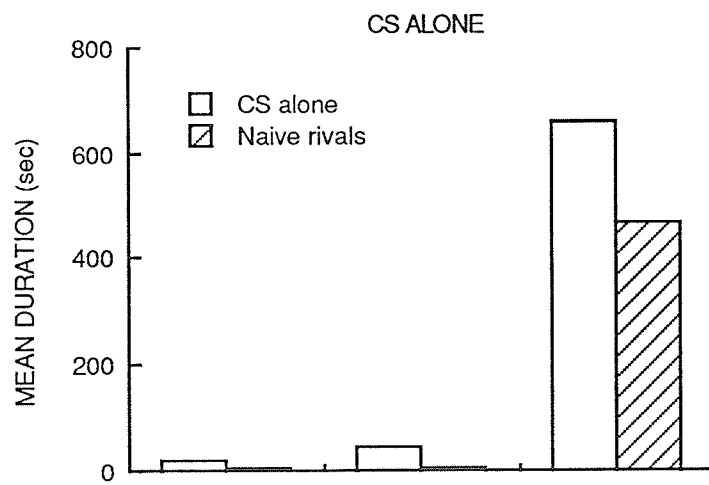
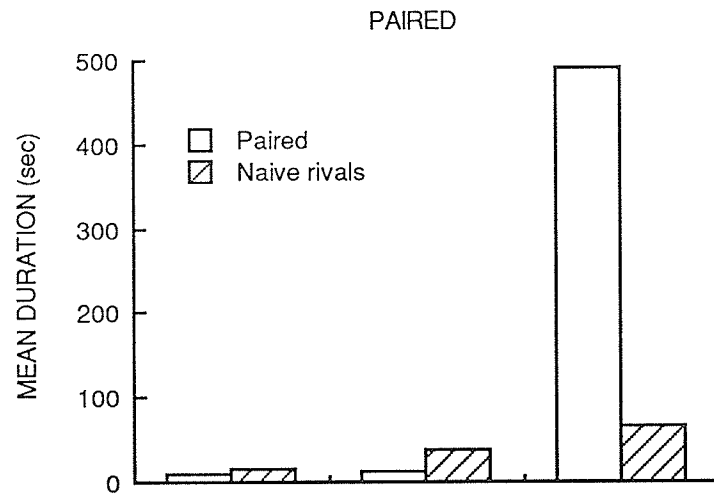
Figure 2. Mean latencies for approach to passage (AP), entrance to passage (EP), and entrance to rival's territory (ERT) for the paired (top frame), CS alone (middle frame), and US alone (bottom frame) groups compared to their naive rivals.



versus their respective naive rivals. As can be seen from the top frame, subjects in the paired group had shorter mean latencies of approach to passage, entrance to passage, and entrance to rival's territory than their naive rivals. Thus, the paired subjects were quicker than their naive rivals to approach and enter the passage, and then enter their rival's territory. The more rapid reaction of the paired subjects suggests that they had an initial advantage over their naive rivals. In contrast, subjects in the CS alone group (middle frame) and US alone group (bottom frame) had much longer latencies of approach to passage, entrance to passage, and entrance to rival's territory than their naive rivals. These longer latencies indicate no initial advantage for CS alone and US alone subjects. ANOVAS and Mann-Whitney U-tests, however, revealed that none of the differences between experimental subjects and their naive rivals were statistically significant.

For each subject, the duration of each bout of approach to passage, entrance to passage, and entrance to rival's territory was calculated by dividing the total duration by the corresponding frequency for each behavior. Figure 3 presents the mean duration of bout for the paired group (top frame), CS alone group (middle frame), and US alone group (bottom frame). As can be seen from the top frame, the paired group had shorter duration of bout values for approach to passage and entrance to passage, and longer duration of bout values for entrance to rival's

Figure 3. Mean duration of bout for approach to passage (AP), entrance to passage (EP), and entrance to rival's territory (ERT) for the paired (top frame), CS alone (middle frame), and US alone (bottom frame) groups compared to their naive rivals.



territory than its naive rivals. The longer time spent by paired subjects in their naive rival's territory suggests a territorial advantage for the paired subjects. However ANOVAs failed to confirm any of the differences noted between paired subjects and their naive rivals to be significant.

As can be seen from the middle frame, CS alone subjects had longer duration of bout values for all three approach behaviors than their naive rivals. An ANOVA revealed a significant difference between the CS alone group and its naive rivals on the duration of bout of approach to passage  $F(1,3) = 9.3, p < .04$  and entrance to passage  $F(1,3) = 20.08, p < .01$ . Thus, in contrast to paired subjects (top frame), CS alone subjects spent more time than their naive rivals approaching and entering the passage. And similar to paired subjects, CS alone subjects spent more time in their naive rival's territory. However, the values of duration of bout for entrance in rival's territory depicted in the frame indicate less of a difference between CS alone subjects and their naive rivals compared to the difference between paired subjects and their naive rivals (top frame). Thus, the territorial advantage of CS alone subjects is of a lesser magnitude than that of the paired subjects.

The pattern of duration of bout values for the US alone group (bottom frame) is similar to that of the CS alone group. US alone subjects had greater duration of bout values than their naive rivals for all three approach behaviors. Thus, US alone



subjects spent more time approaching and entering the passage than their naive rival's, and more time in their naive rival's territory. In addition, the relatively large magnitude of the difference between US alone subjects and their naive rivals on duration of bout of time spent in the rival's territory suggests a territorial advantage for the US alone subjects, similar to that observed for the paired subjects (top frame). However, an ANOVA did not find any of the differences between US alone subjects and their naive rivals to be statistically significant.

Except for the differences found between the CS alone group and its naive rivals on duration of bout, no other comparisons revealed significant differences between experimental groups and their naive rivals. The failure to find significant differences was likely a consequence of the variability of scores across individual subjects.

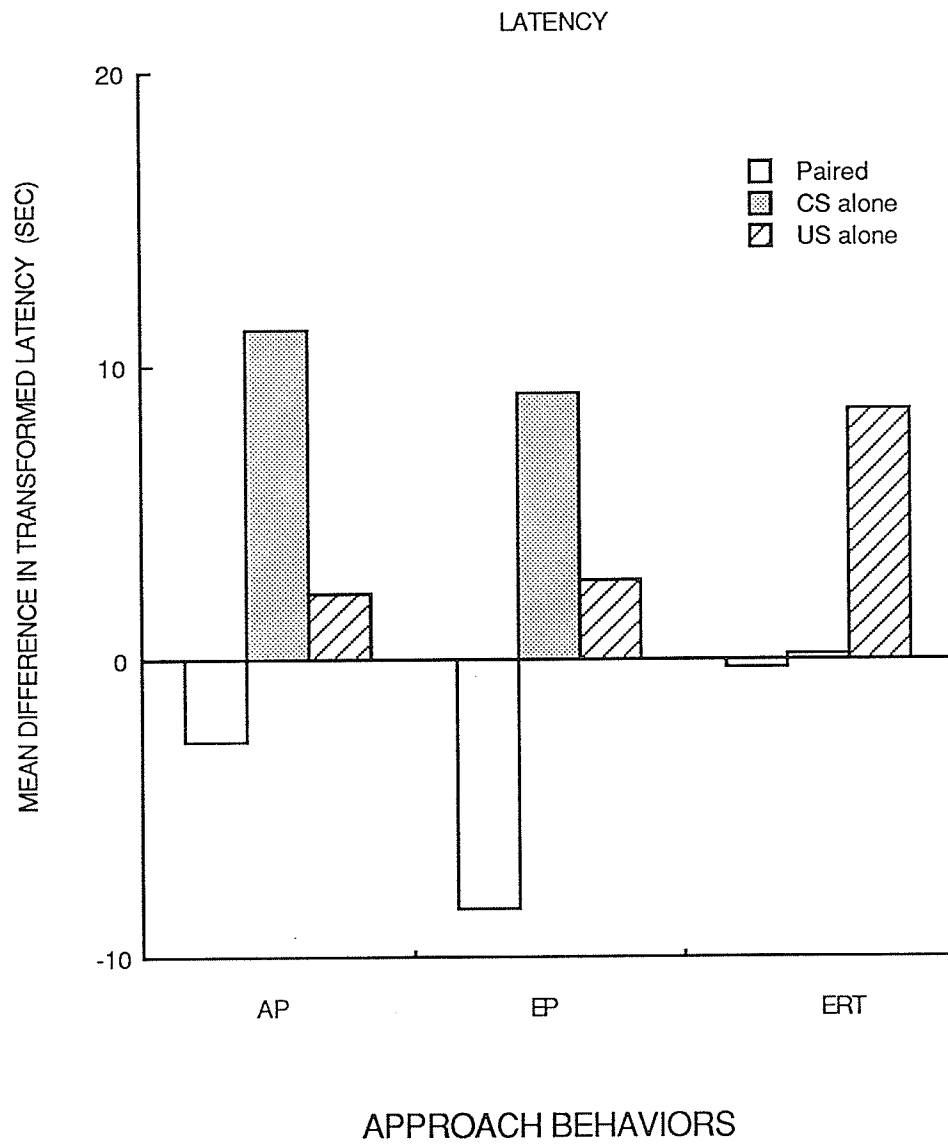
Due to the variability of scores across individual subjects, a square root transformation was carried out to reduce variability for a comparison between groups on the latency and duration of bout of approach behaviors. In addition, to determine whether a relative advantage had been conveyed among the experimental groups, the advantage gained by each subject was obtained by subtracting the score of the naive rival from the score of the experimental subject. Thus, scores were transformed by subtracting the square root of each naive rival's score from the square root of its experimental counterpart's score,

resulting in a difference score.

Figure 4 presents the mean difference scores on the latency of approach behaviors for paired, CS alone, and US alone groups. Negative values for the latency difference scores indicate that subjects had shorter latencies than their naive rivals on a particular behavior. As can be seen from Figure 4, paired subjects had negative latency values, or shorter latencies, for approach and entrance to the passage, and entrance to rival's territory. In contrast, CS alone and US alone subjects had positive values on the latency difference scores, indicating that CS alone and US alone subjects had longer latencies than their naive rivals for approach behaviors. Comparing the paired, CS alone and US alone groups, the shorter latency values for the paired group mean the paired subjects were relatively quicker than subjects in the CS alone and US alone groups to approach and enter the passage, and to enter their naive rival's territory. Thus, the paired subjects exhibited a relative territorial advantage compared to the CS alone and US alone groups. ANOVAs did not find any of the differences between paired, CS alone, and US alone groups to be significant. However, post-hoc orthogonal comparisons revealed that the paired group had a significantly shorter latency to enter the passage than the CS alone group,  $F(1, 3) = 6.07, p < .05$ .

For each subject, the duration of each bout of approach to passage, entrance to passage, and entrance to rival's territory

Figure 4. Mean difference scores on the latency of approach to passage (AP), entrance to passage (EP), and entrance to rival's territory (ERT) for paired, CS alone, and US alone groups.

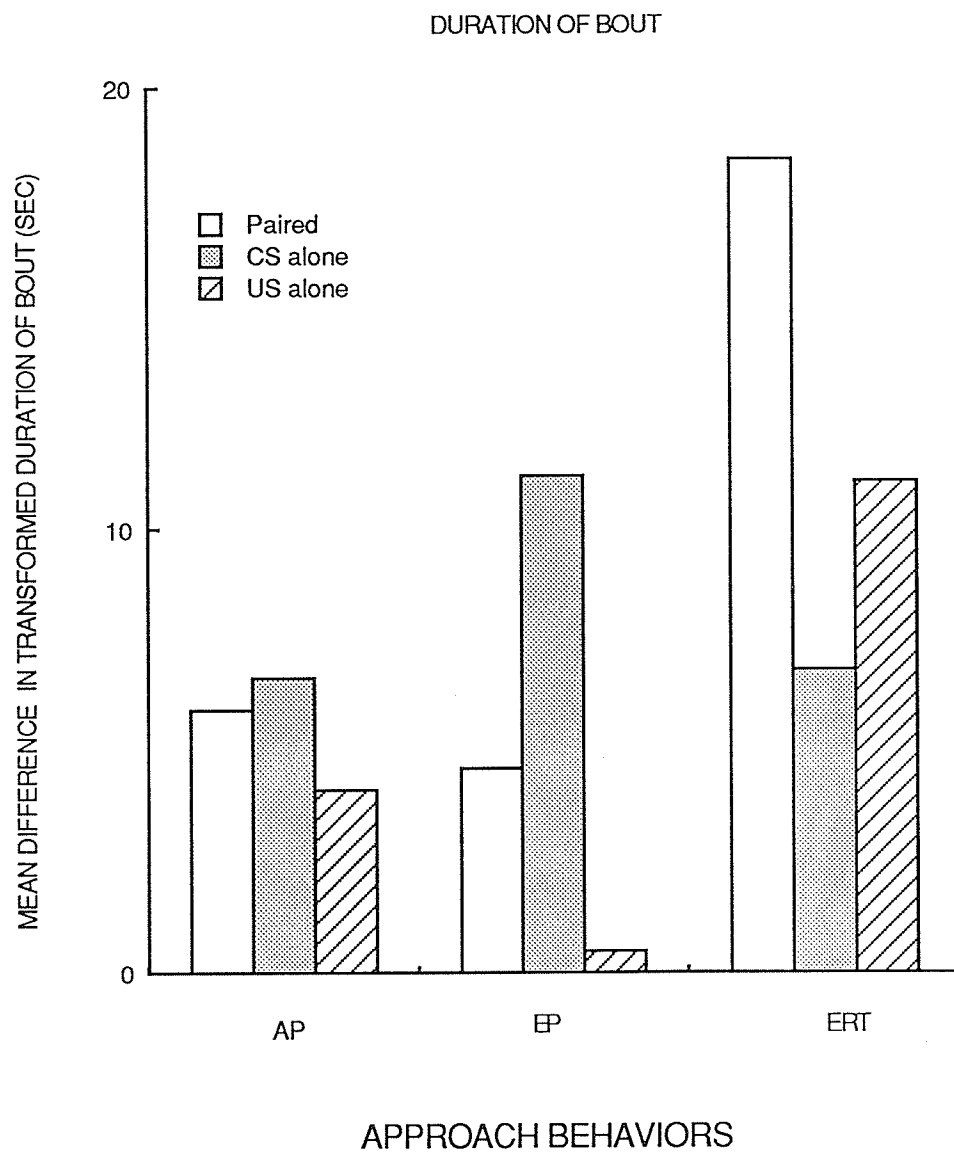


was calculated by dividing the duration difference score by the corresponding frequency difference score for each behavior. Figure 5 presents the mean duration of bout of difference scores for approach to passage, entrance to passage, and entrance to rival's territory for the paired, CS alone, and US alone groups. The positive values for approach behaviors for all three groups mean that subjects in all groups had an advantage over their naive rival's in duration of bout for all approach behaviors. Thus, the values plotted in Figure 5 depict whether the advantage of a particular group was greater or less than the advantage of other groups.

An ANOVA found a difference between groups on duration of bout of entrance to passage,  $F(2, 8) = 3.48, p < .08$ . Post-hoc orthogonal comparisons revealed the difference to be between the CS and US alone groups. No other significant differences were found. However, the values plotted in Figure 5 for duration of bout of entrance to rival's territory indicate a substantial difference between the paired group and the CS alone group. The greater value for the paired group means that subjects in the paired group spent more time in their naive rival's territory than CS alone subjects spent in their naive rival's territory. Thus, the paired group had a greater advantage over its naive rivals than did the CS alone group over its naive rivals.

The relationship between the latency, frequency, and duration of approach behaviors for each experimental group was

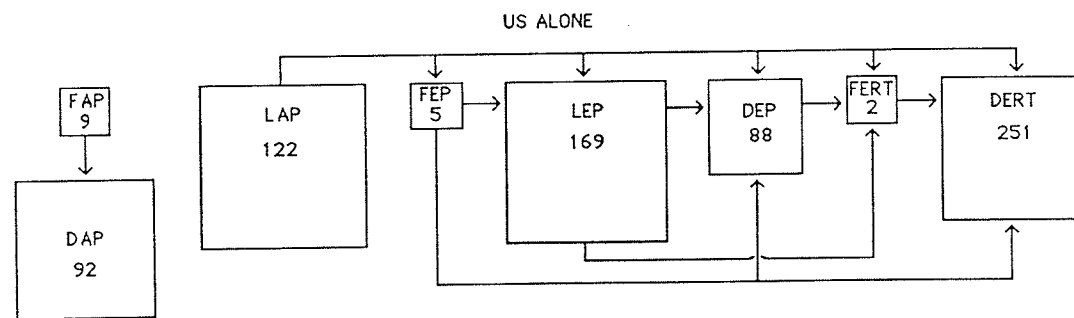
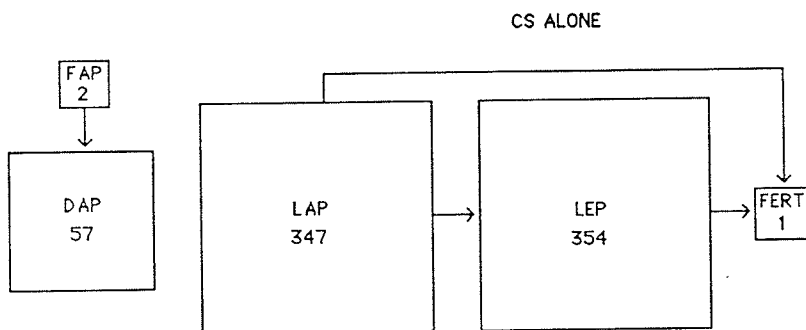
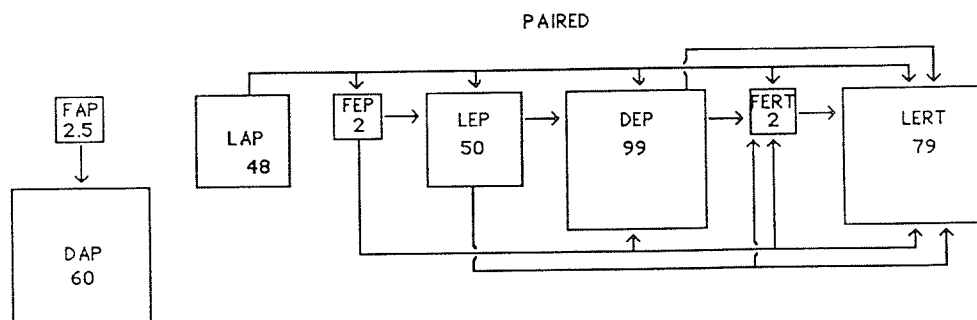
Figure 5. Mean duration of bout of difference scores for approach to passage (AP), entrance to passage (EP), and entrance to rival's territory (ERT) for paired, CS alone, and US alone groups.



examined through a correlation procedure. The resulting correlations are provided in Appendix A. Figure 6 presents a schematic diagram of the significant correlations between approach behaviors for the paired (top frame), CS alone (middle frame), and the US alone (bottom frame) groups. The size of the boxes in the figure are roughly proportional to the magnitude of the mean score for a particular behavior, with larger boxes signifying larger scores. For the paired group (top frame) the correlations reveal a consistent relationship between the latency of approach and entrance to the passage, and entrance to rival's territory, along with connections to the frequency of entrance to the passage and rival's territory and the duration of entrance to the passage. The mean values for each behavior (indicated by the size of the boxes) are small, indicating short latencies and duration, and few occurrences of the behaviors. In contrast, there are far fewer significant correlations between approach behaviors for the CS alone group (middle frame). In particular, the consistent relationship between the latency measures of approach and entrance to the passage, and entrance to rival's territory in the paired group is not evident in the CS alone group. For the CS alone group, approach and entrance to the passage are the only latency measures that are significantly correlated. In addition, the values for the latency behaviors are considerably larger than those for the paired group (top frame). The US alone group (bottom frame) followed a similar



Figure 6. Schematic diagram of the significant correlations between the latency, frequency, and duration of approach behaviors for the paired (top frame), CS alone (middle frame), and US alone (bottom frame) groups. The size of the boxes is roughly proportional to the magnitude of the mean score for a particular behavior. The values within the boxes represent the mean score for a particular behavior in seconds (for latency and duration scores) or in number of occurrences (for frequency scores).



FAP = frequency of approach to passage  
 DAP = duration of approach to passage  
 LAP = latency of approach to passage  
 FEP = frequency of entrance to passage  
 LEP = latency of entrance to passage

DEP = duration of entrance to passage  
 FERT = frequency of entrance to rival's territory  
 LERT = latency of entrance to rival's territory  
 DERT = duration of entrance to rival's territory

pattern to that of the paired group, with many significant correlations between latency, frequency, and duration of approach behaviors. However, as with the CS alone group, there was not a significant correlation between all latency measures for US alone subjects, as only latency of approach and entrance to the passage were significantly correlated. The mean values for the behaviors are also larger than those depicted for the paired group.

A comparison of the three frames of Figure 6 reveals that the paired group, because of the consistent relationship between the latencies of approach behaviors, had a tighter organization of behavior than the CS alone or US alone groups.

Aggressive behavior. Subjects in the paired, CS alone, and US alone groups were compared to their respective naive rivals on the latency of gill-cover extension, lateral display, tail-beating, jaw-locking, biting, and circling during an encounter. Submissive posture was not observed during any of the encounters and therefore was not included in the analysis. Experimental subjects and their respective naive rivals were also compared on the duration of bout of gill-cover extension, lateral display, tail-beating, jaw-locking, and circling. A duration of bout value for biting was not calculated because acts of biting had durations of less than one second. Thus, only the frequency of biting was examined. Figure 7 presents the mean latency of aggressive behaviors, Figure 8 the mean duration of bout of aggressive behaviors, and Figure 9 the mean frequency of biting

Figure 7. Mean latencies of gill-cover extension (GCE), lateral display (LD), tail-beating (TB), jaw-locking (JL), circling (C), and biting (B) for the paired (top frame), CS alone (middle frame), and US alone (bottom frame) groups compared to their naive rivals.

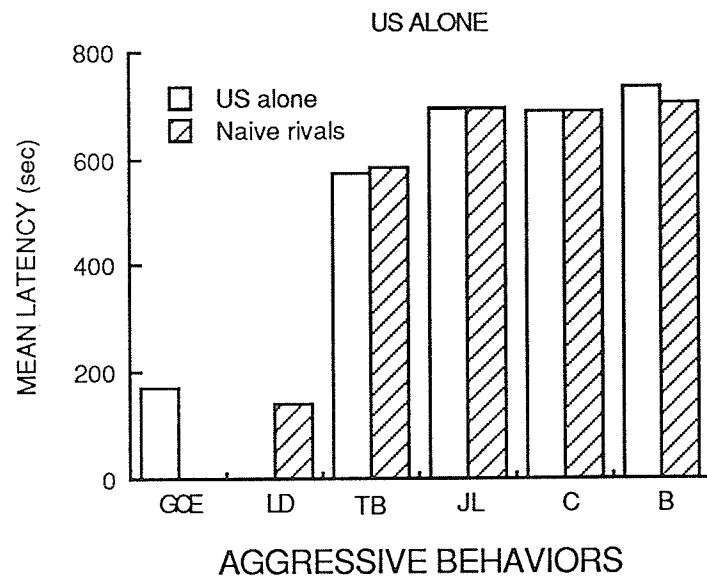
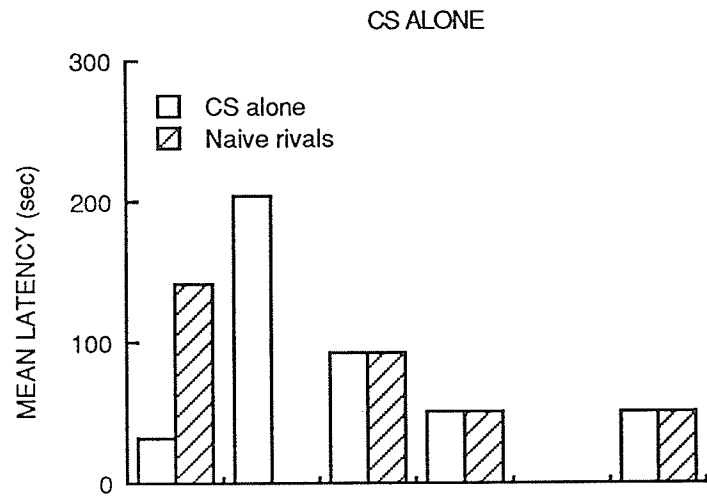
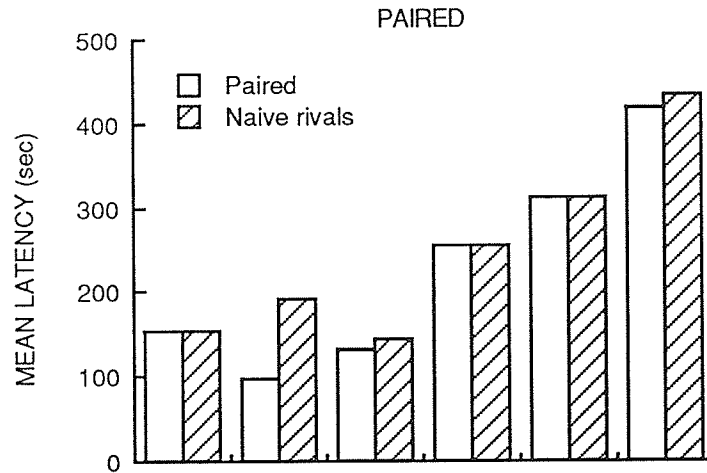
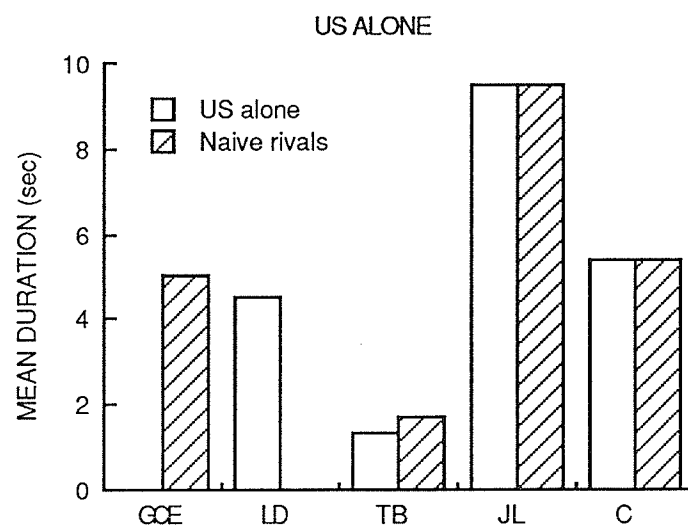
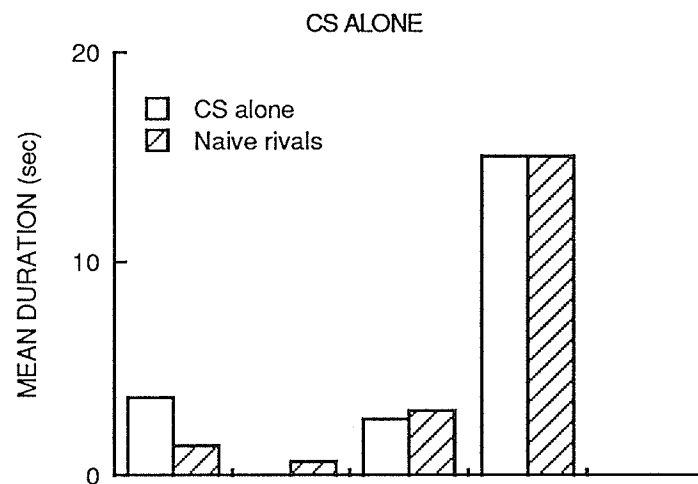
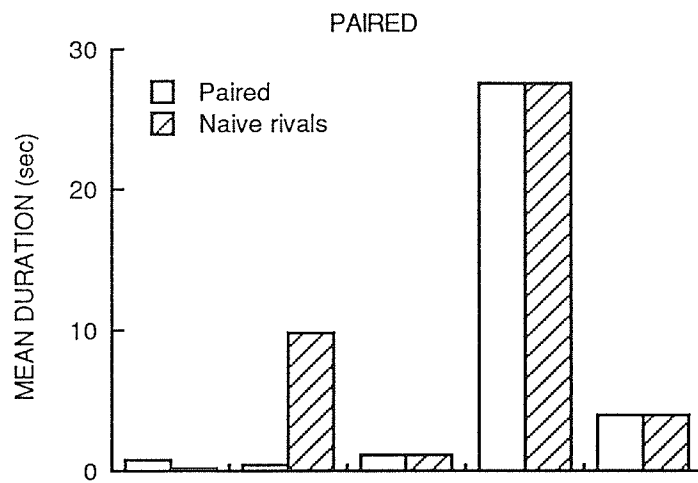


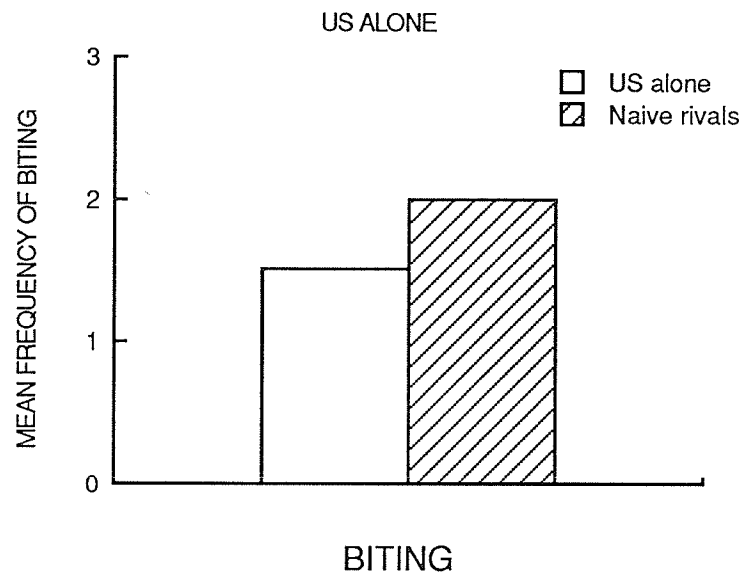
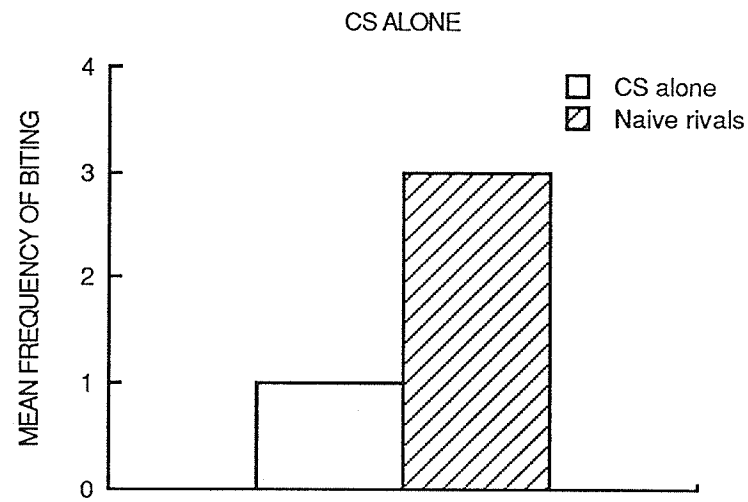
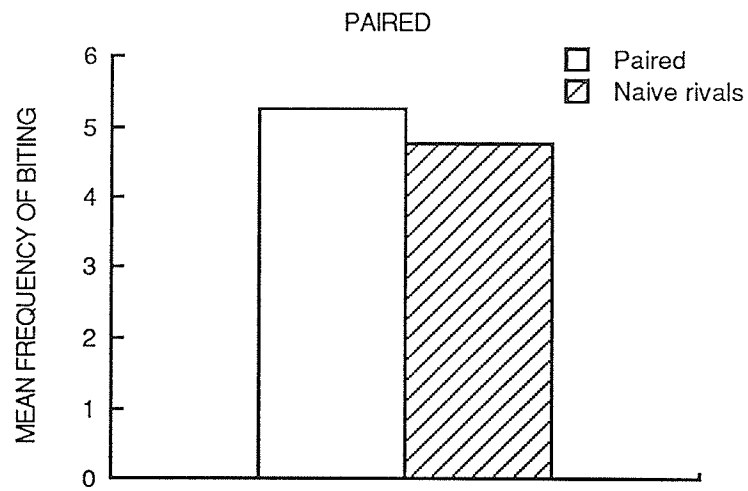
Figure 8. Mean duration of bout for gill-cover extension (GCE), lateral display (LD), tail-beating (TB), jaw-locking (JL), and circling (C) for the paired (top frame), CS alone (middle frame), and US alone (bottom frame) groups compared to their naive rivals.



AGGRESSIVE BEHAVIORS

Figure 9. Mean frequency of biting for the paired (top frame), CS alone (middle frame), and US alone (bottom frame) groups compared to their naive rivals.





for subjects in the paired group (top frame), CS alone group (middle frame), and US alone group (bottom frame) versus their respective naive rivals. Absent values in the figures, such as for circling in the CS alone group (Figure 7, middle frame) indicate that subjects never engaged in a particular behavior. As can be seen from Figures 7, 8, and 9, there are only slight differences between experimental subjects and their naive rivals on all measures except for jaw-locking and circling which were always equal. Because the behaviors of jaw-locking and circling were engaged in simultaneously by opponents, the measures for those behaviors were always equal for experimental subjects and their naive rivals. ANOVAs did not find any of the differences between experimental subjects and their naive rivals on latency and duration of bout of aggressive behaviors or frequency of biting to be statistically significant. The failure to find any significant differences between experimental subjects and their naive rivals can be explained in part by the type of behaviors that were measured. In an encounter, behaviors such as jaw-locking and circling require simultaneous performance by both opponents in an encounter. Other behaviors, such as gill-cover extension and lateral display do not necessarily occur simultaneously, but as revealed in Figures 7 and 8, exhibit only slight differences between opponents. Thus, a more meaningful comparison was one that compared the latency and duration of bout of aggressive behaviors and the frequency of biting between

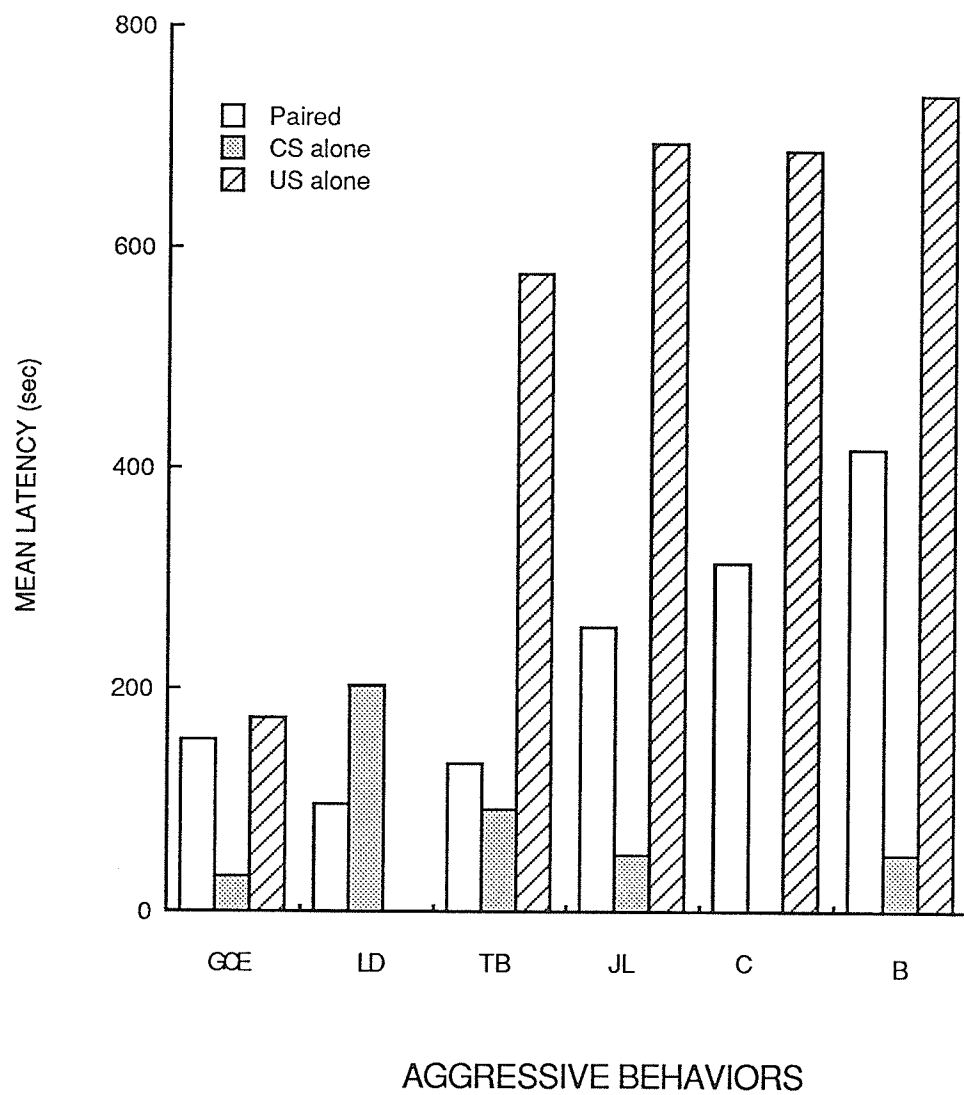
experimental groups.

Similar to the data for approach behaviors, the data for aggressive behaviors exhibited a large amount of variability across individual subjects. Consequently, a square root transformation was carried out to reduce variability. In addition, difference scores were obtained by subtracting the square root of each naive rival's score from the square root of it's experimental counterpart's score. However, the behaviors of jaw-locking and circling were not included in the analyses because the identical scores of naive rival and experimental subjects on those behaviors resulted in difference scores of zero. Analyses of difference scores through the use of ANOVAS failed to find any significant differences between experimental groups on the latency and duration of bout of aggressive behaviors or the frequency of biting. Because the use of difference scores failed to alleviate the problems induced by high variability, and also resulted in the absence of jaw-locking and circling from the analyses, comparisons between groups were done using non-transformed scores.

Figure 10 provides the mean latency of gill-cover extension, lateral display, tail-beating, jaw-locking, circling, and biting for the paired, CS alone, and US alone groups. Absent values for the US alone group on lateral display and the CS alone group on circling indicate subjects did not engage in those particular behaviors. As can be seen from Figure 10, the CS alone group had

Figure 10. Mean latencies of gill-cover extension (GCE), lateral display (LD), tail-beating (TB), jaw-locking (JL), circling (C), and biting (B) for paired, CS alone, and US alone groups. Absent values indicate that subjects did not engage in those particular behaviors.

# LATENCY OF AGGRESSIVE BEHAVIORS



shorter latencies than the paired group and the US alone group on gill-cover extension, tail-beating, jaw-locking, and biting, and longer latency on lateral display than the paired group. The paired group had shorter latencies than the US alone group on gill cover extension, tail-beating, jaw-locking, circling, and biting. An ANOVA did not find any of the differences between groups to be statistically significant.

Figure 11 presents the mean duration of bout for gill-cover extension, lateral display, tail-beating, jaw-locking, and circling for the paired, CS alone, and US alone groups. The absent values on gill-cover extension for the US alone group and lateral display and circling for the CS alone group indicate that subjects did not engage in those particular behaviors. As can be seen from Figure 11, all behaviors except jaw-locking have relatively low duration of bout values, with very little difference between the groups. For the behavior of jaw-locking, the paired group has a considerably longer duration of bout value than that of the CS alone and US alone groups. Although an ANOVA did not find the difference between groups on jaw-locking or any of the other behaviors to be statistically significant, the difference between groups on jaw-locking suggests that subjects in the paired group engaged in more face-to-face combat than subjects in the CS alone or US alone groups.

Figure 12 presents the mean frequency of biting for the paired, CS alone, and US alone groups. As can be seen from

Figure 11. Mean duration of bout for gill-cover extension (GCE), lateral display (LD), tail-beating (TB), jaw-locking (JL), and circling (C) for paired, CS alone, and US alone groups. Absent values indicate that subjects did not engage in that particular behavior.

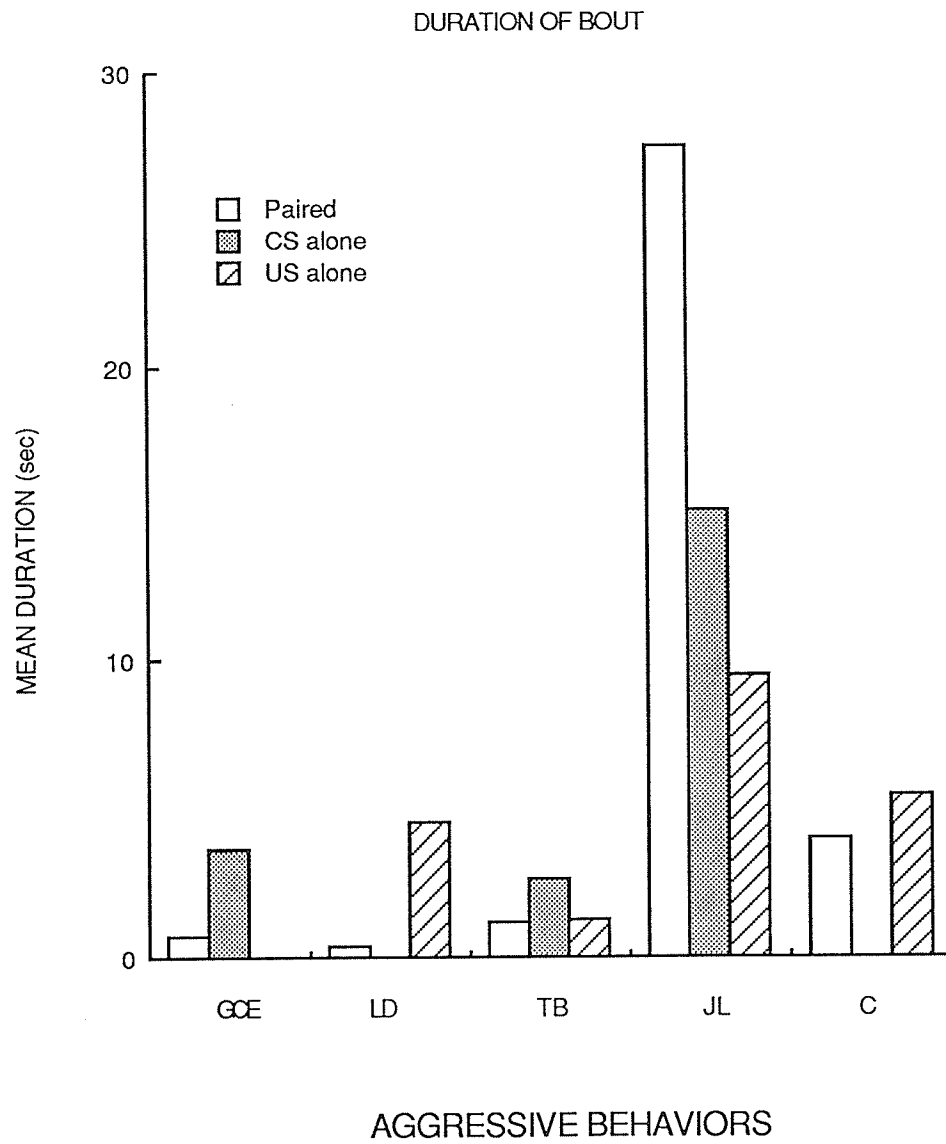
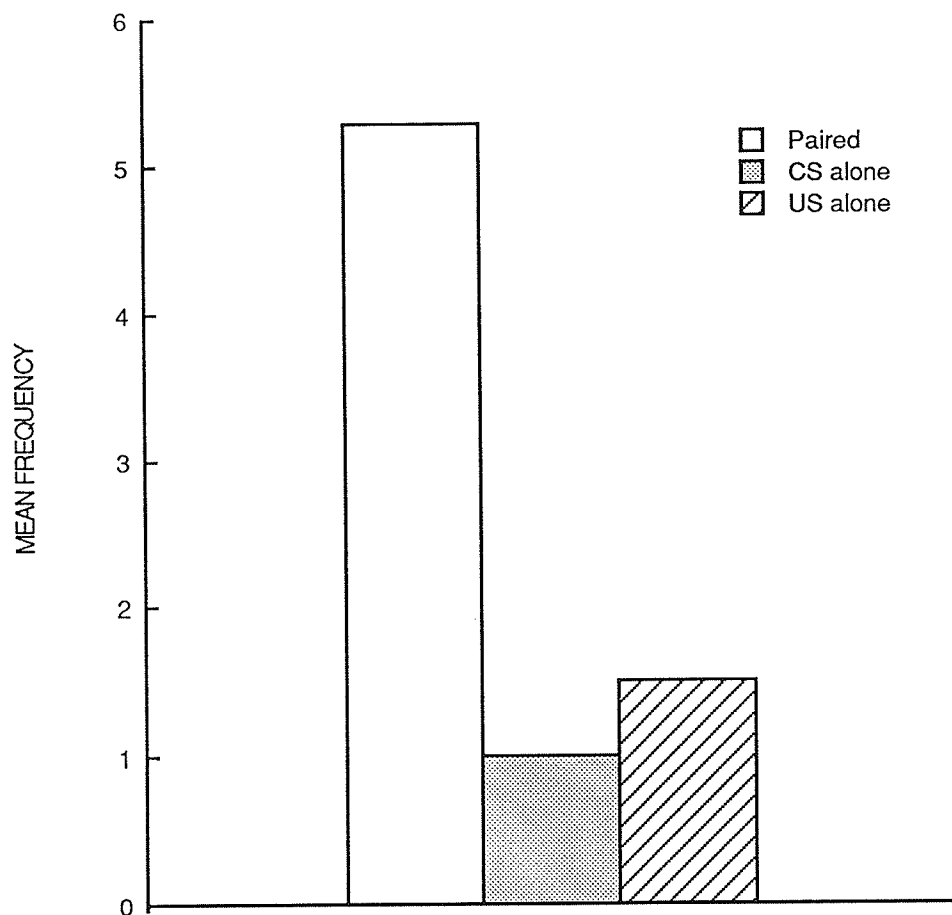




Figure 12. Mean frequency of biting for paired, CS alone, and US alone groups.

# FREQUENCY OF BITING



BITING

Figure 12, subjects in the paired group delivered considerably more bites than subjects in the CS alone or US alone groups. Again, an ANOVA did not find any of the differences between groups to be statistically significant. However, the greater frequency of biting by subjects in the paired group is suggestive of a greater degree of aggression within the paired group, compared to the CS alone or US alone groups.

The relationship between the latency, frequency, and duration of aggressive behaviors was examined through a correlation procedure. Correlations were not carried out for the CS alone group due to the high number of absent values on most dependent variables. The absent values, combined with the small sample size, prevented the computation of meaningful correlations. The resulting correlations for the paired and US alone groups are provided in Appendix B. Figure 13 presents a schematic diagram of the significant correlations between aggressive behaviors for the paired group (top frame) and the US alone group (bottom frame). The size of the boxes in Figure 13 are roughly proportional to the magnitude of the mean score for a particular behavior, with larger boxes signifying larger scores.

For the paired group (top frame), there is a cluster of correlations between the latency, frequency and duration of behaviors in which two opponents are in close proximity to each other (i.e., tail-beating, jaw-locking, and circling). Gill-cover extension and lateral display share fewer significant

Figure 13. Schematic diagram of the significant correlations between the frequency, latency, and duration of aggressive behaviors for the paired (top frame) and US alone (bottom frame) groups. The size of the boxes is roughly proportional to the magnitude of the mean score for a particular behavior. The values within the boxes represent the mean score for a particular behavior in seconds (for latency and duration scores) or in number of occurrences (for frequency scores).



correlations. For the US alone group (bottom frame), the significant correlations between behaviors follow a pattern similar to that of the paired group. For the US alone group, there is a cluster of correlations between the latency, frequency, and duration of tail-beating, jaw-locking, and circling. These behaviors, however, have more connections to the latency of gill-cover extension and the latency and frequency of biting than in the paired group. The clusters of correlations for both the paired and US alone groups are comprised of behaviors that occur in face-to-face combat (i.e., tail-beating, jaw-locking, and circling). Given the occurrence of the clusters, and the fact that display behaviors such as gill-cover extension shared fewer connections (with the exception of the latency of gill-cover extension in the US alone group), the pattern of correlations for both groups suggest an emphasis on face-to-face combat during an aggressive encounter.

The data from both the conditioning and the test phases were characterized by a lack of statistical significance. The exceptions were the significant decreasing linear trend in the CS alone group in the conditioning phase and the significant shorter latency of the paired group on entrance to passage, along with the significant correlations between behaviors in the test phase. However, there is a pattern of non-significant results. Specifically, the paired group appeared to have an advantage over the CS alone and US alone groups on a number of dependent

variables. By chance, any one group would be expected to have an advantage on one third of the dependent variables. A review of the outcomes of the groups on the dependent variables revealed that the paired group had an advantage on 44 percent of the dependent variables, the CS alone group had an advantage on 33 percent of the dependent variables, and the US alone group had an advantage on 22 percent of the dependent variables. To determine whether the observed pattern of outcomes was significantly different from chance, a chi-square test was performed. The results of the chi-square test,  $\chi^2 (2) = 7.34$ ,  $p < .05$ , revealed a significant pattern of outcomes. Therefore, while the variability of the data was too high to obtain statistical significance, the consistent pattern of outcomes provided a basis for the following discussion.

### Discussion

Three goals were sought in the present research. The first goal was to demonstrate Pavlovian conditioning in convict cichlids. The second goal was to show a functional gain of learning. The third goal was to determine whether the conditioned response included a unique aggressive component and was therefore a function-specific conditioned aggressive behavior, or was indicative of a more general alert state. Each of these goals will be discussed in turn. As a general caveat, it should be noted that the absence of statistical confirmation means that much of the following discussion must be considered to be tentative. The basis for the discussion is the consistent pattern of group ordering noted in the result section.

The overall level of conditioned responding in the paired group was low, and did not differ significantly from responding observed in the CS alone and US alone groups. The low level of responding appeared to indicate that little or no learning occurred. However, the failure to obtain clear evidence of learning does not mean that learning did not occur. A distinction must be drawn between learning, the formation of associations, and performance, the demonstration that the associations developed (Kimble, 1961). The performance of conditioned responses (CRs) by the fish would have provided evidence that an association between the light CS and the



conspecific US had been formed. However, the absence of strong indices of conditioning does not necessarily indicate that no associations were formed. Rather, associations may have been formed, but the performance of conditioned responses was prevented by other factors. The factors that may have affected performance include individual differences; competing fear behavior; the relationship between the reproductive cycle and aggressive behavior; the potential effects of pheromones; and, the conditioning parameters. An assessment of the possible contribution of these factors to performance is noted in the following paragraphs.

In an examination of encounters between territory residents and intruders between convict cichlids, Figler and Einhorn (1983) found large amounts of random error produced by individual differences in response to an intruder. Some fish were observed to attack an intruder immediately, while other fish stared at intruders for a long period of time from a distance, or hid behind territory markers. Similarly, the convict cichlids in the present research exhibited individual differences in their responses during the conditioning sessions. While the light CS was on, some fish approached the stimulus panel quickly, while other fish showed no apparent reaction to the CS. Upon stimulus panel door movement and US presentation, some fish approached the panel grid quickly, while others startled and remained motionless on the bottom of the tank near the stimulus panel (freezing

behavior). Thus, the performance of conditioned approach responses was affected by the performance of startling and freezing behavior. It may be that the startling and freezing behavior in the convict cichlids constituted fear behavior that served as a competing response to approach behaviors.

Figler and Einhorn (1983) stated that a frightening stimulus occurring in an already familiar environment elicits fear behavior. The fear behavior inhibits or attenuates the performance of aggressive behavior, although such an effect is often of short duration. In the present research, stimuli that may have caused the startling and freezing behavior in the convict cichlids were the movement of the stimulus panel door, the light CS, and the US fish. The fish may then have made an association between the CS and the frightening stimulus, resulting in the conditioning of fear behavior. It is unlikely that the movement of the stimulus panel door was the cause of startling and freezing behavior, as startling and freezing behavior had dissipated in the fish during the exposure period prior to the conditioning phase. It is also unlikely that the light CS was the cause of startling and freezing behavior as CS alone and paired subjects were observed to approach the light CS during conditioning. Since neither the stimulus panel door movement or the light CS appeared to serve as a frightening stimulus, it may have been that the US fish constituted a fearful stimulus, and caused the occurrence of startling and freezing

behavior. However, because fear and approach behaviors could not be accurately delineated (as described below), it cannot be concluded for certain that the US fish served as a frightening stimulus.

Heiligenberg (1965) has shown that presentation of a frightening stimulus to a cichlid fish, Pelmatochromis kribensis, was associated with a decrease in aggression or an increase in avoidance of an aggression-eliciting stimulus. As such, the behavior produced by the frightening stimulus constitutes a response that competes with the performance of some other response. Thus, the startling and freezing behavior observed in the convict cichlids may have constituted a fear response that competed with the performance of approach responses. However, because of the tank environment, it cannot be determined whether the startling and freezing behavior of the convict cichlids constituted a fear, and thus competing response. The stimulus panel was painted black, and the gravel on the bottom of the tank was dark in color. When seeking to hide, one strategy fish adopt is to blend into their surroundings (Keenleyside, 1979). Since convict cichlids are dark in color, a position on the bottom of the tank near the stimulus panel allowed them to blend into their surroundings. Some fish dug out a home territory near the bottom of the stimulus panel. During conditioning, some fish would either already be positioned near the stimulus panel, or would move to their dug-out territory near the panel. Because approach

to the stimulus panel constituted a conditioned response, the position of the fish near the panel made it difficult to delineate between an approach response or a fear response. In order to be able to conclude that a fish was exhibiting a fear response and thus hiding, the fish's hiding place would have to be separated from the target of approach (the stimulus panel). A method to achieve separation between the hiding place and the target of approach would be to paint the stimulus panel white, and to remove the gravel from the tank. A hiding place could be provided by a dark-colored rock on the far side of the tank. Then, in order to hide, a fish would have to take refuge behind the rock, which would allow for clear delineation between approach and hiding responses. It could then be determined whether the hiding response served as a competing response, and the potential effects of competing responses on the performance of approach responses could be assessed.

Another factor that may have contributed to the low levels of conditioned responding obtained in convict cichlids was the relationship between the reproductive cycle and aggressive behavior. However, for the reasons stated below, it was unlikely that the reproductive cycle was a major factor in the low levels of conditioned responses observed in the convict cichlids.

There is some evidence that the position of a fish in the reproductive cycle (which includes territory defense, preparation of the nest site, spawning or mating, and parental care) can

affect aggressive behavior. Peeke and Peeke (1982) found changes in levels of aggression of convict cichlid pairs that were concurrent with changes in the development stage of the young. The fish in the present study did not have any young present, thereby ruling out changes in aggression caused by the presence of young. Other research has focused upon the role of gonadal hormones in reproductive behavior (e.g., Liley & Stacey, 1983). On the basis of research on an African cichlid Tiapia mariae, Schwank (1980) suggested that aggressive behavior was to some extent governed by endogenous androgen levels. Contrary to Schwank's conclusion, Smith (1969) had concluded that aggressive behavior in centrarchid sunfish (Lepomis megalotis and Lepomis gibbosus) was not dependent on androgen or gonatropin levels, but was influenced more by water temperature and social conditions. In order to assess such conflicting results, Liley and Stacey (1983) suggested that a distinction must be drawn between reproductive and non-reproductive aggression. According to Liley and Stacey, there is considerable evidence to support the role of hormones in all aspects of male reproductive behavior. However, Liley and Stacey stated that non-reproductive aggressive behavior appears to be independent of gonadal control. For example, Johns and Liley (1970) observed that castrated male blue gouramis placed with intact or other castrate males performed agonistic behaviors until a dominance relationship was established. The agonistic behavior of castrates was not observed to differ

qualitatively or quantitatively from that of the intact males. In addition, Liley and Stacey argued that since establishment of dominance, maintenance of territories, and competition for food have been shown in a number of species to occur regardless of age, sex, or season, it is incorrect to assume a hormonal basis for all aggressive behavior.

For the present research, it can be assumed that the convict cichlids were in a non-reproductive state. The reason for this assumption is as follows. Convict cichlids are capable of breeding year round in laboratory conditions (McKaye, 1977). The ability of convict cichlids to breed year round suggests that the presence or absence of suitable mates, the presence or absence of predators, and the availability of food are the primary determinants of breeding in laboratory-held convict cichlids. In the present study, there were no predators and food was abundant. Furthermore, since the fish in the present research were isolated both from females, and, from visual and physical contact with a male conspecific (except during conditioning trials) throughout the research period, it is unlikely that the males were moving through a reproductive cycle. Therefore, the aggressive behavior of the convict cichlids would have to be considered non-reproductive aggressive behavior and as such not likely to be under gonadal control. Consequently, the low levels of conditioned responses obtained in the convict cichlids were not likely due to the effects of reproductive hormones.

Another factor that may have contributed to the low levels of conditioning obtained in convict cichlids was the potential effects of pheromones. Various species of fish have been observed to exhibit a fright reaction when an alarm substance from an injured conspecific is released (Hara, 1971). In addition, fish have been observed to exhibit a fright reaction in response to a predator odor (Hara, 1971). Ingersoll, Bronstein, and Bonventre (1976) found that agonistic displays in male Betta splendens were reduced via chemical remnants of either injured or intact conspecifics. Thus, Betta splendens are capable of reducing some of their aggressiveness in response to chemical factors. An alarm substance released from the skin of a conspecific has been shown to elicit an alarm response of moving to the substrate in zebra danios (Brachydanio rerio) (Suboski, Carty, & McQuoid, 1987). The alarm response in zebra danios has also been shown to be conditionable. Suboski et al. (1987) presented fish with a previously neutral chemosensory stimulus, morpholine, along with an alarm substance. After pairings, the fish were observed to drop to the substrate in response to the morpholine, thereby demonstrating learning. A phenomenon similar to that described by Suboski et al. could have occurred in the convict cichlids. A US fish was moved from its home tank to the stimulus panel enclosure for each conditioning session. It was likely that the movement between tanks constituted a stressful situation for the US fish. Under such conditions, the US fish

may have released an alarm substance that elicited an alarm response, startle and movement to the bottom of the tank, in the convict cichlids. And, similar to the conditioning of alarm responses in the zebra danios, the convict cichlids may have made an association between the previously neutral stimulus, the light CS, and the alarm substance released by the US fish. Then, on later trials the light CS may have evoked a hiding response in the convict cichlids. However, because the potential effects of pheromones could not be assessed in the present research, occurrence of a learned alarm response as described above is highly speculative. Furthermore, both the paired subjects and the US alone subjects responded with threat displays during the US period, which argues against a fear reaction due to pheromones.

The final factor that may have contributed to the low levels of conditioning obtained in convict cichlids was the conditioning parameters. In other species, such conditioning parameters as types of response being conditioned, CS-US interval, CS duration, and CS type have been shown to differentially affect the acquisition of responses.

In aversive classical conditioning, the rate of acquisition of responses has been shown to differ among response systems. Schneiderman (1972) described a study by Yehle (1968) that examined differences in performance among rabbit response systems during aversive classical conditioning. The subjects received



pairings of a tone CS and a shock US. It was observed that decelerative heart rate responses (autonomic responses) occurred almost immediately after CS-US pairings began. In contrast, nictitating membrane responses (somatic responses) did not occur until the second day of acquisition training. According to Schneiderman (1972), during the initial stages of aversive classical conditioning, inhibition of somatic responses, or behavioral freezing, becomes conditioned. Autonomic CRs (e.g., heart rate deceleration) still occur however, because they are compatible with somatic inhibition. As autonomic CRs decrease over time, somatic CRs may then occur. Schneiderman (1972) suggested that it may be that autonomic and somatic CRs reflect the same process, but a specific somatic CR occurs later because it is incompatible with behavioral freezing. An analogous process may have occurred in the convict cichlids in the present research. The startle and freezing behavior of the cichlids may have prevented the occurrence of approach responses. Thus, the startling and freezing behavior and the approach behavior of the fish may have reflected the same learning process. However, because fear and approach responses could not be accurately delineated in the present experiment, such a conclusion could not be substantiated.

Differences in the CS-US interval have also been shown to affect the acquisition of responses in aversive classical conditioning. VanDercar and Schneiderman (1967) found that in

rabbits, heart rate response but not nictitating membrane response became conditioned with a CS-US interval of 6.75 sec, whereas nictitating membrane but not heart rate response became conditioned with a CS-US interval of 0.25 sec.

Effects of CS duration on the acquisition of CRs have been observed in appetitive conditioning. Holland (1980) found that in rats, different forms of CRs were evoked by differences in CS duration. For example, a short duration auditory CS paired with a food US resulted in large amounts of startle and head-jerk behavior and low amounts of magazine behavior. In contrast, a long duration CS paired with a food US resulted in less startle and head-jerk behavior, but more magazine behavior. The magazine behavior of the rats could be conceived as approach behavior, which suggests that a longer duration CS may be positively related to occurrence of approach behavior. Thus, for convict cichlids, it may be that a longer CS duration would result in greater amounts of approach behavior.

The type of CS has been shown to affect the form of the CR in appetitive conditioning. Holland (1977) found that in rats, a CR of head-jerk was evoked by an auditory CS, while CRs of rearing and magazine behavior were evoked by a visual CS. For fish, a CS could be visual, auditory, or chemical. As described earlier, it may have been that a chemical factor acted as a CS and produced startling and freezing behavior in the convict cichlids.

Finally, the qualitative characteristics of associations may be influenced by the choice of behavior being studied. Tait and Saladin (1986) found that both excitatory and inhibitory effects were produced by a common conditioning procedure. Tait and Saladin found that following backward pairings with an aversive (shock) US, a tone CS was an effective punisher of licking in rabbits. This outcome indicated that the CS controlled an excitatory CR. However, retarded acquisition of the nictitating membrane response resulted when forward CS-US pairings were given. This outcome suggests that the CS controlled an inhibitory CR.

The examples described above indicate that the acquisition of CRs can differ across response systems, and can be affected by the conditioning parameters. In the present research, the conditioning parameters may have affected the performance of conditioned approach responses in the convict cichlids. A subsequent pilot study (Appendix C) supported this possibility. The pilot study found that fish which received CS-US pairings in which the light CS remained on throughout the US period exhibited higher levels of conditioned responding than observed in the original experiment. And, fish that received US presentations of 30 seconds (compared to 15 seconds with the original parameters) also showed higher levels of conditioned responding. Thus, it is likely that the conditioning parameters used in the present research were not optimal, and therefore contributed to the low

levels of CRs obtained in the convict cichlids.

Taking into consideration the effects of individual differences, fear behavior and the tank environment, and the conditioning parameters on the levels of conditioned responses obtained in convict cichlids, there are steps that could be taken to achieve better indices of conditioning. The problem of high variability of responding across individuals could be alleviated through the use of a larger sample size. The problem of delineating between fear and approach behaviors could be alleviated by changing the stimulus panel to white and removing the dark gravel from the tank. Finally, the duration of the light CS could be extended throughout the US presentation period, which would also be extended. If the present experiment was repeated with the changes listed above implemented, it is likely that better indices of conditioning would be obtained.

The second goal of the present research was to show a functional gain of learning. A functional gain of learning would be demonstrated if Pavlovian conditioning enabled the paired subjects, compared to the control subjects, to respond faster and with greater aggression than their naive rivals in a signaled encounter. A fish that responds fastest in a signaled encounter will likely have an initial advantage in the encounter. According to Figler and Einhorn (1983), in a territorial dispute between convict cichlids, biting first is a reliable predictor of eventual dominance. Although none of the differences between

groups on the latencies of approach and aggressive behaviors were statistically significant, the pattern of results is suggestive of an advantage for the paired group. Specifically, the shorter latencies of approach behaviors and the greater number of significant correlations between the latencies of approach behaviors in the paired group compared to the CS and US alone groups is suggestive of a greater degree of preparation in the paired subjects. In addition, the shorter latencies of the paired group compared to the US alone group on aggressive behaviors is indicative of an initial advantage for the paired subjects. Once an encounter has begun, the fish that exhibits a greater amount of aggression than its opponent will be the dominant fish. The higher frequency of biting observed in the paired subjects and the greater amount of time spent in their naive rival's territory by the paired subjects compared to the CS alone and US alone subjects is indicative of greater dominance displayed by the paired subjects. Thus, the faster speed and greater aggression of the paired subjects compared to the CS alone and US alone subjects is suggestive of a functional gain of learning. However, due to the lack of statistical confirmation, such a conclusion is preliminary, and in need of further investigation.

The third goal of the present research was to determine whether the conditioned response in the convict cichlids included a unique aggressive component or was indicative of a more general

alert state. Since the conditioned responses consisted only of approach behaviors, and not threat displays of gill-cover extension or lateral display, the conditioned responses observed in the convict cichlids appeared to be indicative of a general alert state. The failure to observe gill-cover extension or lateral display during conditioning may have been in part due to the conditioning parameters that were employed. As noted in the preceding section, the type of conditioned response performed is influenced by the conditioning parameters that are employed. Hollis (1984) suggested that the brief duration of the CS may have been the reason the conditioned responses in the blue gouramis consisted only of fin erection and not tail-beating. Similarly, the occurrence of approach behaviors, but not display behaviors as conditioned responses in the convict cichlids may have resulted from the short duration of the light CS. However, the longer CS duration used in the pilot study (Appendix C) did not result in the occurrence of display behavior as conditioned responses, even though higher levels of approach responses were obtained. A more likely reason for the failure to observe display responses as a conditioned response may be related to the sequence of aggressive behavior in convict cichlids. The usual sequence of aggressive behavior in convict cichlids is gill-cover extension and lateral display, followed by tail-beating, jaw-locking, circling, and biting (Weber & Weber, 1976). However, before engaging in a threat display, a fish must approach an

opponent (or stimulus). Evidence supporting such a sequence comes from the behavior of fish during the conditioning phase and the signaled test encounter. During the conditioning phase approach behaviors only were observed in response to the light CS, while gill-cover extension and lateral display were observed during the US period. During the signaled test encounter, the fish approached and entered the passage, then entered the naive rival's territory, without engaging in display behavior. Only after the fish was close to its naive rival did display behavior and aggressive behavior occur. Thus, the approach behavior of the convict cichlids represented an initial state of arousal or attention that constituted the beginning of a sequence of threat displays and aggressive behavior.

Research conducted with pigeons suggests that approach behavior is strongly controlled by the CS (Eldridge & Pear, 1987) in Pavlovian conditioning. Eldridge and Pear implemented an autoshaping procedure in which a CS (red keylight) was followed by food presentation. Eldridge and Pear observed that pigeons developed approach behavior to the CS at its onset, with key pecks occurring throughout the CS duration. Omission training was then implemented, in which pecks on the key resulted in the omission of food presentation at the end of the CS interval. Eldridge and Pear observed that during omission training, key pecks decreased in probability, but approach behavior to the key was maintained. In convict cichlids, it is likely that the CS is

capable of controlling the occurrence of approach behavior. Other factors, such as visual contact with a conspecific and the potential effects of pheromones, then influence the sequence of displays and aggressive behavior and the outcome of the encounter. Pavlovian conditioning, then, may subserve an arousal/ attention mechanism that functions to prepare a convict cichlid for an interaction.

Hollis (1984) suggested that Pavlovian conditioning may function as a preparatory mechanism by enabling Pavlovian conditioned male gouramis to be more aggressive in a signaled encounter than they would be were the encounter not signaled. Or, it may have been that the CR in Pavlovian conditioned fish represented an early show of strength that produced faster capitulation in unprepared rivals (Hollis, 1984). As such, Pavlovian conditioning would appear to prepare a fish specifically for an aggressive interaction. However, the general nature of the CRs observed in convict cichlids suggests a more general role for the preparatory function of Pavlovian conditioning in fish. It may be that Pavlovian conditioning functions to alert the fish that some biologically significant event (such as the presence of a conspecific or the presence of food) is about to occur. When the event occurs, the Pavlovian conditioned fish is less surprised than a non-conditioned fish. Because it is less surprised, the Pavlovian conditioned fish is likely to have an initial advantage, the form of the advantage



depending upon the type of event.

Hollis (1984) asserted that conditioned fin erection in male blue gouramis represented a function-specific conditioned aggressive behavior. In her prefiguring hypothesis, Hollis hypothesized that the function-specific conditioned aggressive behavior allowed the gouramis to optimize their interaction with a rival. However, since fin erection in gouramis also occurs in food-seeking behavior, Hollis may have been premature in concluding that conditioned fin erection was a function-specific conditioned aggressive behavior. Thus, it was suggested that fin erection in gouramis subserved a general arousal/attention mechanism rather than being a function-specific conditioned aggressive behavior. Although the low levels of conditioned responding in convict cichlids and lack of statistically significant results prevented firm conclusions from being drawn, the present observation that only approach behaviors occurred as conditioned responses was consistent with the hypothesis that the result of Pavlovian conditioning in territorial fish is a general state of arousal/attention as opposed to a function-specific conditioned aggressive behavior. The failure to provide support for the prefiguring hypothesis does not mean, however, that Pavlovian conditioning serves no biological function. It may be that a general alert state, indicated by approach behavior, results in a more aware fish. A more aware fish may then have an initial advantage in an aggressive encounter.

The results of the present study are informative in that they illustrate the need to obtain more concise assessment of Pavlovian conditioning in fish. The results also provide steps to be taken in improving the assessment of Pavlovian conditioning in convict cichlids. The two key steps are changes in the conditioning parameters to produce higher levels of conditioned responses, and changes in the tank environment to allow for accurate identification of behaviors. And finally, although all conclusions are tentative due to the lack of statistical confirmation, the results are informative in that they suggest that the biological function of Pavlovian conditioning in fish is preparatory in nature.

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Appendix A

CORRELATIONS BETWEEN APPROACH BEHAVIORS DURING  
TEST ENCOUNTER FOR PAIRED, CS ALONE, AND US ALONE GROUPS

Table A -1

Correlations Between Approach Behaviors During Test Encounter for Paired Group

	FAP	LAP	DAP	FEP	LEP	DEP	FERT	LERT	DEPT
FAP	-	-0.28	0.99*	-0.38	-0.29	-0.40	-0.32	-0.38	-0.46
LAP		-	-0.34	0.95*	0.99*	0.93*	0.99*	0.95*	0.52
DAP			-	-0.45	-0.35	-0.48	-0.39	-0.46	-0.55
FEP				-	0.96*	0.99*	0.98*	0.99*	0.74
LEP					-	0.93*	0.99*	0.95*	0.54
DEP						-	0.96*	0.99*	0.80
FERT							-	0.98*	0.62
LERT								-	0.76
DEPT									-

NOTE: FAP = frequency of approach to passage  
 LAP = latency of approach to passage  
 DAP = duration of approach to passage  
 FEP = frequency of entrance to passage  
 LEP = latency of entrance to passage

DEP = duration of entrance to passage  
 FERT = frequency of entrance to rival's territory  
 LERT = latency of entrance to rival's territory  
 DEPT = duration of entrance to rival's territory

\*  $p < .05$

Table A - 2

Correlations Between Approach Behaviors During Test Encounter for CS Alone Group

	FAP	LAP	DAP	FEP	LEP	DEP	FERT	LERT	DEPT
FAP	-	0.95	0.99*	0.18	0.94	-0.33	-0.94	-0.84	-0.84
LAP		-	0.98	-0.48	0.99*	-0.61	-0.99*	-0.96	-0.63
DAP			-	-0.30	0.97	-0.44	-0.97	-0.90	-0.77
FEP				-	-0.48	0.98	0.50	0.68	-0.3
LEP					-	-0.61	-0.99*	-0.97	-0.63
DEP						-	0.62	0.78	-0.22
FERT							-	0.97	0.62
LERT								-	0.43
DEPT									-

Note: FAP = frequency of entrance to passage  
 LAP = latency of entrance to passage  
 DAP = duration of approach to passage  
 FEP = frequency of entrance to passage  
 LEP = latency of entrance to passage

DEP = duration of entrance to passage  
 FERT = frequency of entrance to rival's territory  
 LERT = latency of entrance to rival's territory  
 DEPT = duration of entrance to rival's territory

\* p &lt;.05

Table A - 3

Correlations Between Approach Behaviors During Test Encounter for US Alone Group

	FAP	LAP	DAP	FEP	LEP	DEP	FERT	LERT	DERT
FAP	-	-0.16	0.99*	0.01	-0.27	-0.25	-0.40	0.77	0.12
LAP		-	-0.13	0.98*	0.99*	0.99*	0.96*	0.44	0.96*
DAP			-	0.04	-0.24	-0.22	-0.37	0.78	0.14
FEP				-	0.95*	0.96*	0.90	0.59	0.99*
LEP					-	0.99*	0.98*	0.32	0.91
DEP						-	0.98*	0.34	0.92
FERT							-	0.19	0.84
LERT								-	0.67
DERT									-

Note: FAP = frequency of approach to passage  
 LAP = latency of approach to passage  
 DAP = duration of approach to passage  
 FEP = frequency of entrance to passage  
 LEP = latency of entrance to passage

DEP = duration of entrance to passage  
 FERT = frequency of entrance to rival's territory  
 LERT = latency of entrance to rival's territory  
 DERT = duration of entrance to rival's territory

\*  $p < .05$

Appendix B

CORRELATIONS BETWEEN AGGRESSIVE BEHAVIORS DURING  
TEST ENCOUNTER FOR PAIRED AND US ALONE GROUPS



Table B - 1

Correlations Between Aggressive Behaviors During Test Encounter for Paired Group

	FGCE	LGCE	DGCE	FLD	LLD	DLD	FTB	LTB	DTB
FGCE	-	1.00	1.00	-0.22	0.85	0.04	0.57	0.95*	0.13
LGCE		-	1.00	-0.22	0.85	0.04	0.57	0.95*	0.13
DGCE			-	-0.22	0.85	0.04	0.57	0.95*	0.13
FLD				-	0.12	0.94*	-0.39	-0.30	-0.34
LLD					-	0.28	0.72	0.89	0.39
DLD						-	-0.37	-0.10	-0.47
FTB							-	0.79	0.88
LTB								-	0.41
DTB									-
FJL									
LJL									
DJL									
FC									
LC									
DC									
FB									
LB									

Note: FGCE = frequency of gill-cover extension  
 LGCE = latency of gill-cover extension  
 DGCE = duration of gill-cover extension  
 FLD = frequency of lateral display  
 LLD = latency of lateral display

DLD = duration of lateral display  
 FTB = frequency of tail-beating  
 LTB = latency of tail-beating  
 DTB = duration of tail-beating  
 \*  $p < .05$

Table B - 1 (continued)

	FJL	LJL	DJL	FC	LC	DC	FB	LB
FGOE	-0.17	0.79	-0.31	0.21	0.87	0.36	0.40	0.57
LGOE	-0.17	0.79	-0.31	0.21	0.87	0.36	0.40	0.57
DGOE	-0.17	0.79	-0.31	0.21	0.87	0.36	0.40	0.57
FLD	-0.27	-0.37	-0.23	-0.35	-0.35	-0.37	-0.12	0.65
LLD	0.12	0.84	-0.01	0.45	0.88	0.57	0.70	0.79
DLD	-0.48	-0.26	-0.47	-0.46	-0.20	-0.43	-0.17	0.80
FTB	0.70	0.95*	0.59	0.92	0.90	0.97*	0.94*	0.19
LTB	0.12	0.93	-0.02	0.49	0.97*	0.62	0.64	0.50
DTB	0.95	0.71	0.89	0.99*	0.60	0.97*	0.92	-0.09
FJL	-	0.46	0.98*	0.92	0.33	0.85	0.79	-0.27
LJL		-	0.32	0.76	0.98*	0.85	0.85	0.35
DJL			-	0.85	0.18	0.76	0.70	-0.35
FC				-	0.66	0.98*	0.94*	-0.04
LC					-	0.77	0.77	0.41
DC						-	0.96*	0.04
FB							-	0.29
LB								-

Note: FJL = frequency of jaw-locking  
 LJL = latency of jaw-locking  
 DJL = duration of jaw-locking  
 FC = frequency of circling

LC = latency of circling  
 DC = duration of circling  
 FB = frequency of biting  
 LB = latency of biting  
 \* p < .05

Table B - 3

Correlations of Aggressive Behaviors During Test Encounter for US Alone Group

	FGCE	LGCE	DGCE	FLD	LLD	DLD	FTB	LTB	DTB
FGCE	-	0.99*	0.00	0.00	0.00	0.00	0.00	0.12	-0.27
LGCE		-	0.00	0.00	0.00	0.00	-0.02	0.09	-0.30
DGCE			-	0.00	0.00	0.00	0.00	0.00	0.00
FLD				-	0.00	0.00	0.00	0.00	0.00
LLD					-	0.00	0.00	0.00	0.00
DLD						-	0.00	0.00	0.00
FTB							-	0.99*	0.96*
LTB								-	0.91
DTB									-
FJL									
LJL									
DJL									
FC									
LC									
DC									
FB									
LB									

Note: FGCE = frequency of gill-cover extension  
 LGCE = latency of gill-cover extension  
 DGCE = duration of gill-cover extension  
 FLD = frequency of lateral display  
 LLD = latency of lateral display

DLD = duration of lateral display  
 FTB = frequency of tail-beating  
 LTB = latency of tail-beating  
 DTB = duration of tail-beating  
 \*  $p < .05$

Table B - 3 (continued)

	FJL	LJL	DJL	FC	LC	DC	FB	LB
FGCE	0.97*	0.38	0.99*	0.99*	0.31	0.99*	0.17	0.43
LGCE	0.96*	0.36	0.99*	0.98*	0.28	0.99*	0.14	0.41
DGCE	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
FLD	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
LLD	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
DLD	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
FTB	0.22	0.92	0.06	0.10	0.94*	0.06	0.98*	0.89
LTB	0.34	0.96*	0.19	0.22	0.98*	0.18	0.99*	0.94
DTB	-0.05	0.77	-0.21	-0.17	0.82	-0.21	0.89	0.74
FJL	-	0.59	0.98*	0.99*	0.52	0.98*	0.39	0.60
LJL		-	0.45	0.48	0.99*	0.44	0.97*	0.99*
DJL			-	0.99*	0.38	0.99*	0.24	0.49
FC				-	0.41	0.99*	0.27	0.53
LC					-	0.37	0.98*	0.99*
DC						-	0.23	0.49
FB							-	0.96*
LB								-

Note: FJL = frequency of jaw-locking  
 LJL = latency of jaw-locking  
 DJL = duration of jaw-locking  
 FC = frequency of circling

LC = latency of circling  
 DC = duration of circling  
 FB = frequency of biting  
 LB = latency of biting  
 \* p < .05

Appendix C

PILOT STUDY

The observation of low levels of conditioned responding in convict cichlids in the original study may have been in part due to the conditioning parameters used. Thus, a pilot study was conducted in which the CS and US parameters were changed from those used in the original study. For one group, the duration of the light CS was extended to remain on throughout the US presentation. For the second group, the US period was extended to 30 sec. It was expected that these changes would result in a higher level of conditioned responding than those obtained in the original study.

### Method

#### Subjects

The subjects were four adult male convict cichlids. The subjects were selected from laboratory stock and were of similar body length.

#### Apparatus

The apparatus was the same as that used in the original experiment.

#### Procedure

Two of the subjects were randomly assigned to one of two groups. The groups consisted of a CS-duration group and a Long-US group. The housing of the subjects and the pre-exposure period were the same as that of the original study.

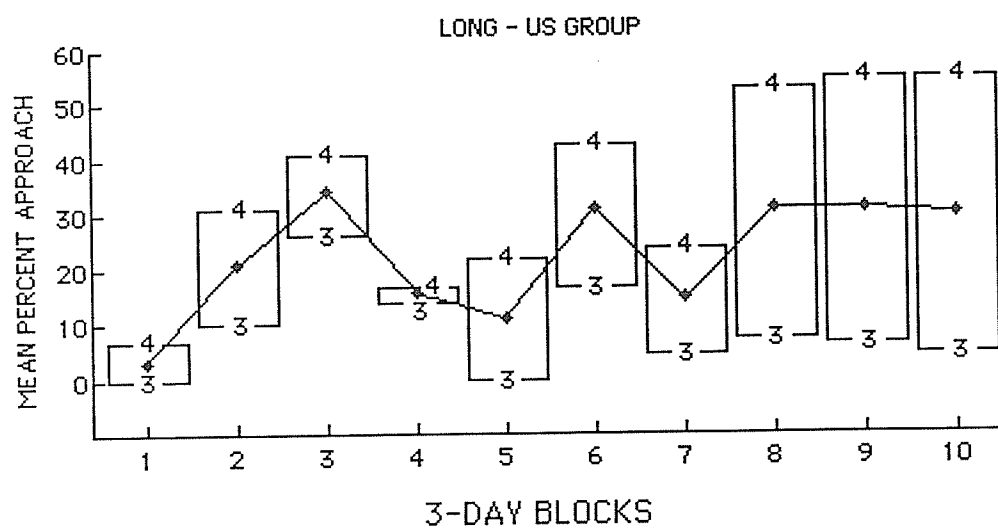
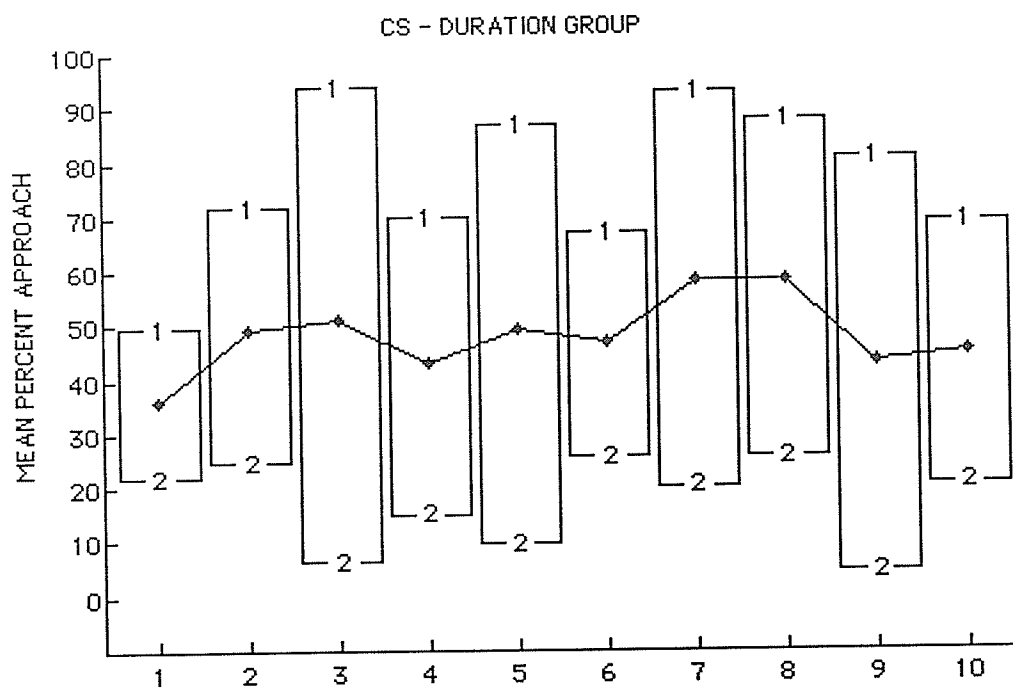
The conditioning procedure was the same as that of the original study except for the changes made in the CS and US parameters. For subjects in the CS-duration group, the light CS remained on throughout the US presentation period. For subjects in the Long-US group, the US period was lengthened to 30 sec. The responses monitored during conditioning were the same as those monitored during the original study.

### Results

ANOVAs were used to analyze the results. As in the original study, only approach behaviors were observed to occur in all subjects. Figure 14 presents the mean percentage approach responses as a function of 10 three-day blocks for the CS-duration group (top frame) and the Long-US group (bottom frame). The mean percentage approach responses of each subject from each group are plotted by subject number. The histograms depict the range of individual subject scores in each group. As can be seen from the top frame, there was a slight increase in responding across blocks for the CS-duration group. Orthogonal components for trend did not find the increase to be significant. However, the scores of individual subjects reveal a high level of responding for subject one. The results of the Long-US group (bottom frame) show an initial increase in responding, then a levelling off of responding. Again, no significant trends were found. However, the scores of subject four depict an increase in

Figure 14. Mean percentage of approach responses as a function of 10 three-day blocks for the CS-duration (top frame) and Long-US (bottom frame) groups.





responding across blocks, which is indicative of the acquisition of a conditioned response.

### Discussion

The pilot study was undertaken in an attempt to increase the levels of conditioned responses obtained in convict cichlids. Although the small sample size of the pilot study prevented statistical confirmation of the results, the change in conditioning parameters appeared to have led to higher levels of conditioned responding than those obtained in the original study. For the CS-duration group, the presence of the light CS during US presentation may have enhanced the association between the CS and US and thereby facilitated the performance of conditioned responses. For the Long-US group, responses were often observed to occur after the initial 15 sec of the US presentation (which comprised the US presentation period in the original study). It may be that the longer US period allowed initial fear reactions to dissipate and the aggressive behaviors to emerge as suggested by Figler and Einhorn (1983). Because the unconditioned response reliably contained approach behavior, a CR consisting of approach behavior, rather than fear behavior, could result as a function of CS-US pairings.

The levels of CRs obtained in the pilot study represent an improvement over those obtained in the original experiment. Thus, in future examinations of Pavlovian conditioning in convict

cichlids, the US presentation period should be at least 30 sec, and the light CS should remain on for the duration of the US presentation.