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The effects of delay in the aggressive display of male Siamese fighting fish: Betta splendens Missoula Montana USA

Baine B. Craft
The University of Montana

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THE EFFECTS OF DELAY IN THE AGGRESSIVE DISPLAY

OF MALE SIAMESE FIGHTING FISH: *BETTA SPLENDENS*

MISSOULA, MONTANA, USA

by

Baine B. Craft

B.S. Mississippi College, USA, 2001

M.A. The University of Montana, USA, 2004

presented in partial fulfillment of the requirements

for the degree of

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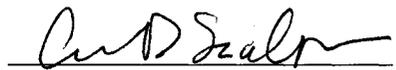
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The Effects of Delay in the Aggressive Display of Male Siamese Fighting Fish: *Betta splendens*

Chairperson: Allen D. Szalda-Petree, Ph.D. _____

Although many studies have been conducted in the area of choice behavior, no extant comparative model or theory completely describes choice behavior. If advances are to be made in the area of choice, the generality of current theories needs to be further examined by studying a variety of species and reinforcements. Due to the relatively small number of studies involving risk-sensitivity and self-control in aquatic species and the ability to investigate valuable reinforcers other than food, additional studies with fish would be beneficial. Specifically, a wealth of data is available regarding the behavior of male Siamese fighting fish (*Betta splendens*) and the species-specific behaviors unique to male *Betta splendens*. Therefore, *Betta splendens* would serve as an excellent animal model with which to examine risk-sensitivity and self-control. To explore self-control and impulsivity using an aggressive display, Experiment 1, ($N = 8$) and risk-sensitivity using an aggressive display, Experiment 2, ($N = 8$), instrumental conditioning of choice behavior was used to determine choice bias in male *Betta splendens*. The results from Experiment 1 revealed a statistically significant choice bias directed toward a self-controlled option. The results from Experiment 2 revealed a statistically significant choice bias directed toward a constant delay or risk-averse option when reward amount remained constant. The results from both experiments are explained in terms of current choice theories and are compared to choice bias in avian and mammalian species when food stimuli are used.

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General Introduction

Although many studies have been conducted in numerous choice situations, a comparative model or theory that accurately describes choice remains elusive. If Shimp, Fremouw, Ingebritsen, and Long (1994) are correct in stating, "One way to make progress on this difficult problem is to systematically increase the temporal and spatial complexity of patterns of simple responses and determine whether empirical phenomena based on the simple responses generalize (96)" then a point of interest that should be considered in examining shifts in choice bias is the response and reward used, as well as, the species studied. A more generalized or complete understanding of current theories or models of choice behavior could be obtained by examining existing models or theories in light of novel response systems, rewards, and species studied.

Several models or theories have been proposed to explain the relationship between foragers' shifts in choice due to extraneous variables and species differences. Molar maximization models, specifically Optimal Foraging Theory (OFT), describe a foraging strategy in which an organism seeks to choose a reward that provides the maximum return per unit time (Pyke, Pulliam, & Charnov, 1977). When presented with an option to choose between two rewards (a constant reward and a variable reward) yielding the same amount, OFT suggests that a forager will be indifferent or will choose the constant reward option. OFT explains such choices as the result of a forager seeking to minimize delay to reward and maximize reward amount, both of which can be experimentally manipulated.

While OFT purports to account for forging decision in animals, several problems with the OFT model become apparent when a forager makes choices that involve variable

or delayed reward. First, OFT does not take into account the limitations or restrictions that prevent an organism from performing optimally (Stephens & Charnov, 1982). Failures in optimal performance are the result of restrictions in the environment or the organisms' evolutionary background (Pyke, Pulliam, & Charnov, 1977). Second, OFT states that a forager seeks to minimize delay in reward. If OFT is an appropriate comparative model to describe foraging behavior, foragers receiving a mean reward amount should be indifferent or choose a constant reward. However, the OFT has been called to question as an adequate description of foraging behavior by experiments in which subjects displayed a choice for a variable reward (e.g., Caraco, Martindale, & Whitman, 1980; Caraco, 1981; Caraco, 1982).

In experiments by Caraco et al., (1980), Caraco (1981), and Caraco (1982), subjects responded differently to variations in food sources as a result of the subject's fitness. For example, Caraco et al., manipulated the food intake of yellow-eyed juncos (*Junco phaeonotus*). Subjects denied the number of seeds per minute required to maintain fitness chose a variable food option as opposed to a constant food option. Subjects provided with the number of seeds per minute required to maintain fitness chose a constant food option as opposed to a variable food option. In other words, subjects with low fitness or a low energy budget chose the variable food option and subjects with a stable fitness or stable energy budget chose the constant food option. The choice of a variable option under any condition or level of fitness deviates from the predictions asserted by the OFT. Thus, in order to provide a more adequate explanation for and description of foraging behavior in situations where a variable option is preferred, the development of a new theory or model was needed.

Depending on the discipline, the problem of predicting and explaining choice in situations where a forager changes or shifts choice preference can be approached in a variety of different ways. For example, ecological and behavioral ethological models (i.e., functional models) have focused on shifts in choice preference based on the potential evolutional history of the species and the functional relevance of shifts in choice. However, psychological models (i.e., mechanical models) of animal choice behavior have been based largely on the use of a relatively uniform set of methods and procedures with a limited variety of species, including rats, pigeons, monkeys, and humans. In addition, the psychological models have focused on the description of shifts in choice based on reward magnitude and delay to reward. A discussion of functional and mechanical models will follow.

Functional Models

Risk-sensitive Foraging Theory was developed to explain a choice bias directed toward a variable or constant option under certain circumstances (i.e., where OFT fails to explain the choice of a variable option). If an organism displays a bias in choice, the organism is said to be risk-sensitive (Smallwood, 1996). For example, as described in Caraco et al., (1980), a new problem arose when subjects' fitness and energy were manipulated. Due to the manipulation of subjects' fitness and energy, subjects' choice shifted between a constant reward and a variable reward. Therefore, choice behavior could not be predicted accurately using OFT.

Using Jensen's inequality, researchers (e.g., Stevens, 1981; Houston, 1991; Smallwood, 1996) examining choice could predict the shift between constant and variable rewards by describing the relationship between fitness and energy as being a

non-linear function. In Jensen's inequality, the function $y=f(x)$, where y represents fitness

and x represents amount of food obtained, demonstrates the interaction between fitness

and obtained food. In other words, as income or the amount of food obtained (x)

increases or decreases, fitness (y) increases or decreases respectively. The prediction of a

forager's expected fitness can be denoted as $E(y)=f[E(x)]$ such that $f[E(x)]=E[f(x)]$ where

the function of x is linear and can be explained by Optimal Foraging Theory. However,

Jensen's inequality states that the function of x is non-linear or $f[E(x)]$ cannot equal

$E[f(x)]$ (see Figure 1 and 2; Smallwood, 1996).

Figure 1a. and 1b.
Jensen's inequality.
Figure 1a and 1b illustrate
fitness on the x-axis
and income on the
y-axis. In Figure 1a, A
(constant option) yields
a higher degree of fitness
than B (variable option).
However, in Figure 1b
B yields higher fitness.

Figure 1a

Figure 1b
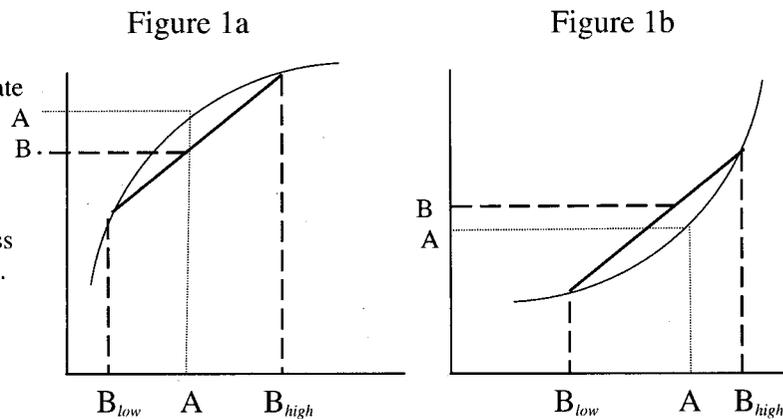
For example, given a hypothetical foraging bout with one choice option delivering

a constant income and another delivering variable income, Jensen's inequality predicts

that a bias will occur due to potential changes in the forager's fitness. If fitness accelerates

negatively with respect to income, Jensen's inequality predicts that the forager will

choose a constant return. However, if fitness accelerates positively with respect to

income, Jensen's inequality predicts that the forager will choose a variable return. While

Optimal Foraging Theory fails to account for such a non-linear relationship, the Daily

Energy Budget Rule (DEB) assumes that the relationship between fitness and energy is

non-linear.

The DEB rule makes the assumption that foraging bouts provide an organism with an amount of energy to survive until the organism can forage again, given an interruption in foraging (for example, overnight) (Houston, 1991). If the foraging bout begins with an organism possessing some initial energy reserve x, then the organism will have to forage for a specific amount of time (T) at some mean rate (μ) until the amount of energy required (R) to survive is obtained. Thus, a forager with a positive energy budget is expressed as $x + \mu T > R$, and a forager with a negative energy budget is expressed as $x + \mu T < R$.

As a forager reaches a negative energy budget, the DEB rule describes the organism as seeking a reward with the greatest amount of return despite the variability or delay of the reward (risk prone; see Figure 2). On the contrary, organisms with a positive energy budget will choose a constant reward in order to maintain a positive energy budget state (risk averse; see Figure 1) (Caraco, 1980). For example, Barnard and Brown (1985) manipulated the food intake of common shrews (*Sorex araneus L.*). In their experiment, common shrews were kept at a negative energy budget by depriving them of the number of worms required to maintain a stable energy budget. Shrews in a negative energy budget chose a reward with the greatest amount of return despite the variability or delay to the reward, in other words, a risk prone foraging strategy. Contrary to the shrews with a negative energy budget, shrews given the number of worms to maintain a positive energy budget chose a constant reward in order to maintain that economic state, in other words, choosing a risk averse foraging strategy. Due to organisms' (such as shrews) susceptibility to variations in energy budget, shifts in choice due to economic state, explained by the DEB rule, can be accurately predicted using the z-score model.

The z-score model predicts that the forager will attempt to minimize the probability of a deficiency in calories (Stephens, 1981). In other words, the z-score model describes an organism (usually small avian or mammalian species) in a positive or negative energy budget, as trying to postpone starvation. If the forager is attempting to minimize a deficiency in calories, the forager will be attentive to the mean return and the variability of rewards. If presented mathematically, the reward required for survival (R) is subtracted from the mean reward (μ) and is divided by the standard deviation of the reward (σ) or $z = (R - \mu)/\sigma$; $\mu = R - z\sigma$ (Stephens & Paton, 1986). Despite predictions made by the z-score model and empirical validations of the DEB rule, researchers (e.g., Gibbon, 1977; Kacelnik & Bateson, 1996) have argued that the DEB rule fails to sufficiently describe foraging behavior.

Kacelnik and Bateson (1996) argued four points in which the DEB rule fails to account for various phenomena demonstrated by foragers. First, the DEB rule, as presented by Stephens (1981), assumes that a forager will choose a strategy, such as risk averse, and will not change that strategy for the remainder of the day. The DEB rule fails to take into account the possibility of the forager changing strategies as the organism's energy budget changes, which is a likely possibility if the organism receives a large return as the result of choosing the variable option. Second, the DEB rule assumes that some minimum caloric level must be met before foraging is interrupted by instances such as nightfall. The DEB rule does not take into account the possibility of a forager that is required to continuously forage such as several small mammalian or avian species. For example, if a forager does not achieve a positive mean net gain, the forager is forced to continue foraging at the risk of starvation. The third problem, the DEB rule fails to

account for any energy expenditure directed toward any behavior other than foraging. For example, the DEB rule describes a static environment with no competing behaviors such that an organism required to care for young, defend a territory, compete for mates or other behaviors that would deplete energy reserves might not be accurately described. Finally, the DEB rule fails to explain variations in delay to reward. For example, if a forager experiences a run of bad luck by choosing the variable option (returning only a small reward amount), the delay to reward will increase until the variable option returns a large reward amount.

Mechanical Models

Matching law predicts that an organism will make choices for a specific option relative to the magnitude of reward delivered (Herrnstein, 1961). For example, in situations where choice options vary in reward magnitude and the delay to reinforcement is constant across choice options, the matching law predicts that the forager will make choices based on the magnitude of reward delivered for each choice option. In situations where the choice options are a larger but delayed reinforcer or a smaller and immediately available reinforcer, matching law would predict a choice bias directed toward the option delivering the larger reward, albeit delayed. However, many species display a choice bias for the smaller and immediate option and thus, suggesting that delay, rather than magnitude, determines choice. By amending the matching law to include a bias coefficient, matching law can predict choice in situations where a choice bias, undermatching, or overmatching would be observed (Baum, 1974; Baum, 1979).

Similar to the matching law, the delay-reduction hypothesis (Fantino, 1969) and the variance discounting hypothesis (Real, 1980) predicts choices based on the delay to

reinforcement and the variability in the delivery of a reinforcer, respectively. If delay to reward is relatively low or if the variability in the delivery of the reinforcer is minimal, the discounting value will be relatively low. However, as delay to reward becomes lengthy or as the reinforcer becomes more variable, the reward value will eventually begin to depreciate; therefore, the discounting value increases. For example, when presented with two choices, one with a minimal delay relative to the reward magnitude and another with a large delay relative to the reward magnitude, the delay-reduction hypothesis would predict a choice preference directed toward the reward option with minimal delay. However, as delay is increased relative to the reward magnitude, choice could be expected to shift. In situations where choice options vary in either reward magnitude or the delay to reinforcement, the variance discounting hypothesis would predict that a choice preference would be observed based on the variance associated with a particular choice option. For example, when presented with two choice options that yield the same mean, the variance discounting hypothesis would predict that the forager would display a choice bias for the option with the least variance.

Scalar Expectancy Theory (SET) was proposed as another plausible explanation for foraging behavior. The SET describes the forager as choosing a reward option based on two principles. First, a forager seems to make a choice based on the expectation of a reward where the expectation of a reward can be described as an increase or decrease in anticipation for the reward. This anticipation or expectation is contingent on the delay to reward and could be expressed as an exponential function but, if delay to reward becomes lengthy, the reward value depreciates or is discounted. In other words, expectation can be described as increasing hyperbolically as delay to reinforcement increases (Gibbon,

1977). For example, if delay to reward is relatively low, then the discounting value will be relatively low. However, as delay to reward becomes lengthy the reward value will eventually begin to depreciate, therefore, the discounting value increases. Second, SET explains a forager's choice based on the value assigned to a reward option (Kacelnik & Bateson, 1996). To discuss the value assigned to a reward option, a description of Weber's Law is necessary.

Weber's Law states that any noticeable difference in an event produces a record of the event. The difference between events is referred to as a Just Noticeable Difference. In light of Weber's Law, SET explains an organism choice, given the option between two rewards that deviate a Just Noticeable Difference, as being contingent on the differential value associated with each option. For example, the forager associates a value with a reward based on the dissimilar quality or quantity of the two reward options. If a forager associates a greater value to one reward option over another, the organism should choose the more valuable reward as predicted by SET.

SET predicts that an organism will associate a higher value with a food option that returns a constant quantity of food with a constant delay over a food option that has a variable quantity and constant delay. On the contrary, an organism will associate a higher value with a food option that returns a constant reward when delay to reward is constant over a food option that has a constant return and a variable delay (Kacelnik & Bateson, 1996). Therefore, a forager's behavior is not completely contingent on nor can it be explained by the organism's fitness or energy budget, but by the forager's record of events (events such as delay to reward or variability in reward) in which a desirable reward was received (See Figure 2). Several experiments provide evidence to support the

predictions made by SET (e.g. Bateson & Kacelnik, 1995, 1997, 1998; Kacelnik &

Bateson, 1996).

Figure 2a and 2b
Scalar Expectancy. Figure 2 illustrates expectation on the y-axis and delay to reward on the x-axis.

a. Fixed Option

b. Variable Option
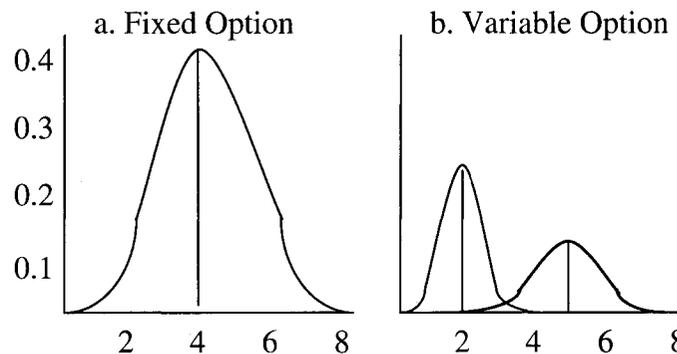
All the aforementioned theories or models provide plausible explanations or

predictions for foraging behavior in specific foraging situations, but researchers have

failed to agree on theories or models that generalize across various choice situations and

describe the ultimate causes of foraging behavior. Given that explanations or predictions

about proximate causes provide only little indication of the ultimate causes for foraging

strategies, determining ultimate causes for choice behavior such as self-control and risk-

sensitivity can only be ascertained by attempting to generalize current theories or models

to new foraging situations. By conducting further studies using different species, the

potential to generalize current theories to other behaviors or species becomes more

probable. In addition, by making these comparisons and expanding the generality of

proximate explanations, development of a unified theory of foraging becomes more

probable.

Comparatively, numerous studies have been conducted with a variety of avian and

mammalian species in both self-control and risk-sensitivity; however, few studies have

been conducted to determine risk-sensitivity or self-control in aquatic species. In light of

the relatively small number of studies involving foraging in aquatic species, Siamese

Fighting Fish (*Betta splendens*) would make an excellent model with which to study self-control and risk-sensitivity for several reasons. First, a wealth of information is available on this species based on research investigating responding under a variety of situations. Second, due to the unique species-specific reproductive behaviors of male *Betta splendens* (Betta), the investigation of reinforcers other than food would be possible. Finally, by using male Betta as subjects to explain the properties governing self-control and risk-sensitive behavior, the generality of self-control and risk-sensitivity could be expanded to include a greater number of aquatic species.

Male Betta splendens and Aggressive Display

Betta are a member of the Anabantidae family and inhabit shallow pools of stagnant water in lower Asia. As the water recedes at the end of the rainy season, male Betta establish and vigorously defend territories. Since the water in their environment is not oxygenated, Betta and related species evolved a labyrinth organ. Compensating for their underdeveloped gills, Betta use the labyrinth organ to obtain oxygen. Male Betta also use the labyrinth organ to mix air, gulped from the surface of the water, with saliva and mucus to form bubble nests. Male Betta construct bubble nests (a mass of bubbles) on the surface of the water (Braddock & Braddock, 1959; Bronstein, 1981; Hogan, 1961).

In order to build a bubble nest, successful males must not only establish, but also maintain suitable territories. For example, after opposing males are driven away, the male Betta establishes a territory in which he builds a bubble nest. By driving away other males, the chances of reproduction increase for the defending male. It is believed that females select mates based on the quality of territories and nesting sites (Hogan, 1961). After building a bubble nest, the male Betta has the possibility of mating with a female

and tending to the eggs he places in the bubble nest after fertilization (Robertson & Sale, 1974).

The mechanisms by which male Betta learn to respond aggressively are not completely understood despite various attempts (c.f. Hollis, 1997). In addition, the exact mechanisms that constitute the reinforcing properties of an aggressive display remain elusive (e.g., Bols, 1976; Bols & Hogan, 1979; Hollis, 1984; Thompson, 1963). However, many researchers have studied a variety of stimuli that reinforce the aggressive display characteristic of male Betta, as well as, influence the choice preferences of male Betta (e.g., Robert & Sale, 1974; Thompson & Sturm, 1965a). In particular, certain qualities of various stimuli (e.g., colors, shapes, movement, etc.) appear to play a vital role in determining the reinforcing properties and choice preferences of such a compound stimulus.

Using male Betta, Thompson and Sturm (1965a) conducted an experiment to study the effects of different colored models, styled after a conspecific, as reinforcers in an operant conditioning experiment. Thompson and Sturm presented one green, one red, or one blue model fish to experimental subjects performing an operant response. Betta swam through a hoop to receive the presentation of a model in the shape of a live male Betta. Thompson and Sturm suggested that the subjects responded differently to different colored models. For example, red Betta responded more aggressively to green or blue models than red models. In addition, Thompson and Sturm (1965b), using classical conditioning, indicated a significant difference between subjects' aggressive response to different color stimuli. Thus, Betta responded to and reacted differently toward specific colors.

In addition to responding differently toward color, male Betta responded differently to models with different shapes and body patterns (Robertson & Sales, 1974). Robertson and Sales studied Betta display toward eight different models comprising of specific shapes and body patterns. Betta displayed aggressive, submissive, or reproductive behavioral responses to models styled after male or female Betta. The model styled after an aggressive male featured long fins, raised opercula, and no body pattern. Subjects displayed the most aggressive behavior in response to the characteristics of the model styled after an aggressive male. In addition, Robertson and Sales (1974) noted that a subject's display toward an aggressive male model of a Betta was indiscernible from a display toward a live conspecific. The absence of any of these features (for example, short fins or a patterned body) resulted in a different response from the subject. Therefore, the results of this experiment suggested that male Betta displayed aggressive behavior in the presence of certain stimuli (e.g., shape and body pattern).

Aside from the importance of coloration, shape, and body pattern, Bols (1976) explained the importance of the stimulus movements to influence choice preference. In three separate experiments, Bols divided subjects into two groups, one given the option to choose a live conspecific and another given the option to choose a Paradise fish (*Macropodus opercularis*, a related species). Bols used a submerged T-maze to determine choice. In the first experiment, Betta chose between a conspecific and a nonconspecific (an empty container). In the second experiment, Betta chose between a conspecific and a nonconspecific (a marble). Finally, in the third experiment, Betta chose between a displaying conspecific and a nondisplaying conspecific. In the first two experiments, subjects chose a conspecific with a higher frequency than the nonconspecific. In the final

experiment, subjects chose the displaying conspecific with a higher frequency than the nondisplaying conspecific. Bols suggested that conspecifics were more reinforcing than nonconspecifics due to the conspecific's display. In other words, a conspecific performed specific movements that were lacking in the nonconspecific's display (Bols, 1976; Bronstein, 1985).

From review of the previously discussed studies, it can be deduced that aggressive display and choice preference in Betta are contingent on stimulus color, shape, body pattern, and movement. The most reinforcing stimuli are those that contain all characteristics mentioned above, in other words, the reinforcer is a compound stimulus. Both a mirror presentation and the presence of a live conspecific possess all the attributes of the compound stimulus. The use of live conspecifics or mirror presentations as stimuli has been a common practice in eliciting and reinforcing aggressive behavior in Betta (e.g., Bols & Hogan, 1979; Bronstein, 1985; Craft, Velkey, & Szalda-Petree, 2003; Hollis, 1984; Thompson, 1963).

Self-control in Male Betta splendens

Self-control is defined as the choice of a larger but delayed reinforcer over a smaller and immediately available reinforcer while the opposite choice has been defined as impulsivity (Ainslie, 1974; Logue, 1981; Rachlin & Green, 1972). A relatively wide literature exists on various factors that influence self-controlled and impulsive choice in humans (Forzano & Logue, 1994; Logue, 1998; Logue, Forzano, & Tobin, 1992; Mischel, Ebbesen, & Zeiss, 1972; Millar & Navarick, 1984; Mischel, Shoda, & Rodriguez, 1989) and pigeons (Ainslie, 1974; Chelonis, King, Logue, & Tobin, 1994; Grosch & Neuringer, 1981; Logue, Rodriquez, Pena-Correal, & Mauro, 1984; Mazur,

1994; Mazur & Logue, 1978; Rachlin & Green, 1972). Overall, results from studies using human subjects have found a general bias towards self-control. This self-control bias signifies that choice is largely controlled by the relative magnitude of the reward. In contrast, a general impulsive bias has been demonstrated for most non-human animals examined, signifying that choice is controlled by the relative delay to reward.

The choice between self-control and impulsivity in specific situations, such as the aforementioned experiments, potentially reflects each species' specific biological system of responding in that given situation (Collier, 1981; Green & Estle, 2003). That is, the choice bias observed for a given species may be the result of both a specific evolutionary history and situational variables. For example, in most experiments, the delay for a self-controlled choice is six seconds while the delay for an impulsive choice is 0.1 seconds. Given the methodological and procedure constraints of these experiments, the generic choice process for any species cannot be globally categorized as self-controlled or impulsive. For example, studies have revealed shifts in choice bias as the result of variability in delay to reinforcement (Chelonis, et al., 1994), increased effort requirements (Chelonis, Logue, Sheehy & Mao, 1998), reinforcer value (Grosch & Neuringer, 1981), precommitment (Ainslie, 1974; Rachlin & Green, 1972) and fading (Logue, 1981; Logue, et al., 1984; Mazur & Logue, 1978). In addition, by implementing a competing or distractor stimulus during the inter-trial interval or the delay to reinforcement in the self-control option, choice bias shifts from impulsive to self-controlled (Grosch & Neuringer, 1981; Logue & Pena-Correal, 1984; Mazur, 1994; Mischel, et al., 1972).

It is necessary to note that the bulk of the animal literature on self-control is based on results from studies using pigeons as subjects. However, even though limited, the literature investigating self-control in mammalian species tends to show a general impulsive choice bias pattern similar to the bias typically observed with pigeons (Boehme, Blakely, & Poling, 1986; Chelonis, et al., 1998; Eisenberger, Weier, Masterson, & Theis, 1989; Green & Estle, 2003; Kararek & Collier, 1973; Tobin, Chelonis, & Logue, 1993; Tobin & Logue, 1994; Flora & Workman, 1995; van Haaren, van Hest, & van de Poll, 1988), with the exception of two experiments involving macaque monkeys in which nearly exclusive self-control was observed (Szalda-Petree, Craft, Martin, & Deditius-Island, 2004; Tobin, Logue, Chelonis, Ackerman, & May, 1996).

To date, no studies in aquatic species have attempted to examine choice bias where the choices were a long delay, large reward versus short delay, small reward. Additionally, all studies examining self-control and impulsivity have used food reinforcement. Using Betta as subjects in which to study self-control and impulsivity could make the existing literature regarding self-control and impulsivity research more comprehensive.

Currently, no studies in self-control and impulsivity have been conducted using male Betta. However, in a study by Lattal and Metzger (1994), male Betta responding, directed toward a 15 s mirror presentation, decreased as delay to reinforcement increased from 0 s to 10 s and 10s to 25 s delay. This study is consistent with the operant responding observed in mammalian and avian species being provided with food reinforcement such that, as delay increased, operant responding decreased. Results from

this experiment revealed that Betta were sensitive to delay to reinforcement when the reinforcement was an aggressive display. Therefore, it could be possible that Betta would display a choice bias in a self-control procedure when using aggressive display as reinforcement.

<center>Experiment 1</center>

To explore self-control and impulsivity in the aggressive display of Betta, instrumental conditioning of choice behavior was used to determine choice bias directed toward access to a mirror image. It was predicted that choices would significantly differ from chance performance.

Method

Subjects. The subjects ($N=8$) were healthy adult male Siamese fighting fish (*Betta splendens*) obtained from a local supplier. The naïve subjects' length averaged 6 cm, and the fish were red or blue in color.

Apparatus. The apparatus was a modified T-maze similar to the apparatus used in the experiment by Bols (1976). The T-maze (see Figure 1 for diagram of T-maze apparatus) consisted of a start box (20 x 5 x 11 cm), goal box (20 x 5 x 11 cm), and a choice chamber (10 x 5x 11 cm). The T-maze was submerged in a tank (65 x 45 x 15 cm; approximately 30 L). Each tank consisted of a gravel floor, a temperature gauge, a submerged tank heater, an air stone, and a T-maze. All latency measures were recorded using a digital stopwatch.

Subjects were housed in the entire T-maze with the exception of the three sessions each day (see Figure 1, T-maze between sessions). The water used in the apparatus was de-chlorinated before subjects are introduced and water temperatures were regulated at

25 °C throughout the experiment. Subjects were fed eight Betta Baby Pellets (Hikari,

Himeji Japan) per day, two pellets after the 8 a.m. and 12 p.m. session and four pellets

after the 4 p.m. session. The light cycle was maintained 12 h : 12 h light/dark cycle.

Procedure. The experiment consisted of three sessions each day (8 a.m., 12 p.m.,

4 p.m.) with two trials per session for a total of six trials/day. The two trials were

delivered approximately 20 min apart. For all trials, subjects swam away from the

researcher (see Figure 1, T-maze during sessions).

To ensure that each subject experienced both choices, all subjects were exposed to

forced choice trials. Forced choices were established by blocking one of the choice

options, leaving the opposite unimpeded. The order of exposure to the reward options in

the forced choice trials was counterbalanced to eliminate any potential primacy or

recency effects. The first day consisted of only forced choice trials (six forced choice

trials total). During the forced choice trials, subjects were forced to choose either the

longer, larger option or the shorter, smaller option and then the alternate option on the

subsequent trial. For the remainder of the experiment, the first two trials of each day were

forced choice trials. Following the forced choice trials in the 8 a.m. session, subjects were

presented with two free choice trials in the 12 p.m. session and two free choice trials in

the 4 p.m. session. During the free choice trials, subjects were allowed to choose from

both options.

The two choice options consisted of a short delay, small reward choice (i.e.,

impulsive) and a long delay, large reward choice (i.e., self-control). The impulsive option

resulted in a delay of 0.1 seconds followed by the delivery of 2 seconds exposure to a

mirror. The self-controlled option resulted in a delay of 15 seconds followed by the

delivery 15 seconds of exposure to a mirror. The side for stimulus presentation was counterbalanced across subjects to eliminate any potential side bias. Choice was recorded for each trial and continued until there was no upward or downward monotonic trend in choices across five consecutive days.

At the beginning of each trial, the subject swam into the start box and the start box guillotine door was put into place. Once the choice door and mirrors were in place in the goal box, the start box guillotine door was raised, beginning the trial and the start box latency measure. After leaving the start box, the subject entered the choice chamber ending the start box latency measure and beginning the choice latency (i.e., the measurement of the amount of time taken until a choice was made). Once the subject swam through a choice door in the goal box, the choice latency measure ended. The subject was then presented with the delay to and exposure to the mirror relative to the choice made. Following the exposure to the mirror, the subject was returned to the start box and remained there until the next trial began, or if both trials had been completed, the subject was allowed to swim freely throughout the maze.

Results

The number of self-control choices was averaged across the last five days for each subject. A one-sample t-test conducted on the mean number of self-control choices revealed a significant bias for the long delay and large reward option compared to chance performance ($t(7) = 2.91, p < .05, d = 1.03$).

Table 1.

Number of choices (20 trials total) averaged across the last five days and median choice latencies (40 trials total) averaged across the total 10 days.

	Choices		Choice latency (sec)	
	Mean	SEM	Median	IQR
Self-control	15.6		4.81	25th Percentile = 3.77 75th Percentile = 6.14
		0.10		
Impulsive	4.4		5.04	25th Percentile = 4.53 75th Percentile = 15.82

Discussion

In the current experiment, male Betta displayed a self-controlled choice bias. In other words, a larger duration of exposure to a mirror with a longer delay to exposure to a mirror was preferred over a smaller duration of exposure to a mirror with a shorter delay to exposure to a mirror. Clearly, subjects in the current experiment were more sensitive to manipulations in duration of exposure to a mirror image than to the delay to the mirror exposure. For example, if delay to reinforcement was controlling choice in the current experiment, subjects' should have responded more toward the impulsive option or the option with the lesser delay to reinforcement. In light of the observed choice preference for the larger reward amount (despite a lengthy delay) in the current experiment, the present experiment can be explained by stating that the magnitude of the reward or the duration of exposure to a mirror was controlling choice, as opposed to delay.

The sensitivity of an organism to the magnitude or duration of the presentation of a mirror image (a pseudo-sexual, aggressive, social encounter) as a type of reward is unique to the literature regarding self-control and impulsivity. No studies in the area of

self-control and impulsivity have examined the effects of differential delays to and magnitude of a social encounter on choice preference. However, the current experiment reveals conclusive evidence to support a bias in choice between a self-controlled and impulsive option where the reinforcement is exposure to a mirror image or a social encounter.

The choice bias observed in the present study can be explained by assuming that the aggressive responding or the social encounters of male Betta functions under the same parameters as foraging strategies for food. Such a choice bias for food rewards have been observed in other species using methodology similar to the current study (Ainslie, 1974; Chelonis, et al., 1994; Chelonis, Logue, Sheehy & Mao, 1998; Grosch & Neuringer, 1981; Logue, 1981; Logue & Pena-Correal, 1984; Logue, et al., 1984; Mazur, 1994; Mazur & Logue, 1978; Mischel, et al., 1972; Rachlin & Green, 1972; Szalda-Petree, Craft, Martin, & Deditius-Island, 2004; Tobin, Logue, Chelonis, Ackerman, & May, 1996).

Provided that the aggressive responding of male Betta functions under the same parameters as foraging for food and is, therefore, analogous to food reinforcement, the sensitivity of Betta to the magnitude or duration of the presentation of a mirror in the current experiment is also unique in that a self-control choice bias has only been observed in relatively few experiments using food reinforcements (Szalda-Petree, Craft, Martin, & Deditius-Island, 2004; Tobin, Logue, Chelonis, Ackerman, & May, 1996). The bulk of the self-control and impulsivity literature typically reveals a choice bias directed toward the impulsive option in pigeons (Ainslie, 1974; Chelonis, King, Logue, & Tobin, 1994; Grosch & Neuringer, 1981; Logue, Rodriquez, Pena-Correal, & Mauro, 1984; Mazur,

1994; Mazur & Logue, 1978; Rachlin & Green, 1972) and rats (Boehme, Blakely, & Poling, 1986; Chelonis, et al., 1998; Eisenberger, Weier, Masterson, & Theis, 1989; Green & Estle, 2003; Kararek & Collier, 1973; Tobin, Chelonis, & Logue, 1993; Tobin & Logue, 1994; Flora & Workman, 1995; van Haaren, van Hest, & van de Poll, 1988). It is only when alterations in procedures are made such as variability in delay to reinforcement (Chelonis, et al., 1994), increased effort requirements (Chelonis, Logue, Sheehy & Mao, 1998), reinforcer value (Grosch & Neuringer, 1981), precommitment (Ainslie, 1974; Rachlin & Green, 1972), or fading (Logue, 1981; Logue, et al., 1984; Mazur & Logue, 1978) that a shift from impulsivity to self-controlled is observed. Therefore, the observed choice bias in the current experiment is inconsistent with the findings from previous research investigating the effects of delay to reinforcement.

The choice between self-control and impulsivity in specific situations, such as in the current experiments, potentially reflects species' specific biological system of responding in that given situation (Collier, 1981; Green & Estle, 2003). That is, the choice bias observed for male Betta may be the result of both a specific evolutionary history and situational variables. For example, males Betta must not only establish, but also maintain suitable territories in which to mate. By driving away other males, the chances of reproduction increase for the defending male. Additionally, it is believed that females select mates based on the quality of territories and nesting sites (Hogan, 1961). After building a bubble nest, the male Betta has the possibility of mating with a female and tending to the eggs he places in the bubble nest after fertilization (Robertson & Sale, 1974). By displaying a choice preference for a larger amount of exposure to a mirror, the subject or defending male may be increasing the probability of establishing a quality

territory in which to build a bubble nest and, in turn, increasing the probability of reproducing. Therefore, such a choice preference could be the result of male Betta specific evolutionary history.

Given the evidence from the present study, it is possible that the use of a mirror image or conspecific as a reward could provide a beneficial model in which to examine social encounters under various contingencies and subsequently, further expand current theories of choice that are based largely on food rewards to include social encounters. By further expanding current theories to include explanations of rewards other than food, such as social encounters, the better researchers and clinicians could be at predicting and controlling more nebulous choice situations. Future studies should attempt to determine the factors that contribute to shifts in choice for exposure to a mirror image.

Risk-Sensitivity in male Betta splendens

Much like other small avian and mammalian organisms studied in risk-sensitivity experiments using food rewards, fish have been shown to be affected by variations in reward options (i.e., Roche, Dravet, Bolyard & Rowland, 1998). In addition, Jack Dempsey cichlids, bitterlings, and spined sticklebacks have been shown to shift from risk averse to risk prone strategies as the result of changes in energy budgets, thus exhibiting risk-sensitive behavior (e.g., Roche, Dravet, Bolyard & Rowland, 1998; Young, Clayton, & Barnard, 1990; Croy & Hughes, 1991).

Roche, Dravet, Bolyard and Rowland (1998) examined the choice bias in Jack Dempsey cichlids, *Chichlasoma octofasciatum*. A stable energy budget was determined by allowing subjects to freely feed, measuring the number of food pellets consumed per hour, and then manipulating their energy budget by controlling the number of pellets

consumed prior to and during experimentation. Subjects maintained on a positive energy budget were given a choice between a constant food reward and a variable food reward in both a discrete-choice treatment and a free-choice treatment. Subjects preferred the constant food reward as opposed to the variable food reward in both the free-choice and discrete-choice treatments. Therefore, male Jack Dempsey cichlids responded in a risk-averse manner when on a positive energy budget compared to a negative energy budget.

Young, Clayton, and Barnard (1990) revealed risk-sensitive behavior in male bitterlings, *Rhodeus sericus* using a free choice design. Before the experiment began, one group of subjects was deprived of food for three hours, which maintained the subjects at or above the required energy budget (positive energy budget). Subjects with a positive energy budget choose a constant food reward (risk averse) as opposed to a variable food option, which yielded a mean of one pellet. In another group, subjects were deprived of food for 48 hours before the experiment began. Subjects with a negative energy budget chose the variable food reward (risk prone). Therefore, male bitterlings responded in accordance with predictions made by the Risk-sensitive Foraging Theory and the Daily Energy Budget rule.

Finally, in an experiment by Croy and Hughes (1991), spined sticklebacks (*Spinachia spinachia*) were deprived food for 24 hours before the beginning of the experiment. Subjects were then allowed to sample two food reward sites, one containing a constant reward and the other site containing a variable reward. Researchers revealed that subjects responded differently toward food reward sites as the result of energy reserves. At the beginning of the sampling procedure, subjects with a negative energy budget chose to sample the variable food site as opposed to the constant food site. As

subjects became satiated, choice of food site shifted to the constant food site. Therefore, male spined sticklebacks responded in accordance with the Risk-sensitive Foraging Theory and the Daily Energy Budget rule. Additionally, provided that the exposure during daily trials has determined an energy budget for aggressive display, the daily energy budget rule could explain a choice bias for the constant or variable option such that a variable choice bias would reflect a negative energy budget and a constant choice bias would reflect a positive energy budget.

To date, no studies in aquatic species have attempted to examine the effects of a variable versus a constant delay when reinforcement was held constant. Additionally, all risk-sensitivity studies using aquatic species have used food reinforcement. Using Betta as subjects in a risk-sensitivity experiment could make the existing literature regarding risk-sensitivity research more comprehensive.

Currently, no studies investigating risk-sensitivity have used male Betta as subjects. However, as discussed in Experiment 1, in a study by Lattal and Metzger (1994), male Betta responded differently to a 15 s mirror presentation when delay to reinforcement was 0 s, 10 s, and 25 s. This study is consistent with the operant responding observed in mammalian and avian species being provided with food reinforcement such that, as delay increased, operant responding decreased. Results from this experiment revealed that Betta were sensitive to delay to reinforcement when the reinforcement was an aggressive display. Therefore, it could be possible that Betta would display a choice bias in a risk-sensitivity procedure when using aggressive display as reinforcement.

Experiment 2

To explore risk-sensitivity in the aggressive display of Betta, instrumental conditioning of choice behavior was used to determine choice bias directed toward access to a mirror image. Risk-sensitive foraging experiments traditionally have examined the effects of two dimensions of variability in food reward: variability in amount and variability in delay. Experiment 2 was designed to investigate variability in delay to access to a mirror image. Subjects were expected to display a significant preference for the option with either the constant or the variable delay.

Method

Subjects and Apparatus. The subjects ($N=8$) and apparatus were equivalent to those described in Experiment 1.

Procedure. The procedure was identical to Experiment 2 with three exceptions: the delay associated with each option, the duration of exposure to the mirror, and the direction in which the trials were conducted in the T-maze. First, choices consisted of a variable delay to exposure to a mirror (19s [$p=.5$] or 1 s [$p=.5$]) and a constant delay to exposure to a mirror (10 s [p=1.0]). Second, the duration of exposure was held constant for both choices at 10 s. Third, for the first trial of each session, the subject swam toward the researcher in order to reach the goal box. For the second trial of each session (see Figure 1, T-maze during sessions), the subject swam away from the researcher to reach the goal box.

Results

The total number of constant reward choices was averaged across the last five days for each subject. A one-sample t-test was conducted on the proportion of constant

reward choices during the first trial of each session and during the second trial of each session. No significant difference was observed between the constant delay to reward choices ($t(7) = -0.63$, $p \geq .05$, d = -0.22) and chance performance for the data from the first trial of each session. A significant difference was observed between the constant delay to reward choices ($t(7) = 2.75$, $p < .05$, d = 0.97) and chance performance for the data from the second trial of each session (see Table 2).

Table2.

Number of choices (10 trials total) averaged across the last five days for the second trial data.

	Choices	
	Mean	SEM
Constant Delay to Reward (Risk-Averse)	7.3	0.08
Variable Delay to Reward (Risk Prone)	2.7	

Discussion

In the present experiment, subjects did not display a statistically significant preference for a constant over a variable delay to a mirror during the first trial of each session or when the subjects swam toward the researcher in order to reach the goal box. However, subjects did display a statistically significant preference for a constant over a variable delay to a mirror during the second trial of each session or when the subjects swam away from the researcher in order to reach the goal box.

The differential responding by subjects in the first trial of each session and in the second trial of each session may be attributed to the influence of the researcher. In the first trials of each session, the subject was required to swim toward the researcher in

order to reach the goal box. This required the experimenter to reach his or her hand directly over portions of the T-maze (such as the choice chamber) and manipulate parts of the apparatus (e.g., guillotine doors) directly above and beside the subject. In addition, the subject was required to swim toward the researcher and thus, the researcher was in the subjects' visual field throughout the duration of the trial. Being that the researcher was manipulating parts of the apparatus in such proximity to and in the subjects' visual field, the subjects may have been distracted or startled by the researcher's movements and were not considered to have chosen freely. Therefore, no choice preference (i.e., indifference) was observed during those trials.

In the second trial of each session (see Figure 1, T-maze during sessions), subjects swam away from the researcher in order to reach the goal box. By swimming away from the researcher, the experimenter was never required to manipulate parts of the apparatus by placing his or her hand directly above the subject or parts of the T-maze in which the subject would be swimming. Additionally, the subjects were required to swim away from the researcher, and, therefore, the researcher was not in the subjects' visual field for the duration of the trial. Being that the researcher was not manipulating parts of the apparatus in close proximity to the subjects or in the subjects' visual field, subjects were considered to have chosen freely without the influence of the researcher. Therefore, a choice preference (i.e., risk averse) was observed directed toward the choice option that delivered a constant delay to reinforcement during the second trial of each session.

The effects of delay to reinforcement on responding in the second trial data from the current experiment support and add to evidence from the study by Lattal and Metzger (1994). In the study by Lattal and Metzger, subjects' responding decreased as delay to

exposure to a mirror presentation increased. Similarly, subject choice in the current experiment was sensitive to delay. However, the ratio between delays in the choice options in the current experiment were equivalent and thus, subject choice should have been indifferent. Therefore, the observed choice bias suggested that choice in Betta was not only contingent on delay but to variability in delay to reinforcement. This observed choice bias can be explained in light of the Scalar Expectancy Theory and the variance-reduction hypothesis.

The data from the second trial of each session in the current experiment is consistent with the predictions made by the Scalar Expectancy Theory (Kacelnik & Bateson, 1996). Scalar Expectancy Theory states that a value will be assigned to a choice option based on a just noticeable difference in those choice options. For example, in previous research using similar manipulations with a food reward, subjects preferred to choose an option with a constant delay when manipulations in delay to reinforcement were varied and access to reinforcement were held constant. Similarly, Betta displayed a risk-averse choice bias or, in other words, a choice bias directed toward the choice option with a constant delay. The observed choice bias in previous research was, according to Scalar Expectancy Theory, due to the higher value associated with the constant option and the resulting expectation of that reward option.

As well as supporting predictions made by the Scalar Expectancy Theory, the data from the second trial of each session in the current experiment are consistent with predictions made by the variance-discounting hypothesis. In terms of the variance-discounting hypothesis, subjects would be expected to display a preference for the constant delay and, in turn, minimize variability (Real, 1980). For example, according to

variance-discounting hypothesis, subjects in the current experiment displayed a choice bias for the constant reward due to a decrease in or discounted value associated with the reward option followed by the variable delay. On the contrary, the reward followed by the constant delay did not decrease in value and thus, was more preferable relative to the variable delay option.

Moreover, the current experiment reveals evidence to support a bias in choice between a constant or a variable delay option where the reinforcement to follow was exposure to a mirror image. The use of exposure to a mirror image (a pseudo-sexual, aggressive, social encounter) as a type of reward is unique to the literature regarding risk-sensitivity. Given the evidence from the current experiment, it is possible that the use of a mirror image or conspecific as a reward could provide a beneficial model in which to examine social encounters under various contingencies and subsequently, further expand current theories of choice that are based largely on food rewards to include social encounters. By further expanding current theories to include explanations of rewards other than food, such as social encounters, the better researchers and clinicians could be at predicting and controlling more nebulous choice situations. Therefore, future studies should attempt to determine the factors that contribute to an energy budget for exposure to a mirror image.

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Figure 1

T-maze between sessions

T-maze during sessions

Choice door

Start box door

Start box (20 x 11 cm)

Choice chamber (10 x 11 cm)

Goal box (20 x 11 cm)

RESEARCHER