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Patterns of Female Mating Preferences for Sarotherodon caroli, from Barombi Mbo

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PATTERNS OF FEMALE MATING PREFERENCES FOR SAROTHERODON CAROLI,
FROM BAROMBI MBO

A Thesis

by

ILEANA RUBY ALVARADO

Submitted to Texas A&M International University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

May 2020

Major Subject: Biology

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ABSTRACT

Patterns of Female Mating Preferences for *Sarotherodon caroli,* from Barombi Mbo
(May 2020)

Ileana Ruby Alvarado, B.S., Texas A&M International University;

Chair of Committee: Dr. Michael R. Kidd

Cichlid fish are widely studied for their explosive speciation, which has led to a distinct variety of morphological characteristics and complex reproductive strategies. Cichlids display a variety of parental care strategies, including maternal-only, paternal only, and bi-parental which differentiates them from other vertebrate families. The African cichlid *Sarotherodon caroli* is endemic to the crater Lake Barombi Mbo located in Western Cameroon. *Sarotherodon caroli* is a monogamous species and their mating strategy involves defending their territory together one week prior to spawning. The purpose of this experiment is to quantify *Sarotherodon caroli* mate choice behavior in order to behaviorally define monogamy in this species. In a two-way mate choice experiment, the female *Sarotherodon caroli,* will spawn with the large male more frequently than the small male. Quantifying the behaviors that define monogamy in this species will provide the foundation for future hormone manipulation studies.

ACKNOWLEDGEMENTS

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CHAPTER 1

INTRODUCTION

1.1 Mating System

A mating system is defined as the general behavioral strategy employed in obtaining mates and is of great importance as it allows us to understand the evolutionary processes of biological diversity caused by direct or indirect selection pressures (Emlen and Oring 1977; Jungwirth et al. 2016). Mating systems are comprised of the following features: the number of mates acquired, the manner of mate acquisition (courtship, coercion, and forced copulation), the presence and characteristics of any pair bonds, and the patterns of parental care provided by each sex (Emlen and Oring 1977; Wootton and Smith 2014). Mating systems can be genetically fixed, with individuals using one system throughout their lifetime such as the externally fertilizing monogamous largemouth bass, *Micropterus salmoides* (Taylor et al. 2003). Mating systems can also be conditional with any individual potentially using one or more strategies depending on its phenotype or social and environmental conditions, such as resource distribution, risk of predation, the need for cooperation in hunting or brood care, mate availability and the timing of reproduction (Godin 1995; Rogers 1987). The damselfish *Dascyllus marginatus* can be monogamous, polygynous or promiscuous depending on the size of the coral which forms its breeding ground (Fricke 1980). Mating systems are also influenced by the limiting sex in a population. When one sex becomes a limiting factor for the other, the result is an increase intrasexual competition among the gender competing for the limited sex and often results in sexual selection (Emlen and Oring 1977). Sexual selection is determined by the degree to which critical resources are differentially controlled by members of the limited sex, by the availability of members of the limiting sex, and by the process of mate selection (Emlen and Oring 1977).

_____
This thesis follows the model of *Evolution*.

Operational sex ratio (OSR) is defined as the average ratio of fertilizable females to sexually active males and it is affected by the degree of spatial and temporal clumping for the limiting sex. When the OSR is skewed towards males, polygyny is expected, when the skew is toward females, polyandry should occur.

1.2 Types of Mating Systems

Monogamy occurs when individuals restrict their reproductive behavior to just one partner for one breeding season or longer (Sefc et al. 2009). Monogamy is more likely to occur if two individuals are required to effectively feed, incubate or guard young, defend a territory, or because of a shortage of mate availability (Taylor et al. 2003). Monogamous species exhibit courtship behavior and pair formation before selecting and defending a potential breeding territory (Itzkowitz and Nyby 1982; Gumm and Itzkowitz 2007). Individuals first assess each other as potential mates upon their first encounter. The monogamous cichlid *Cichlasoma citrinellum*, displays courtship behavior and pair formation as both sexes have preference for large, more aggressive, and experienced partners (Barlow 1986). A larger body size may increase the chances of offspring survival as it can intimidate potential predators and keep them away (Balshine-Earn 1996). Additionally, a larger mouth brooding female can store more eggs in the buccal cavity which increases the reproductive success of the male (Noonan 1983). However, the stability of their pair bond can be broken by the removal of their offspring or by the selection of a new mate (Gumm and Itzkowitz 2007). The selection of a new mate can be caused by an encounter of a new available partner that is more attractive in genetic quality or territory ownership than their current mates (Breukelen and Draud 2005).

Polygamy is used when individuals of either sex have more than one mate (Davies et al. 2012). Polygamy is more prevalent when one sex is predisposed to assume most of the parental

care, parental care duties are minimal, and there is an abundance of food resources which enables a single parent to provide full parental care (Emlen and Oring 1977). Polygamy can take different forms such as such as polygyny, polyandry, and polygynandry.

Polygyny is the mating relationship between one male and two or more females. Polygyny is more likely to occur when there is an abundance of females as a result of environmental or behavioral conditions and males have the capacity to monopolize them (Emlen and Oring 1977). Studies have shown that males benefit by this mating system as they maximize their reproductive output by fertilizing as many eggs as possible, while females do so by concentrating on maximum egg production (Emlen and Oring 1977). Polygyny is seen in the red-winged blackbird, *Agelaius phoeniceus* (Westneat 1993). Polygyny can be costly as mate guarding or investing time attracting females can reduce the time and energy to participate in parental care (Westneat et al. 1990). This is seen in birds as reduced paternal assistance reduces the reproductive success for female birds paired with polygynous males as females have lower post-fledging survival rates and rear fewer clutches per season (Webster 1991).

Polyandry occurs when a female has multiple mates in a breeding season, however the male only mates with one female (Taylor and Knight 2008). In this mating system, females increase their fitness by competing and defending resources that are essential to males. This often leads to the monopolization of a territory that allows females to mate with multiple males. Additionally, the male is often the sole provider of parental care (Emlen and Oring 1977). This behavior in which the traditional sex roles become reversed is seen in the Wattled Jacanas, *Jacana jacana* located in Central America. Since females have to compete for males, females exhibit greater ornamental features, are selected for greater competitiveness and display a larger body size than male jacanas. Additionally, females that are larger and heavier are more

successful in obtaining and holding large numbers of mates than smaller and lighter females (Emlen and Wrege 2004).

Polygynandry occurs when both females and males have two or more mates in a breeding season (Barlow 1991; Davies et al. 2012). In polygynandry, the males typically have territorial defense of a nesting site which attracts multiple females to mate in that site (Harding et al. 2003). Such mating strategy is seen in the sea spider, *Ammothea hilgendorfi*, a marine anthropod in which the female transfers her eggs to a male which uses a specialized pair of legs called ovigers, to hold and externally fertilize the eggs. Genetic analysis revealed both males and females have multiple mates and supported that polygynandry occurs in nature in this species (Barreto and Avise 2008).

Promiscuity occurs when both males and females have multiple mates during a breeding season (Wootton and Smith 2014). This differs from polygynandry, where the possibility of a mate selection exists. Females can benefit from promiscuity as insurance against male sterility, have access to higher quality territories, brood diversity, and avoidance of inbreeding. It can also be costly as females have a high risk of contracting disease, predation, and copulation brutality (Avise et al. 2002). Such behavior can be observed in a lek. A lek-based mating system is characterized by an aggregation of adult males with females visiting that localized area for the sole purpose of egg fertilization (Kellogg et al. 2000). This behavior is seen in cichlids *Astatotilapia flaviijosephi* and *Oreochromis mossambicus* (Werner and Lotem 2003; Nelson 1995). The adult males do not contribute resources or parental care and there is no pair-bonding between the male and female (Mckaye 1983; Mckaye et al. 1990). Such behavior is seen on the Lake Malawi cichlid *Pseudotropheus zebra*, as genetic markers revealed multiple paternity in a brood.

1.3 Differences in Reproductive Investments

An organism must at some point allocate time and resources to reproduction to ensure its reproductive success. Studies have shown that reproductive investment should be high when the expected returns in fitness are high. Abiotic or biotic factors can influence adjustments in reproductive investment (Harris and Uller 2009). Previous studies suggest that females are expected to be the limiting sex because rate of egg production is slower than the male's rate of producing sperm (Barlow 1991). Females maximize their reproductive success by investing greater material in offspring and as a result are expected to be more discriminatory than males with respect to mate quality (Howard 1978; Gwynne 1982; Breed et al. 1980; Borgia 1981). Males are commonly viewed as the sex that increases their reproductive success by maximizing the number of fertilizations rather than the quality of females (Howard 1978). This is based in the assumption that a male provides relatively inexpensive gametes to females allowing a male with sufficient reserves to inseminate many females. In order to increase the number of fertilizations, males invest energy into secondary sexual characters that can be used as weapons against other individuals, attractive ornaments, or any other indicator of its fitness (Berg and Finstad 2008). Female katydids *Conocephalus nigropleurum* show preference for males with a longer singing call as it represented an increased energetic contribution that could only be made by large males that produce large-sized spermatophores, which contain proteins that are important for female reproduction (Gwynne 1982). In bower birds, females prefer to mate with males who have well decorated bowers because only the most dominant males can accumulate such elaborate decorations and it is thought to be a good indication of their quality as sires (Borgia 1985). Female mate choice is an important mechanism for sexually dimorphic traits; however, males can also become selective when they invest a large contribution to parental care.

This leads to sexual selection in females which causes certain traits to evolve to increase their chances of reproduction (Henson and Warner 1997; Dugatkin and FitzGerald 1997). Within a monogamous mating system, both sexes are expected to be more selective as there is an equal investment in offspring (Santangelo and Itzkowitz 2004). In a polygamous mating system, the sex that invests more in parental care is expected to be more selective. In a polyandry mating system, the male will be expected to be more selective. In a polygynous mating system, the female will be expected to be the most selective sex (Barlow 1991).

1.4 Alternative Mating Strategies

Alternative mating strategies are defined as a set of evolved behavioral and morphological characteristics with the purpose of obtaining fertilizations in both males and females (Taborsky et al. 2008). Alternative mating strategies refers to the different methods conspecifics or intrasexual competitors use for reproductive competitions, while mating strategies refers to the mating system used more frequently by a species (Howard 1978). Alternative mating strategies are common in the animal kingdom and are often correlated with morphological traits such as plumage variation in birds, throat color polymorphisms in lizards, and color or size polymorphisms in fish (Sinervo and Zamudio 2001). Other examples include behavioral alternatives such as territoriality vs. floating, monopolization vs. scramble competition, or investment in primary access to a resource vs. social parasitism (Taborsky et al. 2008). Alternative reproductive strategies may be fixed for a lifetime or flexible depending on its phenotype or prevailing social and environmental conditions (Taborsky 2001; Godin 1995). Also, flexible alternative reproductive strategies can be simultaneous, performed at the same time or sequential, performed in a fixed or reversible sequence (Taborsky et al. 2008). Additionally, alternative mating strategies can be expressed within a species, or even within an

individual during its lifetime (Avise et al. 2002). For instance, the ocellated wrasse, *Symphodus ocellatus*, displays the following alternative mating strategies: large "bourgeois" males, satellite males, parasitism or cuckoldry, (Henson and Warner 1997). A bourgeois male establishes and defends its territory and often tends to progeny. When males are territorial, they tend to invest in recruiting females to spawning sites, actively defending against male intruders, and developing traits that attract females, or that signal male quality (Howard 1978; Taborsky 2001). Males can also adopt alternative non-territorial behaviors. For instance, intermediate sized males can mimic females in order to gain access to the nest for spawning. Additionally, these satellite males may provide a resource, such as territory defense, to burgeois males and are permitted to court and spawn with females (Henson and Warner 1997; Taborsky 2001; Avise et al. 2002). Parasitic behavior occurs when a male remains inconspicuous in order to attain fertilization by depositing sperm at the spawning site before eggs are laid (Taborsky 2001). Parasitic behavior is seen in *S. ocellatus*, as the small males parasitize a bourgeois male by sneaking into the nest and "stealing' fertilizations (Avise et al. 2002). This behavior benefits the parasitic males as they fertilize eggs by exploiting the reproductive investment of territorial males without the costly investment of production of conspicuous signals and energetically demanding structures to attract mates and parental investment to provide and protect offspring (Taborsky et al. 2008).

Although females do not typically compete directly for resources or mates, they also display alternative reproductive behaviors. Females can display copying behavior, in which younger or less experienced females copy the mate choices of other females. Experimental evidence suggests the female trinidian guppy, *Poecilia reticulata*, copy the choice of mates made by other females by viewing such interactions and remembering the identity of the chosen male, and subsequently choosing that male in future sexual reproductions (Dugatkin 1992).

Additionally, females can resist coercion when males attempt to force copulations (Henson and Warner 1997). Most of these alternative mating strategies result from critical values that determine the choice of an individual such as relative body size and condition, the intensity of intrasexual competition, local population density, sequence of residence, and environmental conditions (Taborsky 2001).

Alternative mating strategies evolve by pursuing divergent allocation tactics or by exploiting the investment of competitors without their cost, which maximizes fitness (Taborsky et al. 2008). This may occur by sexual selection that leads to high investment in structures that promote mate acquisition by indirectly or directly benefiting their mates, which can cause variation in the success of the chosen sex (Taborsky et al. 2008). For instance, if some males are successful in obtaining mates, the other males will be unsuccessful which prompts alternative mating strategies to be used to compensate for reproductive competition. Alternative reproductive strategies may coexist in a population either as consequence of frequency-dependent selection with equal average fitness outcomes among different tactics or by opportunistic adoption of parasitic tactics among less competitive males that are unable to obtain primary access to females (Sato et al. 2004). The evolution of alternative mating strategies is also due to different reproductive niches. Selection may favor multiple phenotypes that are specialized to exploit reproductive opportunities in each reproductive niche (Taborsky et al. 2008). For instance, in the dimorphic insect species *Prokelisia dolus,* Langellotto and Denno (2001) found that when female density was low and in sparse vegetation, males with the ability of flight had a mating advantage over their flightless competitors. However, flightless males thrived in a contiguous vegetation with increased female density as they communicate

acoustically via plant substrate-borne vibrations from distances up to 1 m and would locate and arrive at calling females before their winged dimorphic rivals.

1.5 Cichlids

Cichlidae is a family of diverse teleost fishes that are widespread. There are three primary evolutionary clades which include African, Neotropical and Malagasy/Indian lineages (Maruska 2014). The cichlids of the Great Lakes of Africa have become a powerful model system for studying evolution due to their adaptive radiations and explosive speciation (Maan et al. 2004, Kornfield and Smith 2000). The three largest African lakes, Lake Victoria, Lake Tanganyika, and Lake Malawi contain approximately 1500 cichlid species (Genner and Turner 2005). Lake Victoria contains between 450-535 endemic cichlid species, Lake Tanganyika contains 160-185 species, and Lake Malawi contains 450-600 species (Genner and Turner 2005). As a result of their ecological and behavioral diversity, they display remarkable diversity in phenotypic variation, mating systems, social behavior, parental care strategies, and alternative reproductive strategies.

Cichlids display various alternative mating strategies such as territoriality, satellite males, and parasitism (Martin and Taborsky 1997). The shell brooding cichlid *Lamprologus callipterus*, exhibits parasitic behavior. Parasitic males resemble and mimic females or act inconspicuous to sneak in towards the shell where spawning occurs to steal fertilizations from dominant males (Sato et al. 2004). An example of cooperative behavior is seen in the cichlid *Neolamprologus brichardi*, in which the young produced will stay with the family to help defend the territory. However, reproductively mature helpers can expel the former female breeder or split off from the territory and form a harem (Taborsky 2001).

1.6 Cichlid Mating Systems

Cichlids display variation in their mating systems such as monogamy, polygyny, and polyandry (Sefc et al. 2009, Garvy et al. 2015). Monogamous cichlids, such as the *Cichlasoma nigrofaciatum* (Noonan 1983), initiate mating behavior by pair formation and gradually transition into the part of courtship and pair bonding phase, which lasts a few days (Barlow 1991) before they spawn (Gumm and Itzkowitz 2007). *Lamprologus callipterus* display polygynous behavior as males have a harem and defend their gastropod shell which serves as nests in which the females and brood reside. Polyandrous behavior is rare among cichlids but has been reported in *Julidochromis marlieri* (Awata et al. 2006). In this species, the female mates with more than one male, tends to be larger and more aggressive than the male and conducts little to no parental care (Yamagishi and Kohda 1996). Promiscuous mating is seen in the Lake Malawi cichlid, *Cyrtocara eucinostomus*, as males and females aggregate in an arena for spawning without the presence of pair bonding or male parental role (McKaye 1983). Mating systems are influenced by the patterns of parental care and has proceeded from monogamy to bi-parental care to polygamy with maternal care (Barlow 1991).

1.7 Cichlid Parental Care Systems

The diverse range of parental care performed by cichlids allows the opportunity to study evolutionary transitions in parental care (Balshine-Earn and Earn 1998). Parental care is defined as any investment by a parent in an individual offspring with the purpose of increasing the offspring's chance of fitness survival (Stiver and Alonzo 2009). Cichlids perform parental care by substrate guarding or by mouth brooding. Substrate spawning occurs when cichlids lay their eggs on a substrate or crevice and defend their brood by chasing away predators and by providing food resources to their brood (Mckaye 1977). Mouthbrooding cichlids provide care by holding their eggs in their buccal cavity after fertilization, until their offspring become free-

swimming (Lee et al. 2016). Substrate guarding is believed to be the ancestral parental care state in cichlids (Goodwin et al. 1998) and the evolution to mouthbrooding was due to an increased protection from predators, lack of availability of substrates for breeding, and the ability to move fry to suitable habitats. Additionally, the loss of adhesive threads on eggs and the oral transport of offspring by substrate guarders may have been the first step toward the evolution of mouthbrooding (Baylis 1981). Mouthbrooding is energetically costly due to the parents eating less, which results in its delayed growth and gonadal recovery (Sefc 2011). Furthermore, parental care in cichlids can be further characterized as maternal only, paternal only, biparental, alloparental, and communal parental care (Kidd et al. 2012). The black-chinned *Sarotherodon melanotheron* displays paternal care as the male picks up the fertilized eggs and incubates them in his mouth until the eggs become free-swimming fry (Kishida and Specker 2000). Biparental care occurs when both the female and the male provide care in maintaining their brood and is considered the ancestral state to uniparental care, primarily due to reduction of care by males (Goodwin et al. 1998). The cichlid *Boulengerochromis microlepsis* displays biparental care as both parents guard the brood from potential predators (Kuwamura 1997). The haplochromine cichlid *Astatotilapia flaviijosephi,* shows maternal only care as the female is the sole provider of the parental care (Werner and Lotem 2003). Alloparental care is demonstrated when parents care for non-descendant young through brood mixing and/or extra-pair mating. Alloparental care can be the outcome of parasitic behavior as it incurs the costs of conventional care without providing a fitness benefit. (Wisenden 1999). This is seen in the cichlid species *Perissodus microlepsis* where genetic analysis revealed 28 % of the broods sampled were unrelated to either parents most probably due to the farming out method (Lee et al. 2016). Communal care is observed when individuals of a social system care for the young non-discriminately such as seen in

Neolamprologus brichardi (Taborsky 2001). Goodwin et al. (1998) suggest that transitions from bi-parental care to female only care were primarily due to a reduction in care by males. Male desertion may have been caused by a male- biased operational ratio, however, only the males who are successful in competing or attracting females have the alternative of either abandoning a female or contributing to parental care (Gonzalez-Voyer et al. 2008; Sefc 2011).

1.8 Cichlid Mate Choice

Mate choice is defined as any pattern of behavior displayed by one sex, that leads to an increased possibility of mating with members of the opposite sex (Kokko et al. 2003; Lamprecht and Rebhan 1997). Selecting a mate is a complex process that involves searching, sampling, information gathering and decision making (Choudhury and Black 1993). During mate choice, individuals assess potential mates by the participation in courtship displays, which is not only used for both sexes to synchronize their behavior for successful mating, but also to advertise their genetic quality (Kidd et al. 2013; Candolin 2003). Cues used in mate choice can be informative and indicate direct or indirect fitness benefits, or may be uninformative cues that facilitate mate choice, but have no effect on the fitness of the receiver (Candolin 2003). Direct fitness benefits include the selection of a mate based on the basis of assessed traits (Genner et al. 2008). The male convict cichlid, *Cichlasoma nigrofasciatum*, prefers to court with large females rather than small females (Beeching and Hopp 1999). because they may produce more eggs and thus increase the male's reproductive success. Additionally, females prefer to mate with larger males because they have access to higher quality habitats and better resources. In the convict cichlid, females benefited from mating with larger males by being in a superior breeding site, repelling offspring predators, and raising more offspring to independence than smaller males (Gagliardi-Seeley et al. 2009). Indirect benefits include the genetic contribution of the male that

will increase the quality of the offspring (Laubu et al. 2017). These studies show that being of larger size may also be an indication of good genes and plays a role in influencing their choice to mate with a particular individual (Beeching and Hopp 1999, Gagliardi-Seeley et al. 2009).

Additionally, cichlids such as the *Pseudotropheus zebra* may utilize the bet-hedging strategy, in which females show preference for a particular mate, but continue to invest in assessing other potential mates (Parker and Kornfield 1996; Santangelo and Itzkowitz 2004). Potential costs to the females choosing between available males include, increases in vulnerability to predators, time and energy expenditures, risk of harassment and injury from conspecifics or heterospecifics, risks of contracting diseases or parasites, lost mating opportunities, and reduced male parental care (Godin and Briggs 1996). Females incur these cost as failing to mate with males possessing certain elements such as the ability to inseminate an entire clutch of eggs, overall relatedness and parasite resistance, exceed the cost of searching for additional mates (Parker and Kornfield 1996).

Measuring mate choice is rather difficult as matings may be infrequent or occur rapidly (Couldridge and Alexander 2001). Barlow (2002) suggested three experiments to quantify female mate choice in fishes: free access, female only access, and retrained access. In each experiment, females were presented with two or more males of varying qualities. Most field observations and manipulations fall into the free access experiments (Kidd et al. 2006). In this setting, all individuals are allowed to directly interact with each other. Free access studies have been conducted on the bi-parental spawning cichlid *Cichlasoma nigrofasciatum* to gain an understanding of their mating preferences (Beeching and Hopp 1999). This type of experimental setting has also been used on the lekking cichlid species *Cyrtocara eucinostomus,* in order to investigate what male qualities females base their mating decision (McKaye 1983). The female

only access category can be used when females are smaller than males. In this setting, size selective barriers are used to limit male to male interaction but still allow the female access to males (Kidd et al. 2006). In the restrained access class, all subjects are confined by transparent barriers limiting the cues available to the female. This category offers maximum control over the testing variables as all subjects are confined to their individual compartments (Barlow 2002). Restrained access studies have been used on the cichlid *Sarotherodon galilaeus* to investigate the association preference of that species (Balshine-Earn 1996). Couldridge and Alexander (2001) suggest that the time females spent in association near a male is a good indicator of a female's choice in Malawian cichlids. However, Kidd et al. (2013) found that female time spent in association or in the bower did not influence the final mate choice until the actual day of spawning.

1.9 Cichlid Mate Choice in Polygamous and Promiscuous Species

Association preference is also influenced by a female's reproductive cycle. Kidd et al. (2013) found that reproductive female *Astatotilapia burtoni*, prefer to associate with larger males only on the day of spawning and displayed circling spawning behavior in the larger male's bower. Any day other than spawning, non-reproductive females preferred to associate with the smaller males. These changes in behavior are influenced by neurochemicals, hormones, and pheromones (Kidd et al. 2010, Kidd et al. 2013). The different hormones circulating in a reproductive cycle are estradiol (E2), 11-ketotestosteron (11-KT), progesterone (P), and prostaglandin F2α (PGF2). Estradiol is known to promote the development and maintenance of the female sexual characters (Taghizadeh et al. 2013). Prostaglandin (F2α) is a reproductive hormone that is produced in mature reproductive tissues of all female vertebrates (Munakata and Kobayashi 2010). It is an essential hormone as it promotes ovulation and sexual behavior in

female fish (Kidd et al. 2010) and plays a role in the coordination of gamete release between males and females of many teleost species (Robison et al. 1998; Cole and Stacey 2006). Kidd et al. (2012) found that 17 β estradiol peaked 6 days prior to spawning followed by a simultaneous rise in progesterone and testosterone four days prior to spawning, and PGF2 levels peaked three days prior to spawning in the cichlid *A. burtoni*. Additionally, Kidd et al. (2013) found that PGF_2 dramatically shifts the association preferences of non-reproductive females from smaller and less aggressive males to larger males. Hormone studies are instrumental in understanding how sexual selection can influence evolution of female selectivity and male characters.
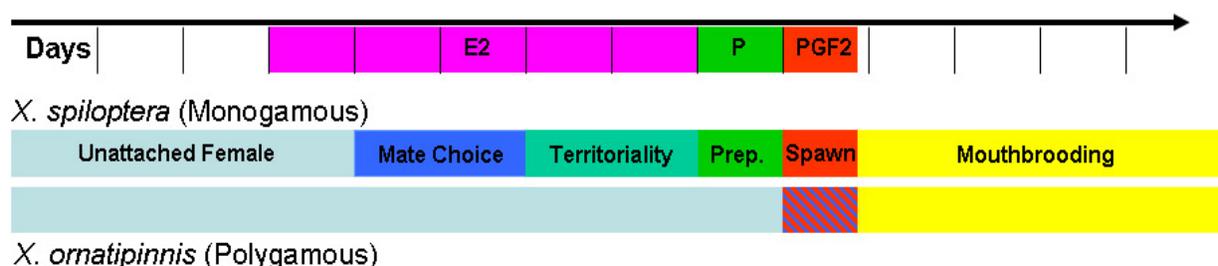
Figure. 1.1: Temporal patterns of reproductive states for monogamous and polygamous cichlid species relative to associated gonadal hormones (E, P, PGF2) based on preliminary data. In contrast to monogamous species, polygamous females choose a mate and spawn simultaneously (stripped area) and do not go through a territoriality and site preparation (Prep) stage.

1.10 Barombi Mbo-Location, Impacts, Monophyly Evolution

Barombi Mbo is a small volcanic crater lake located in SouthWest Cameroon. This lake contains 11 endemic cichlid species that based on their morphological description, are all part of tilapiine lineage (Schliewen et al. 1994). Genetic data (Martin et al. 2015) indicated the lakes of Cameroon originated through monophyly (Schliewen et al. 1994) as the riverine species *Sarotherodon galilaeus* (Oreochromini) colonized the crater lake Barombi Mbo and founded the Barombi Mbo radiation of species. This lake has been used as an example of sympatric speciation as the lake's conical basin is 2.15 km in diameter and is too small to restrict gene flow

(Reid 1990, Martin et al. 2015). There are no apparent migration-barriers along the shore and gene flow from outside the lake is restricted by crater rims that isolate the lake from nearby river systems (Schliewen and Klee 2004; Kornfield and Smith 2000). Additionally, mitochondrial and nuclear (AFLP) methods have been tested to support this phylogeny and species within the radiation were more closely related to each other than to any riverine outgroup (Schliewen et al. 1994; Schliewen and Klee 2004). However, recent studies using genome wide analysis suggest that these species are not as isolated as previously suggested and speciation there has been from riverine populations (Richards et al. 2018).

1.11 *Sarotherodon caroli*

The African cichlid *Sarotherodon caroli,* is endemic to the crater lake Barombi Mbo located in western Cameroon. Early description synonymized *S. caroli* with *S. linnellii*, however differences in the pharyngeal blade and the full body jet-black adult coloration allows the two species to be differentiated (Trewavas et al. 1972; Schliewen and Klee 2004). Most species in the genus *Sarotherodon* are classified as monogamous cichlids with bi-parental behavior (Fishelson and Hilzerman 2002). For instance, *S. galilaeus* is a species that forms temporary pair-bonds and both sexes can participate in territorial behavior and parental care (Schwank and Rana 1991; Zeilstra and Oliveira 2003). After spawning, both males and females may incubate their eggs or fry in their mouth. Males may switch partners after spawning or stay with their partners for future spawning (Zeilstra and Oliveira 2003). It has been suggested that *S. caroli* are ovophilic, maternal mouth brooders that undergo weak pair-bonding before spawning, however, the pair bond breaks after spawning and the female is left to tend to the brood (Trewavas et al. 1972; Lamboj 2004).

The objective of this study is to quantify *S. caroli* mate choice behavior and association preferences to gain an understanding of their reproductive behavior. I hypothesize that when placed in a two-way mate choice experiment, the *S. caroli* female will spawn with the large male more frequently than the small male, thus displaying positive assortative mating. Since it has been reported that this species develops a weak pair bond, I hypothesize that female association preference for the large male will increase earlier in the ovulatory cycle than it does for the polygamous species *A. burtoni*. Instead, *S. caroli* is expected to follow a pattern more like a biparental species. By quantifying their behavior, we hope to gain a better understanding of their pair bond formation, mate choice behavior, and the female's reproductive behavior, within this mating strategy.

CHAPTER 2

METHODS

2.1 Animals

The cichlids for this study were maintained in the laboratory at Texas A&M International University IACUC #2016-1. Fish used in this study had no prior experience in mate-choice and parental behavior. They may have mated before, just not experimentally. All fish subjects were housed in a community 227-l tank with terracotta shelters strategically arranged to facilitate the establishment and maintenance of territories necessary for reproduction (Kidd et al. 2013). Fish were maintained on a 12:12 L/D cycle, kept at a constant water temperature 30-33°C, and at a pH of 7.0-8.0. Fish were fed cichlid flake food every day and spirulina enriched brine shrimp every other day.

2.2 Community Breeding Tank

The community breeding tank was comprised of territorial males and females and was established to encourage female spawning. In order to understand the female's ovulatory cycle, the eggs of the females that spawned in the community breeding tank were removed. This resets the female's ovulatory cycle as it causes a premature cessation of the oral gestation period and the acceleration of vitellogenesis (Tacon et al. 2000). After spawning within a community setting, the female subjects were transferred to a dichotomous experimental tank (Fig. 2.1).

2.3 Experimental Design

This restrained access tested the response of the female to adjacent males. The experimental arena comprised of two males placed in opposite extremities of the tank. The central compartment consisted of a female who had spawned within three days in the community tank. The standard length, which is the measurement of the mouth to the caudal peduncle of the

fish was recorded for all individuals. The males with a greater standard length than the females were labeled as the larger male and those who were less than the female's standard length were used as the small male. The larger male is considered more attractive than the smaller male as females will spawn with the larger male most of the time (Kidd et al. 2013). All fish were separated by a semipermeable and transparent partition, which allowed the passage of hormones, courting, and the display of reproductive behavior but prevented any physical contact. The placement of the males was randomized to avoid any potential side bias associated with female preference for one side of the aquarium (Dechaume-Moncharmont et al. 2011). All three fish had a terracotta pot that served as shelter and a shared bower. The shared bower is of extreme importance as it was the area in which spawning behavior took place. Reproduction behavior such as nipping, throat puffing, head nodding and body quivering, which is the vibration of the body musculature is seen when both female and male are in the bower. Fish also display reproductive behavior by either swimming slowly over the nest, rubbing the genital tube on the substrate and spawn quivering, which is the vibration of the body while passing the nest. Lastly, egg deposition or sperm release can occur during a spawning quiver (Aronson 1945). Although the fish are separated by the semipermeable partition, fertilization can still occur.
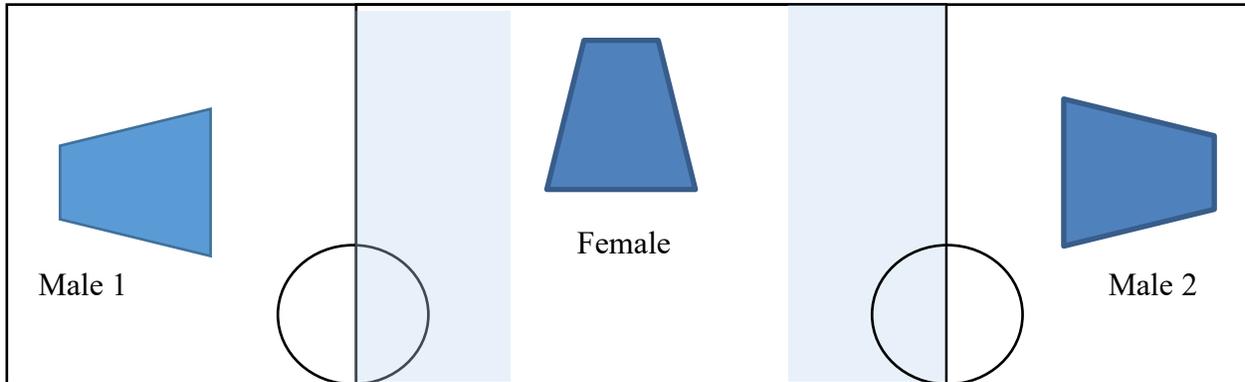
Figure. 2.1: Dichotomous choice paradigm. Females were placed in the center compartment with males on either side. They were separated by a transparent semipermeable partition. Each compartment contains a shelter. The circles represent bower location, where reproductive behavior was displayed, and blue shadowing represent association zones.

2.4 Behavior Analysis

Female reproductive behavior

Female reproductive behavior was continuously recorded for 4 hours using a recording camera (eg. Video Insight ©) for 30 days at 10 in the morning. The following behavior was analyzed: association time, time in the bower, and number of bites. Time spent by the female in each part of the aquarium was used to provide an index of female preference for each of the two males. The time in bower represented the time the female spent in the area in which the most sexual behavior was displayed. The number of bites was annotated when the female attempted to bite either male across the partition.

In order to understand the framework of the ovulatory cycle of the female *S. caroli*, the already known ovulatory cycle of the cichlid species, *A. burtoni* was used as reference. The ovulatory cycle of the *A. burtoni* is two weeks (Kidd et al. 2013), therefore, the behavior of the female *S. caroli* was scored in two parts: forward and backward scoring. Forward scoring is the analysis of behavior of the female after spawning in the community breeding tank. Forward scoring was comprised of the following 12 days: 2, 6, 10, 14, 18, 22, 24, 26, 27, 28, 29, and 30

days after spawning, respectively. Backward scoring is the analysis of behavior of the female after spawning in the experimental tank. In order to account and understand the ovulatory cycle of the female, backward scoring was comprised of day 0, which was the day of spawning in the experimental tank. Additionally, day -1 was the day before spawning, and day -2 was two days after spawning. Backward scoring also compromised of the following days: -3, - 4, -5, -6, -7, -11, -30, -20, and-14, respectively for a total of 12 days. Forward and backward scoring was necessary to map the ovulatory cycle of the female. Essentially to understand when the female began to be receptive to the males and have accountability of the behavior throughout her cycle.

2.5 Statistical Analysis

All this information was analyzed by Excel to see whether female association, time spent in the bower, and the bites displayed throughout her cycle, had any significant relevance. To test for significance, an analysis of variance and a Tukey Post Hoc test was conducted in SPSS. Significance is considered as $p<0.05$.

CHAPTER 3

RESULTS

3.1 Female Association Preference Throughout Her Ovulatory cycle

All ten females spent more time associating with the large male than the small male throughout her ovulatory cycle. However, there is no significant difference with the amount of time the female spends with the large male (Table 3.2) and the day of her reproductive cycle ($p=$ .567). Interestingly, there is significance ($p=.001$) with the amount of time the female associates with the small male and the day of the female's cycle (Table 3.1). The time the female spends with the small male three days before spawning ($p=.003$) and on the day of spawning ($p=.004$) has significant relevance (Table 3.3) It is during the last three days of spawning that the female has an increased association preference with the large male and significant decline of association preference for the small male (Fig. 3.1).

Table 3.1. Analysis of variance for female association preference throughout her ovulatory cycle for the small male. ANOVA analysis indicates a significant difference for female association preference throughout her ovulatory cycle with the small male ($p= .001$). The R. Squared value is .214 (Adjusted R Squared=.121).

Source	Type III Sum of Squares	Df	Mean Square	F	Sig.
Corrected Model	344762.608[a]	23	14989.679	2.299	.001
Intercept	907945.346	1	907945.346	139.253	.000
Day	344762.608	23	14989.679	2.299	**.001**
Error	1264900.259	194	6520.104		
Total	2581977.000	218			
Corrected Total	1609662.867	217			

Table 3.2. Analysis of variance for female association preference throughout her ovulatory cycle with the large male. The R squared value is .099 (Adjusted R Squared =.008). There is no significant difference (p = .567) between the days the female spends in association with the large male throughout her ovulatory cycle.

Source	Type III Sum of Squares	Df	Mean Square	F	Sig.
Corrected Model	688271.387[a]	23	29924.843	.923	.567
Intercept	14341013.691	1	14341013.691	442.507	.000
Day	688271.387	23	29924.843	.923	**.567**
Error	6287262.728	194	32408.571		
Total	21912167.000	218			
Corrected Total	6975534.115	217			
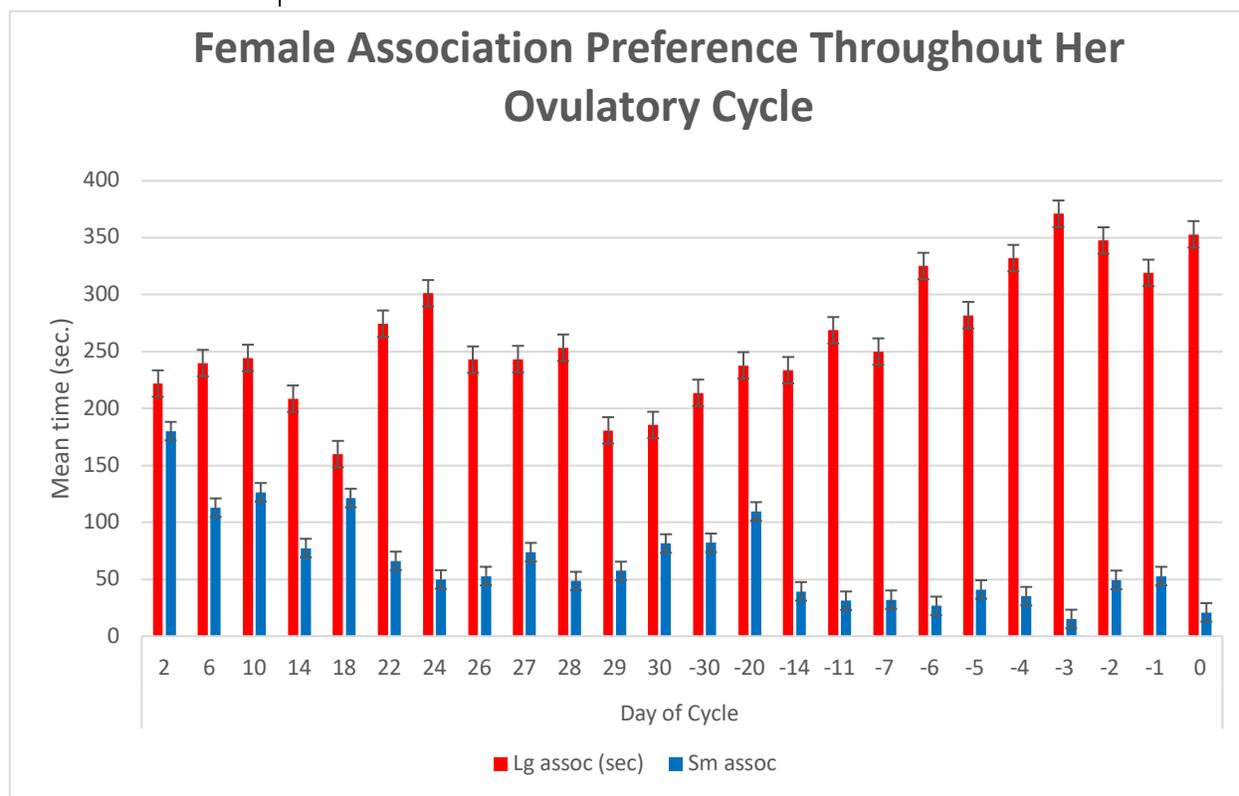
Figure. 3.1. The mean time in terms of seconds of female association preference throughout her ovulatory cycle. The time spent in association with the large male is depicted in red the time the female spent in association with the small male is shown in blue. Whiskers represent the standard deviation of the data.

Table 3.3. Tukey Test on female association preference for the small male. Tukey Test depicts a difference in female association preference for the small male on Day 0 (p=.004) and on Day -3 (p=.003).

(I)Day	(J) Day	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval Lower Bound	Upper Bound
Day 2	Day 6	67.20	36.111	.973	-66.07	200.47
	Day 10	53.70	36.111	.999	-79.57	186.97
	Day 14	102.70	36.111	.411	-30.57	235.97
	Day 18	58.70	36.111	.995	-74.57	191.97
	Day 22	114.00	36.111	.216	-19.27	247.27
	Day 24	130.30	36.111	.064	-2.97	263.57
	Day 26	127.30	36.111	.082	-5.97	260.57
	Day 27	106.30	36.111	.342	-26.97	239.57
	Day 28	131.70	36.111	.057	-1.57	264.97
	Day 29	122.80	36.111	.117	-10.47	256.07
	Day 30	98.70	36.111	.495	-34.57	231.97
	Day 0	**159.20**	**36.111**	**.004**	**25.93**	**292.47**
	Day -1	127.32	37.101	.107	-9.60	264.25
	Day -2	130.66	37.101	.083	-6.27	267.58
	Day -3	**164.99**	**37.101**	**.003**	**28.06**	**301.92**
	Day -4	144.99	37.101	.025	8.06	281.92
	Day -5	139.10	37.101	.042	2.17	276.03
	Day -6	153.53	39.793	.029	6.67	300.39
	Day -7	148.10	39.793	.045	1.24	294.96
	Day -11	149.00	36.111	.011	15.73	282.27
	Day -14	140.73	38.302	.053	-.63	282.08
	Day -20	70.53	39.793	.985	-76.33	217.39
	Day -30	98.10	47.771	.926	-78.21	274.41

3.2 Female Bower Association Throughout Her Ovulatory cycle

The time females spent in the bower of the small and large male varied throughout her reproductive cycle. Table 3.4 shows interaction between the amount of time females spent in the bower of both males and the day of her reproductive cycle (p = .000). Further analysis demonstrated no significant difference in the amount of time the female spent in the small male's bower (p =.357) over the course of her ovulatory cycle (Table 3.5). However, there is a significant difference of how much time the female spent in the bower of the large male (p < 0.05) over the course of her ovulatory cycle (Table 3.6). Additionally, female preference for the large male bower begins to increase 6 days before it finally peaks on the day of spawning (Fig. 3.2). This study found that in *S. caroli*, the male bower the female prefers during the last days of her cycle is reflective of her final mate choice. It is during this period that various reproductive behavior such as quivering was displayed.

Table 3.4. Analysis of variance for female bower preference for the small and large male. The R. Squared value is .295 (Adjusted R. Squared= .210). There is interaction between the amount of time females spend in the bower of both males and the day of her reproductive cycle (p = .000).

Source	Type III Sum of Squares	Df	Mean Square	F	Sig.
Corrected Model	262630.311[a]	47	5587.879	3.457	.000
Intercept	129283.565	1	129283.565	79.994	.000
Male Size	71632.828	1	71632.828	44.323	.000
Day	81819.165	23	3557.355	2.201	.001
Male size X Day	107672.134	23	4681.397	2.897	**.000**
Error	627071.586	388	1616.164		

Table 3.4. Continued

Source	Type III Sum of Squares	Df	Mean Square	F	Sig.
Total	1021031.000	436			
Corrected Total	889701.897	435			

Table 3.5. Analysis of variance for female bower preference for the small male. The R. Squared value is .115 (Adjusted R. Squared= .010). The amount of time females spend in the bower of the small male throughout her reproductive cycle is not significant (p = .357).

Source	Type III Sum of Squares	Df	Mean Square	F	Sig.
Corrected Model	10108.793[a]	23	439.513	1.092	.357
Intercept	4224.380	1	4224.380	10.496	.001
Day	10108.793	23	439.513	1.092	**.357**
Error	78077.684	194	402.462		
Total	92414.000	218			
Corrected Total	88186.477	217			

Table 3.6. Analysis of variance for female bower preference for the large male. The R. Squared value is .246 (Adjusted R Squared= .157). There is significance (p =.000) for female bower preference for large male throughout the reproductive cycle.

Source	Type III Sum of Squares	Df	Mean Square	F	Sig.
Corrected Model	179382.506[a]	23	7799.239	2.756	.000
Intercept	196692.013	1	196692.013	69.506	.000
Day	179382.506	23	7799.239	2.756	**.000**
Error	548993.902	194	2829.865		

Table 3.6. Continued

Source	Type III Sum of Squares	Df	Mean Square	F	Sig.
Total	928617.000	218			
Corrected Total	728376.408	217			
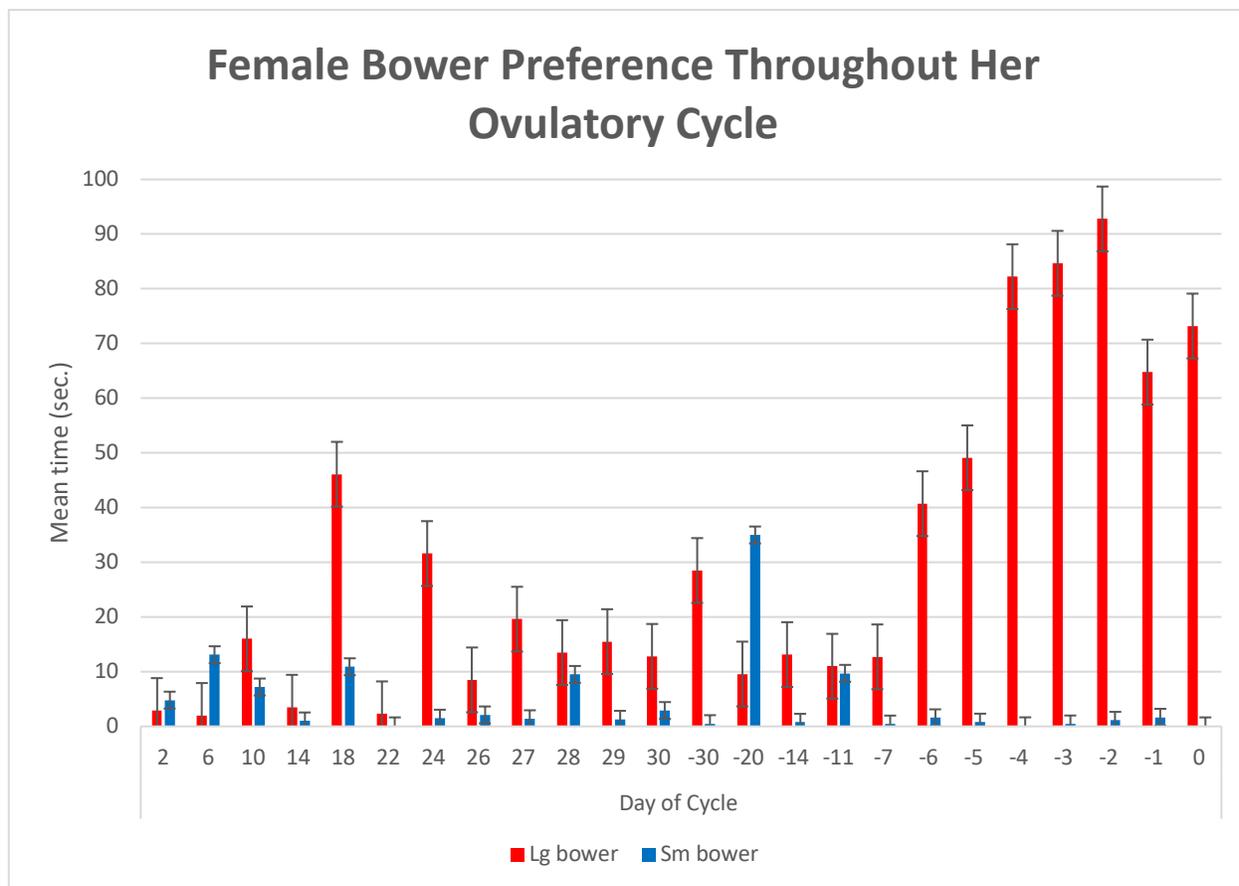
Figure. 3.2. Female Bower Preference Throughout Her Ovulatory Cycle. The time spent in the bower was measures in seconds. The large male is shown in red and the small male is represented in blue. Whiskers represent the standard deviation of the data

3.3 Female Reproductive Cycle

Of the 10 experimental runs, 9 females were recorded picking up eggs on the bower of the large male (Fisher's Exact Test: 0.0325, Table 3.8) when the lights turned on at 8:30 am. The reproductive display of behavior was not observed on the video software as it stopped recording

at 7:30pm and *S. caroli* species preferred to spawn late in the evening rather than the morning, as previously documented in the cichlid *Cyrtocara eucinostomus* (Mckaye 1983).

The female displayed an association preference for the large male after spending an average of 67 days in the dichotomous tank. The maximum amount of time a female spent in the experimental tank was 120 days and the least time spent was 36 days (Table 3.7). On the days leading up to spawning, the female would invest more time in the bower of the more attractive large male ($\bar{x}$= 69.63 sec.) than the less attractive ($\bar{x}$ = 0.82 sec.) small male. On the day of spawning, the female would deposit her eggs in the bower of the large male.

Table 3.7. Female descriptive statistics. A total of 10 females were used in this study. The average female standard length is 11.1 cm, the average female fecundity in a social setting is 51.2 eggs and in an experimental setting it is 88.7 eggs. The average periodicity is 67.2 days and the females were seen spawning with the male a total of 9 times.

Female	Date of Spawn	SL (cm)	Fecundity	Exp Spawn	Periodicity	Exp Fecundity	Male Chosen
SCF-002	03/26/15	11.7	58	06/21/15	87	81	Large
SCF-005	06/27/15	12.2	63	10/25/15	120	87	Not observed
SCF-006	09/14/15	11.3	43	11/18/15	65	86	Not observed
SCF-007	11/6/15	10.6	39	12/25/15	49	67	Large
SCF-008	11/18/16	11.5	63	02/15/16	90	114	Large
SCF-009	03/07/16	10.2	36	04/12/16	36	80	Not observed
SCF-010	03/16/16	10.1	34	05/02/16	47	76	Not observed
SCF-011	04/22/16	10.7	70	06/16/16	55	92	Not observed

Table 3.7. Continued

Female	Date of Spawn	SL (cm)	Fecundity	Exp Spawn	Periodicity	Exp Fecundity	Male Chosen
SCF-012	07/12/16	11.7	62	09/22/16	72	109	Not observed
SCF-013	07/30/16	11	44	09/19/16	51	95	Large

Table 3.8. Fisher's Exact Test for female mating. A total of 9 females were observed picking eggs from the bower. The result is significant as The Fisher Exact Test statistic value is 0.0325.

	Random Mating	Observed	Marginal Row Totals
Large Male	5	9	14
Small Male	5	0	5
Marginal Column Totals	10	9	19
The Fisher Exact Test statistic value is 0.0325. The result is significant at p<.05.			

3.4 Female Bites Throughout Her Ovulatory Cycle

The number of female bites also varied throughout the female reproductive cycle. The female displayed more bites towards the small male on day 2, day 6, and day 18. Table 3.9 shows interaction between the number of bites towards both males and the day of the female's ovulatory cycle (p=0.39). Additionally, the female displayed more bites towards the large male the following days before spawning: 7 days, 6 days, 3 days, 1 day, and on the day of spawning (Fig. 3.3). However, further analysis shows no significant difference for the bites displayed towards the small male (p =.012, Table 3.10) or the large male (p = .320, Table 3.11).

Table 3.9. Analysis of variance of female bites to the small and large male. The R Squared value is .144 (Adjusted R Squared= 0.041). There is interaction between the number of bites to the large and small male and the day of the female ovulatory cycle as the significant value is .39.

Source	Type III Sum of Squares	Df	Mean Square	F	Sig.
Corrected Model	123.785[a]	47	2.634	1.391	.051
Intercept	161.430	1	161.430	85.254	.000
Day	51.348	23	2.233	1.179	.260
Male Size	2.680	1	2.680	1.415	.235
Day X Male size	69.940	23	3.041	1.606	**.039**
Error	734.681	388	1.894		
Total	1037.000	436			
Corrected Total	858.466	435			

Table 3.10. Analysis of variance of female bites to the small male. The R Squared value is .181 (Adjusted R Squared=.084). The bites the females display to the small male throughout her ovulatory cycle is not significant (p =.012).

Source	Type III Sum of Squares	Df	Mean Square	F	Sig.
Corrected Model	58.344[a]	23	2.537	1.869	.012
Intercept	61.255	1	61.255	45.140	.000
Day	58.344	23	2.537	1.869	**.012**
Error	263.257	194	1.357		
Total	391.000	218			
Corrected Total	321.601	217			

Table 3.11. Analysis of variance of female bites to the large male. The R Squared value is .118 (Adjusted R Squared= 0.13). The number of bites the female displays to the large male throughout her ovulatory cycle is not significant (p=.320).

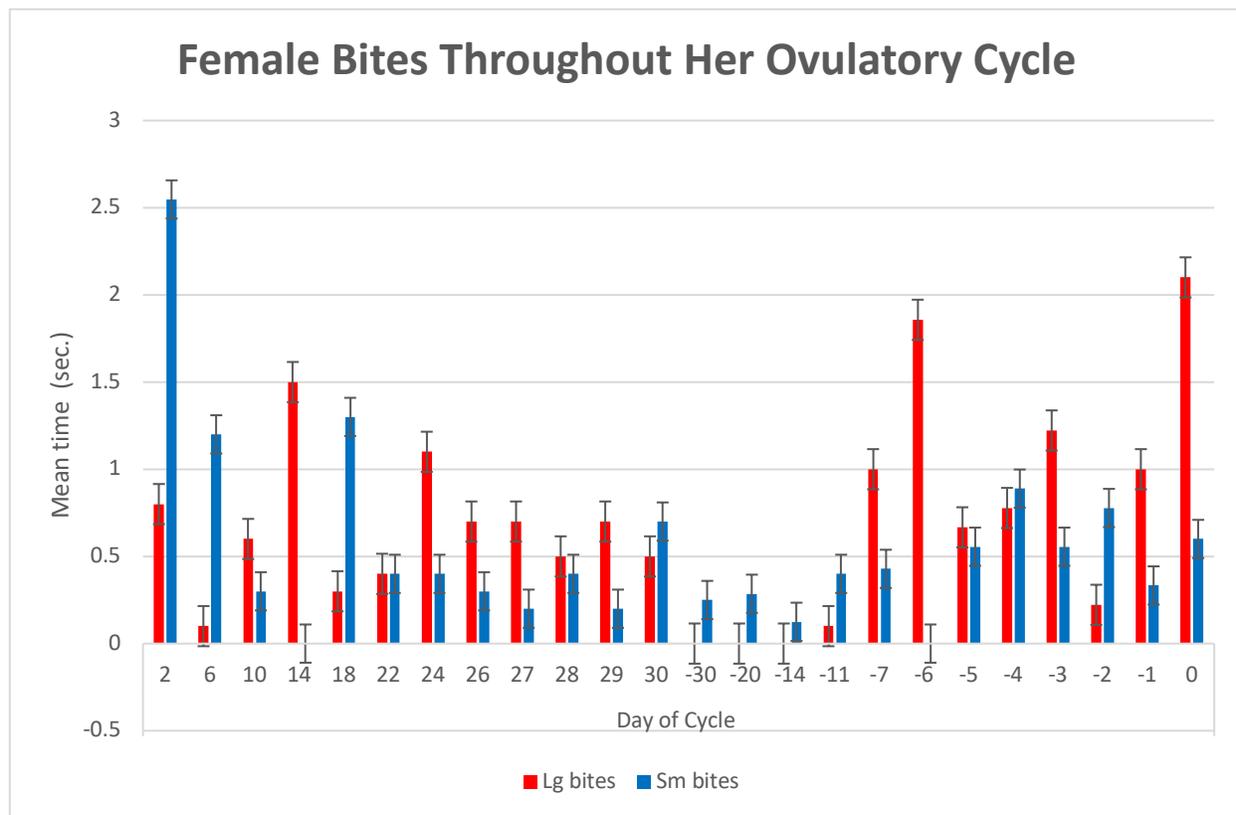| Source	Type III Sum of Squares	Df	Mean Square	F	Sig.
Corrected Model	62.943[a]	23	2.737	1.126	.320
Intercept	102.855	1	102.855	42.327	.000
Day	62.943	23	2.737	1.126	**.320**
Error	471.424	194	2.430		
Total	646.000	218			
Corrected Total	534.367	217			

Figure. 3.3. Female Bites Preference Throughout Her Ovulatory Cycle. The large male is demonstrated in red and the small male is represented in blue. Whiskers represent the standard deviation of the data.

CHAPTER 4

DISCUSSION

4.1 Female Association Time

Studies often use female association time with a male to measure a female mate preference without affirming the actual mating choice. This study demonstrates that in S. *caroli*, association time is predictive of the final choice of mate throughout the female reproductive cycle. Nine females displaying this behavior were seen spawning with the larger male, which supports the use of association time as an indication of preference. This is consistent with a previous study which found that in a binary choice, *S. galilaeus* females spent more time in front of the aquarium holding the larger of two individuals of the opposite sex (Balshine-Earn 1996). In contrast, (Kidd et al. 2013) found that in the lekking cichlid species *A. burtoni*, association time is predictive of the final choice of mate, however, only on the day of spawning. During the rest of the ovulatory cycle the females spent more time with the larger male.

The difference between female association time between the species *A. burtoni* and *S. caroli* might be the due to the hormones being expressed throughout the female's reproductive cycle. Steroid hormones are associated with a reproductive cycle as a mechanism to coordinate the timing of female reproductive effort with a maximum change for reproductive success (Ramsey et al. 2011). Estradiol is responsible for stimulating vitellogenesis in teleost and is secreted by the female gonads during the pre-spawning period (Taghizadeh et al. 2013). Prostaglandin plays a role in the coordination of gamete release between males and females of many teleost and induces spawning behaviors regardless of reproductive state (Kidd et al. 2010; Kidd et al. 2013). The effects of hormones on mate choice varies between mating systems. In the case of the polygamous cichlid *A. burtoni,* 17 β estradiol peaks prior to spawning followed by a

simultaneous rise in progestin and testosterone four days prior to spawning. Additionally, PGF2 levels peaked three days prior to spawning (Kidd et al. 2013). In this study, it was found that *S. caroli* females increase their time in association with the large male 14 days before spawning. This indicates that females select their spawning partner two weeks before spawning and employs a similar reproductive pattern as a monogamous species. In monogamous species, estradiol is circulating in a female's reproductive cycle two weeks or months prior to spawning. When estradiol is at its peak, it influences mate choice as it increases the time spent in association with the selected male. Progesterone is also present in monogamous species and it plays a role in territoriality and spawning preparation time.

4.2 Female Time Spent in Bower

Female association is a predictor of mate choice however, the bower is where reproductive behavior and spawning occurs. Bower size and shape vary between species and are considered manifestations of male behavior and characteristics (Kellogg et al. 2000). In lekking species, elevated male mating success is associated with increased bower size and bowers located in central locations (McKaye 1991). A major finding of this study is that female *S. caroli* spent more time in the bower of the large male instead of the small male on the final week before selecting a spawning partner. Additionally, time spent in the preferred bower during the last week was indicative of the final mate choice. On the contrary, in promiscuous species such as the *A. burtoni,* female time spent in the bower did not reflect the final choice until the day of spawning (Kidd et al. 2013). Surprisingly, the female would also spend significantly more time on the small male's bower and dramatically shift their bower preference to the large male on the day of spawning.

This study also found that in this species the time females spent in association and in the preferred bower was not reciprocal throughout the reproductive cycle. The female *S. caroli* displayed association preference for the large male at an early stage of the reproductive cycle, however, the time spent in the bowers of both males varied and finally increased bower preference for the large male near the completion of the cycle. A possible explanation is that the female is utilizing the bet-hedging strategy to select a potential mate. By using this tactic, the female continues to invest in assessing other potential mates even though they already favor a mate (Santangelo and Itzkowitz 2004). Under the bet-hedging hypothesis two factors influence the probability of becoming the first sire: body size and male fighting performances (Watson 1991). The female *S. caroli* may have already made her decision to spawn with the large male a week before spawning and invested time in the large male's bower the following days to engage in sexual displays such as quivering, lateral movements, and engaging biting behavior. In lekking cichlids, bet-hedging could take form in different ways such as to optimize genetic diversity, account for various female preferences in the population, or to hedge against imperfect selection criteria due to variation among males in the heritability of preferred traits (Kellogg et al. 1995). Bet-hedging is also supported in convict cichlids as studies have demonstrated the both females and male can switch partners when a higher quality mate appears (Triefenback and Itzkowitz 1998). Additionally, sierra dome spiders, *Linyphia litigiosa*, utilize the bet-hedging strategy and evaluate males by series of stringent tests of size and vigor to secure the best genetic material to produce the fittest offspring (Watson 1991).

The final stages of the estrous cycle are characterized by rapid changes in behavior categorized as proceptive, receptive, and lordosis, which are mediated by estradiol and progesterone (Fernandez- Guasti et al. 1991; Edwards and Pfeifle 1983). Proceptive behavior is

the reaction by the female toward the male to initiate and maintain sexual interaction (Edwards and Pfeifle 1983). In female rats, hopping and darting has been identified as proceptive behavior (Edwards and Pfeifle 1983). Receptive behavior indicates the female's willingness to accept male copulation and lordosis is the female's response to male copulation that facilitates fertilization of the eggs. In rats, estradiol is involved in the control of lordosis behavior and progesterone is essential for the display of proceptivity (Fernandez-Guasti et al. 1991). In fish, proceptive behavior is seen when the female visits the male's bower, however the proceptive female is not yet ready to spawn (Barlow 1992). Receptive behavior is seen when both the female and male engage in circling behavior in which the female and male make contact by touching nose to tail and swimming in tight circles (Kellogg et al. 2000). Lastly, lordosis analogous behavior is seen when the male curves and inverts his body towards the female (Villars et al. 1985) and fertilization occurs. In the *A. burtoni* species, females are generally proceptive throughout their cycle and become receptive once they are ready to spawn (Kidd et al. 2013). In contrast, *S. caroli* females become receptive a week before spawning, when they increase their bower visitations. Additionally, females might be engaging in proceptive behavior by having preference for the large male at the beginning of their cycle.

4.3 Female Spawns

This study reveals that when presented with a choice, female *S. caroli* prefer to spawn with the large male. In binary choice experiments, both males and females have shown a preference for large partners over small ones (Balshine-Earn 1996; Beeching and Hopp 1999). This size-based male preference has been seen in the polygamous species *A. burtoni* and bi-parental species, *Cichlasoma nigrofasciatum* and *Amatitliana nigrofasciatum* (Noonan 1983). Females show preference for larger males as they provide superior protection for eggs by having

the ability to clear its territory of offspring predators due to a more intimidating appearance (Balshine-Earn 1996; Gagliardi-Seeley and Itzkowitz 2006). Larger males are also more successful in male-male agnostic contests (Keenleyside et al. 1985) and in convict cichlids, size is directly correlated to fighting ability (Koops and Grant 1993). Additionally, large size males raise a higher percentage of young to independence than small males (Wisenden 1995). Balshine-Earn (1996) found that larger males are more likely to have more energetic resources than small males and therefore be able to invest more in raising a brood. Additionally, the cichlid *Astatotilapia flaviijosephi*, males preferred to court larger sized females (Werner and Lotem 2003). Females also increase their immediate fecundity when they receive direct benefits such as territory quality or paternal care. In a size assortative mating study on the cichlid *Cichlasoma nigrofasciatum* and *Neetrophus nematopus*, young surviving past 3 weeks had larger sized parents (McKaye 1986). Preference for large size mates is seen in other animals such as the fly *Scatophaga stercoraria*. Studies found that when females were free to select mates they showed preference for large-sized males as they are less likely to be physically harmed during male competition, have a more rapid copulation and oviposition, and a greater ability to escape during copulation as reports found that smaller-than average flies were most commonly eaten (Borgia 1981).

This study also reports the spawning behavior of the female *S. caroli* as it was visually monitored in the laboratory and the brooding female was also documented on the video recording. This species prefers to spawn in the evening, unlike most teleost such as the *Cyrtocara eucinostomus*, which prefer to spawn in the morning (Mckaye 1983). This new information allows future studies on this species to be better executed or replicated as experiments can be scheduled during the spawning time preferences of the *S. caroli*. By

adjusting recording equipment during the evening when *S. caroli* are the most active in displaying spawning behavior, more information about to their mating preference, courtship, and pair bonding formation and its duration can be better understood.

4.4 Female Bites

We observed a large amount of variation in the number of bites the female displayed towards both males. However, the female increased the number of bites towards the larger male six days before spawning in the experimental setting. A possible reasoning is that the female bites the larger male more frequently a week before spawning in an attempt to establish a pair bond. This can be an assumption as the time the female spends in the bower also increased during this time. The formation of a pair bond is usually seen in monogamous animals and is characterized by mutual friendliness and efforts to maintain proximity (Lamprecht and Rebhan 1997). Interestingly, in the monogamous convict cichlids, *Cichlasoma nigrofasciatum*, pair formation occurs in the latter part of the territoriality phase with minimal courtship behavior (Mackereth and Keenleyside 1993). Courtship is viewed as a phase for potential mates to advertise their quality (Santangelo and Itzkowitz 2002; Gumm and Itzkowitz 2007). A courtship bout will often start by an interested male approaching the female (Werner and Lotem 2003). Males can then display body quivers and fast turns towards the female (Kellogg et al. 2000). A more intense courtship will ensue if the female remains in the same location or approaches the male (Werner and Lotem 2003) and is characterized by males and females spending an increase amount of time together two days prior to spawning. In the species *Archocentrus nigrofasciatus*, males expressed their mate preferences through courtship whereas females did so through time spent with selected male (Santangelo and Itzkowitz 2004). This may be the result of polygamous species performing multiple levels of mate assessment at the moment of spawning while

monogamous species performing mate assessment during pair formation days prior to spawning. Additionally, Barlow et al. (1977) found that no pairs can form if the female shows any signs of fear. In the *Cichlasoma cyanoguttatus,* females were more successful in re-establishing the pair bond when displaying more female aggression against the male than those females who did not display the same level of aggression (Makie and Itzkowitz 1985). Additionally, McKaye and Barlow (1976) report that aggression by and against a pair is at its highest when a pair is attempting to acquire a territory. Further analysis is encouraged to understand the underlying reason there is a lot variability in the amount of bites the female displays to both males.

CHAPTER 5

CONCLUSION

This study explores the behavior of the female *S. caroli* throughout the reproductive cycle. In this species, females had an association preference for the large male instead of the small male. Female preference for more attractive large males may be due to advantages the females receive such as brood survival, better resources, and predator defense. Additionally, females had preference for the bower of the large male six days before spawning, which was indicative of their mate selection. Unlike the polygamous cichlid species *A. burtoni*, which have a bower preference for the large male on the day of spawning (Kidd et al. 2013). Female bower preference peaked on the days prior to spawning probably due to females utilizing the bet-hedging strategy. This is not uncommon as other animals such as the *P. zebra* have used the bet-hedging strategy to maximize the opportunity to select the most attractive mate.

A more detailed study is encouraged in order to understand the underlying reason as to how pair formation occurs in this species. One reason there is variation in the number of bites is due to the dual nature of bites. Bites can be used to display courtship behavior; however, it can also be used to display aggression. The variation in the number of bites towards both males gives the opportunity to better understand female aggression towards the male she rejects and the formation of a pair bond for the male she chooses as a mating partner. Additionally, although a semi-permeable partition is an excellent structure to study mate choice, perhaps a partition that allows tactile interaction can provide insight such as how pair formation occurs in this species and to disentangle the duality of bite behavior.

This study also allows the opportunity to expand mate choice into a hormonal study to have a better understanding of the reproductive cycle of the female *S. caroli*. Since the

reproductive behavior of a female *S. caroli* resembles that of a monogamous species, the hormone that can be used to expand this project is estradiol. In order to test the effect estradiol has on the reproductive cycle of female *S. caroli*, a non-reproductive female must be injected with estradiol. Based on the results of this study, if estradiol has a role in the reproductive cycle of *S. caroli* females, the non-reproductive female will increase the time she spends in the bower of the large male a week prior to spawning. Additionally, this study can also be expanded to test how the male's behavior and hormone release influence the mate choice of a female. A complete profile of hormonal and physiological stages across the reproductive cycle of *S. caroli* is encouraged to increase our understanding of the effects of endocrine releasers to female behavior and mate choice.

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