Cost Avoidance in Mating Systems: Theory and Lessons from Coho Salmon (*Oncorhynchus kisutch*)

By

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If I told you what it takes to reach the highest high
You'd laugh and say
'Nothing's that simple'
But you've been told many times before
Messiah's pointed to the door
And no one had the guts to leave the temple

-The Who-

For Seren –
a finer sneaker there never was

And
For Shay

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Abstract of the dissertation

This work integrates theory and empirical study to develop and support a new hypothesis of sexual selection. The Cost Avoidance Hypothesis (CAH) (Chapter 1) states that to achieve reproductive success, un-preferred males should coerce females by imposing pre-copulatory costs on those females. In this way, females choose to mate with these un-preferred males to avoid incurring further costs. The CAH additionally states that females and preferred males should cooperate to ensure low-cost reproduction. This cooperation between members of a mating pair is predicted to minimize pre-copulatory costs, even in the face of coercion. Thus, the simultaneous occurrence of coercion and cooperation in mating systems is likely to be an important force in sexual selection.

The CAH is examined in coho salmon (*Oncorhynchus kisutch*). This species is well known for the occurrence of two male phenotypes. These phenotypes, known as "hooknoses" and "jacks," represent males who have taken alternative life-history paths. The large hooknose is three years of age at maturity while the small jack matures at only two years of age. Mature hooknoses are fighters, gaining access to females with force, while jacks draw little attention to themselves by hiding and moving in towards females when the opportunity arises. But the behavior of adult males belies the circumstances that carry a growing juvenile along a given path to maturity. Other researchers have shown that large juveniles are those most likely to mature early, as jacks. Chapter 2 shows that the distribution of resources in the natal habitat plays an important role in directing the growth rate of juveniles and the subsequent expression of alternative reproductive phenotypes. When resources are clumped, the growth rates of individuals vying for those resources vary. Conversely, when resources are evenly spread, individuals grow at similar rates. Under clumped resources, the expression of alternative phenotypes is higher than under evenly spread resources. Chapter 3 tests the predictions that female coho salmon prefer to mate with early maturing jacks, and given this mating preference, hooknoses coerce females to mate by increasing pre-copulatory costs. Data collected in a field study of wild spawning coho salmon support these predictions.

Chapter 1

The Adaptive Value of Cheap Sex: Cost Avoidance in Mating Systems

Abstract of the chapter

By considering the simultaneous effects of inter- and intra sexual interactions, I provide new insight into mating systems and the adaptive value of elaborate sexually selected traits. I present a model of optimal mate choice in which females prefer males with high heritable viability. In the model, male phenotypes are indicative of their viability. In order for males of lower fitness to attain reproductive success, they must contend free female mate choice by coercing females. Females and preferred high fitness males then must cooperate to facilitate mating and avoid the costs of coercion. This simultaneous coercion and cooperation provides an arena in which there is selection for non-preferred males to develop traits useful in coercion. When the costs of coercion are high relative to the benefits of cooperation, females may choose to mate with low fitness non-preferred males. In cases where coercion is common, cooperation to secure preferred matings may occur quickly. Indeed, I suggest that elaborate male traits are often those that are useful in coercion and that quick, efficient "sneak" mating by seemingly drab males may be a means to facilitate preferred matings. Where coercion cannot be avoided, females may evolve life history characteristics that minimize the fitness costs of mating with non-preferred males.

Introduction

Sexual selection is a cornerstone in phenotypic evolution because it gives rise to elaborate traits. Darwin (1871) suggested that sexual selection is the outcome of two types of relationships, intrasexual and intersexual. Perhaps because of this initial division of the mechanisms of sexual selection, many explanations of the evolution of sexually selected traits examine either the outcome of competitive interactions between males (e.g. Souroukis and Cade 1993) or the mating preferences of females (e.g. Ryan 1980; Aspbury and Basolo 2002). This approach has proven successful in describing the forces acting on phenotypic evolution in many controlled contexts. Alternatively, one-sided views of the processes giving rise to sexual selection may cause some interpretations of empirical work to suffer because they come from a confined perspective (Alonzo and Sinervo 2001; Kennedy 1992; Qvarnstrom and Forsgren 1998). With this in mind I consider here the simultaneous effects of intra- and intersexual relationships on phenotypic evolution.

Individuals maximize their evolutionary fitness by increasing their reproductive success. The active choice of preferred mates and mate coercion are two conflicting means by which members of alternate sexes attempt to maximize their reproductive success. The occurrence of inter-sexual conflict is ubiquitous (Elgar et al. 2000; Herberstein et al. 2002), and leads to selection for new sexual phenotypes (Parker 1979). However, instances where mates cooperate in order to consummate reproduction have been largely overlooked. Presumably, situations where females encounter preferred males should lead to cooperation to facilitate reproduction rather than to contention between mates.

A mating preference is an internal property of an individual (after Heisler et al 1987). In contrast, a choice is the physical manifestation of the underlying preference and all factors that may affect the outcome of and the ability to actively pursue that preference (Wagner 1998). As a result, mate choice can vary as a function of the preference and the current situation. Thus, there is a fundamentally important distinction between mate choice and mating preference. Mate choice is directly measurable and the difficult task is to determine whether an observed choice reflects an adaptive preference.

In the case where a female prefers a male, it would behoove that male, if he finds the female suitable, to facilitate mating. Reciprocally, it would benefit the female to act in a manner that allows easy fertilization of her eggs by the preferred male. In short, preferred mates should cooperate to assure mating. The process of facilitating reproduction would be easiest if preferred mates possessed some honest phenotypic signal of their mating value (Zahavi 1977; Kodric-Brown and Brown 1984) relative to other members of the population such that further assessment is unnecessary (Luttbeg 1996). In situations where such preferred mates are encountered, mating should occur in an efficient manner so that the costs associated with mating are low for both parties. This cost reduction should occur because when individuals mate, their fitness functions become linked due to a shared interest in jointly produced offspring. Thus, mates that are cooperating should act to limit the costs they impose on each other because such costs reduce their expected fitness. In contrast, individuals that are not preferred by members of the opposite sex can attain mates only through coercion. Coercion is the induction of a choice that is not a preference. There may be costs associated with this imposed choice, or the lack of making it (Clutton-Brock and Parker 1995). For example these costs may result from many actions that represent both intra- and intersexual relationships, including disrupting preferred matings, directly harassing the intended mate (e.g. (Jaeger et al. 2002), controlling resources (Sato 1994), attracting predators (e.g. Rosenthal et al 2001; (Herberstein et al. 2002) and punishing refusal to mate (Clutton-Brock and Parker 1995). When females are confronted with the costs associated with coercion by non-preferred males, they may make the choice to mate with these males rather than pay such costs. In these cases, the mate choice observed is not the choice of a preferred mate.

An example illustrates the point. In coho salmon, *Oncorhynchus kisutch*, there are two male-types (Gross 1985). One type, called a hooknose, is large and brightly colored. It fights for access to females and actively guards them. The other type, called a jack, is small and cryptically colored. This type usually darts in to fertilize eggs when females oviposit and is considered to be a “sneaky” mater. In addition to the observed phenotypic differences in this species, there are life-history differences among the male-types. Jacks mature a full year earlier than the hooknosed males of their cohort because, as juveniles, they attain high growth rates (Hager and Noble 1976; Bilton 1978). This earlier maturation means that jacks are more likely to survive to reproduction than hooknoses (Gross 1985; Gross 1991). There is a genetic component to early maturation (Iwamoto et al 1984), but a male cannot mature as a jack unless he acquires and defends a superior feeding station as a juvenile and grows to a threshold size (as described in Thorpe 1994 for Atlantic salmon, *Salmo salar*). In short, the phenotype of jack male coho salmon is an honest signal of the life history trajectory they have taken. Individuals following this life history trajectory are far more likely to survive to maturity than those taking the alternative (hooknose) path (Gross 1985). It is possible that female coho salmon indeed prefer to mate with jacks (Gross 1996) because jacks carry genes that confer high viability. Arguably, these males that are merely a fraction of the size of females would have a difficult time physically coercing females. I suggest that in the salmon mating system, and many others, the elaborate traits of fighter males have evolved not in response to female preferences for them, but rather, to limit females' ability to choose freely.

Here, I present a model that allows for simultaneous coercion and cooperation to occur in mating systems. I assume that female mating preferences are for males with high heritable viability (Williams 1966; Andersson 1994). I then ask what consequences these predicted preferences have for non-preferred males. The model shows that non-preferred males might coerce female mate choice decisions to favor them and that preferred males may facilitate female preference. I consider the possibility that in species with alternative male phenotypes ("sneakers" and "fighters"), it is the small "sneaker" male that females prefer. These males are often more likely to survive to maturity. In this new interpretation, sneaking is a means to facilitate mating quickly and efficiently in the face of the costs associated with coercion by non-preferred males. Large "fighter" or "courting" males acquire mates through coercion. I then discuss the reproductive phenotypes expected to evolve in light of the coercion-cooperation paradigm.

The Model

Evolutionary game theory predicts the phenotypes likely to evolve when the optimal behavior of one organism depends on the actions of others (Maynard-Smith 1982; Parker and Maynard-Smith 1990). Thus, game theory is appropriate for modeling the evolution of mating systems because when individuals mate, their fitness depends on the actions of each other as well as those of individuals with whom they do not mate. When there is initially more than one type of mate, we can determine stable frequencies of alternatives and/or the behavioral responses that maintain alternatives in a population. We can also describe the factors likely to lead to the loss of one alternative from a population.

In the model presented here, phenotypes are heritable (as per Maynard-Smith 1982). In addition to phenotypic heritability, I assume that there is a phenotype by life history correlation. In other words, the phenotype of an individual is an indicator of the life history path that it has followed (Gustafsson et al. 1995). Heritable variation in life histories should lead to variation in the fitness prospects of individuals in a population (Falconer and Mackay 1996; Roff 2002). These fitness differences occur because if there is a particular life history pathway that fares best in a given environment, variation in life histories will equate to viability differences among the members of a population. Females prefer those males with highest viability, and the phenotypes of males are indicators of this viability. As such, the model presented here is a “good genes” model (Andersson 1994; but see Kokko 2001).

In this model there are two male-types, one of high viability (Type I), and one of low viability (Type II). Imagine that these viability differences arise as a result of differential development (e.g., Morris and Ryan 1990) or variation in habitat use by the two male-types (e.g., Greeff 1998). The model as presented calculates the fitness of individuals where the probability of a male siring its like male-type equals 1. This though, is not a necessary assumption. The only necessary assumption is that there is some probability that Type I males sire Type I offspring at a higher rate than Type II males do. An individual's expected fitness (//) is the number of offspring it will have that survive to maturity given no variation in generation time. For females this fitness then varies with the ratio of Type I and Type II offspring and with respect to the social situation in which mating occurs.

In the model, females must make a choice between Type I (high viability) and Type II (low viability) males. For simplicity, males of a given phenotype are identical, although this is easily modified. All individuals mate only once. Presented here are the expected fitness payoffs (//) for a female who chooses either Type I or Type II males and the male fitness payoffs given female choice. Two versions of the model are presented, one for internal and one for external fertilization. Under internal fertilization, a female can mate with only one male so the chosen mate's fitness equals that of the female. Conversely, with external fertilization it is possible that more than one male fertilizes a female's eggs. In this case the proportion of the female's eggs fertilized by a male determines his fitness payoff. A female's fitness, and thus the fitness of her mate(s), is influenced by the frequency of Type I males (F) within the operational sex ratio, and by the behaviors of all prospective mates. Note that F is not explicitly the frequency of Type I males in the population, rather it is the frequency of Type I males at a mating event. As such, the operational male-type frequency can be modified by the actions of individuals at the mating event.

The remaining parameters in the model are:

V, male viability

/ /, a cooperation parameter, and

C, the cost of coercion.

Subscripts denote the male-type (1, high viability and 2, low viability) to which a parameter is ascribed. For example, if the female chooses Type I males, she cooperates with them ($\square_1$), while at the same time she is coerced by Type II males (C_2). A female's expected fitness is a function of the relative frequency of each type of male ($\square(F)$).

For the model under internal fertilization the payoffs to a female for a given choice are expressed as follows:

Choose Type I $$\square(F)_1 = \left[1 \square C_2(1 \square F)\right]^{\square_1} V_1, \qquad (1.1)$$

Choose Type II $$\square(F)_2 = [1 \square C_1 F]^{\square_2} V_2, \qquad (1.2)$$

Take the best $$\square(F) = \max\left\{\square(F)_1, \square(F)_2\right\}. \qquad (1.3)$$

When $V_1 > V_2$ and $\dfrac{\left(1 - C_1 F\right)^{\square_2}}{\left(1 - C_2 (1 - F)\right)^{\square_1}} < 1$, then

$\square(F)_1 > \square(F)_2$. (1.4)

When $V_1 > V_2$ and $\dfrac{\left(1 - C_1 F\right)^{\square_2}}{\left(1 - C_2 (1 - F)\right)^{\square_1}} > 1$,

$\square(F)_1 \square \square(F)_2$, and finally (1.5)

when $V_1 > V_2$ and $\dfrac{\left(1 - C_1 F\right)^{\square_2}}{\left(1 - C_2 (1 - F)\right)^{\square_1}} = \dfrac{V_1}{V_2}$,

$\square(F)_1 = \square(F)_2$. (1.6)

Cost is simply reflected as a reduction in the female's overall clutch size of 1. Overall cost increases with the frequency of the non-chosen male-type. As $\square \square\ 0$, cooperation between the female and the chosen male-type becomes more and more coordinated. Thus, $\square = 0$ might be considered perfect cooperation and $\square =$ no cooperation at all.

Now turning to males, the payoffs to males given female choice are expressed for Type I ‘s as follws:

When $\square(F)_1 \geq \square(F)_2$, $\square(F) = \square(F)_1$ and otherwise $\square(F)$=0. (1.7)

Then for Type II males:

When $\square(F)_2 \geq \square(F)_1$, $\square(F) = \square(F)_2$ and otherwise $\square(F) = 0$. (1.8)

With external fertilization females can opt not to directly choose any male-type. When females do not choose, they simply oviposit and male-types fertilize a female’s eggs in proportion to their frequencies at the mating patch, and no cost is accrued by the female. This lack of direct female choice is an assumption of models of sperm competition under external fertilization (Ball and Parker 1996; Ball and Parker 1997; Parker et al. 1996) though the model presented here leaves aside sperm competition for simplicity. If a female chooses a particular male-type and cooperation ensues, chosen males fertilize some greater proportion of eggs than random. Females can either accept some cost for enacting their preference, or avoid this cost by not choosing. Thus, in the external fertilization model, the subscript *N* denotes no choice.

For the model under external fertilization the payoffs to a female for a given choice are:

Choose Type I: $\square(F)_1 = \left(1 \square C_2(1 \square F)\right) \square F^{\square_1} V_1 + (1 \square F^{\square_1})\left(FV_1 + (1 \square F)V_2\right) \square$ (2.1)

Choose Type II: $\square(F)_2 = (1 - C_1F)\left[(1-F)^{\square_2} V_2 + \left[1-(1-F)^{\square_2}\right]\left(FV_1 + (1-F)V_2\right)\right]$ (2.2)

No Choice: $\square(F)_N = FV_1 + (1-F)V_2$ (2.3)

Take the best: $\square(F) = \max\left\{\square(F)_1, \square(F)_2, \square(F)_N\right\}.$ (2.4)

When $V_1 > V_2$

$\square(F)_1 \geq or \square\square(F)_2 \square\square(F)_N.$ (2.5)

With external fertilization, it is possible that more than one male fertilizes a female's eggs. For example, in equation (2.1), a female choosing to mate with Type I males will cooperate with Type I males. Cooperation effectively increases the frequency of Type I's available to the female ($F^{\square_1}$). $F^{\square_1}$ then represents some proportion of the female's eggs fertilized by Type I males. The remainder of the eggs, $1 - F^{\square_1}$, are fertilized by all of the males present (Type I and Type II) in proportion to their frequency at the mating site ($FV_1 + (1-F)V_2$). At the same time, Type II males will attempt to coerce the female to choose otherwise. Type II's do this by imposing a cost on females who choose Type I's ($\left(1 - C_2(1-F)\right)$). If this cost is too great, females should avoid it and not choose Type I males.

Thus, the payoffs to males given female choice are written*:*

Type I:

When $\square(F)_1 > \square(F)_2$ and $\square(F)_1 > \square(F)_N$,

$$\square(F) = \left(1 - C_2(1 - F)\right)\left[F^{\square_1} V_1 + (1 - F^{\square_1}) F V_1\right]. \qquad (2.6)$$

When $\square(F)_2 > \square(F)_1$ and $\square(F)_2 > \square(F)_N$,

$$\square(F) = \left(1 - C_1 F\right)\left[1 - (1 - F)^{\square_2}\right] F V_1. \qquad (2.7)$$

When $\square(F)_1 \square \square(F)_N \geq \square(F)_2$,

$$\square(F) = F V_1. \qquad (2.8)$$

Type II:

When $\square(F)_1 > \square(F)_2$ and $\square(F)_1 > \square(F)_N$,

$$\square(F) = \left(1 - C_2(1 - F)\right)\left(1 - F\right)^{\square_1}\left(1 - F\right) V_2. \qquad (2.9)$$

When $\square(F)_2 > \square(F)_1$ and $\square(F)_2 > \square(F)_N$,

$$\square(F) = \left(1 \square C_1 F\right)\left[(1 \square F)^{\square_2} V_2 + \left[1 \square (1 \square F)^{\square_2}\right](1 \square F)V_2\right]. \tag{2.10}$$

When $\square(F)_1 \square \square(F)_N \geq \square(F)_2$,

$$\square(F) = (1 \square F)V_2. \tag{2.11}$$

Analysis

To determine the optimal behavior of males in the model, I allowed males of both high and low viability to be any of four basic behavioral phenotypes. These were 1) do nothing (neither coerce nor cooperate), 2) coerce, 3) cooperate, and 4) coerce/cooperate. These male phenotypes were then allowed to “compete” for mates. Competition for mates was resolved by determining the optimal female mate choice for a given pair of male-types when males were encountered simultaneously (Table 1.1). For internal fertilization, the male-type chosen was considered the winner. With external fertilization, though, often the optimal behavior for females is to exhibit no mate choice. As such, under external fertilization, low viability males were ascribed a win if females made no choice. High viability males were winners if the optimal female choice was to cooperate with them for mating. In addition, the frequency of male-types competing for mates was varied, as were the abilities to coerce or cooperate. In this way, the model was analyzed under several different conditions (parameter sets). This analysis allowed the comparison of the relative success of different male tactics.

Note that with internal fertilization, males of the same viability class (high or low), but otherwise alternative phenotypes (i.e. coercer or cooperator) are able to compete against each other. Thus with internal fertilization, there are 7 possible encounters for a given male phenotype for each parameter set (Table 1.1A). With external fertilization, however, females control the timing of oviposition. In this case, when females simultaneously encounter males that represent the same fitness expectations, the optimal decision is to make no choice. For example, when a coercing male and a male of equal viability who imposes no cost are encountered at the same time, the female will not choose between them. In this case, external fertilization allows females to avoid costs by making no mate choice in situations where mate choice will not increase her expected fitness payoff. Thus for male phenotypes under external fertilization, there were 4 relevant encounters per parameter set (Table 1.1B).

Visualizing the outcome

For a given set of parameter values, one can plot on a single line the number of winning encounters for males playing a particular phenotypic strategy against the other strategies. Figure 1.1A represents the number of times a Type I cooperator “wins” in these encounters under external fertilization. Note that of the parameters on the line only some may comprise the strategy plotted. Other parameters represent the contender strategies. For example, in Figure 1.1, only the parameter a1 ($\square_1$ in the model) is part of the “Type I pure cooperator” phenotype. The other parameters, C1, C2 and a2 (C_1, C_2

and $\square_2$ respectively) are components of alternative phenotypes, against which the pure cooperator competes. F is the frequency of the Type I males. Thus, by looking at the figure, we can determine how many of the encounters with alternative male phenotypes the phenotype of interest wins for the denoted parameter set.

Plotting several such parameter sets together gives an impression of how successful a given phenotypic strategy is across a number of situations (Figure 1.1B). By connecting the points on the individual lines to produce a polygon, we can see the overall success of a strategy. Comparing graphs of the payoffs to each strategy gives a picture of which strategy is most successful and under which parameter values it succeeds or fails. The strategy that covers the largest area across the range of parameter values is the most successful. Any strategy that fits entirely within the area of another strategy always loses to that strategy.

Constraints

The ability of a male to coerce can be determined by a constraint function. The constraint can be such that its largest negative effect is on low viability males, or on high viability males. When the ability to coerce increases with viability ($C=Vx$; where x is a positive constant), this constrains the ability of low viability males to coerce and is no different from the assumption of many models that high viability males are most vigorous (e.g. Zahavi 1977; Kodric-Brown and Brown 1984).

With an alternative constraint, the ability to coerce decreases with viability ($C = \frac{x}{V}$). This type of constraint may arise in species where high viability males, those most likely to survive to maturity, mature earlier than low viability males at a small size (e.g. Gross 1985; Morris and Ryan 1990). Conceivably, such small highly viable males are incapable of delivering a substantial cost to females. In many such species, large males mature later and are far less likely to survive to maturity. They are low viability males capable of delivering a substantial cost. This constraint favoring low viability males may also appear in species where males who invest less in weaponry live longer than those who invest heavily in weaponry (e.g. Radwan and Bogacz 2000).

Results

The models suggest there should be positive frequency dependent selection on male phenotypes. This result is contrary to much research that indicates negative frequency dependent selection on male phenotypes (Gross 1985; Hamilton 1979; Hunt and Simmons 2002). This positive frequency dependent selection results from female ability to make optimal mate choice decisions in the presence of simultaneous coercion and cooperation by males conferring unequal fitness. When the ability to collaborate with preferred high viability males is high, females choose these males. It is easiest for females to collaborate with preferred males when they are common. Conversely, the cost of coercion increases for females when coercers are prevalent. Thus, considering the female perspective indicates that male phenotypes find themselves in yet another conflict. From an individual male's perspective, it is best to be of the rare phenotype to avoid direct competition with similar males, but at the same time it is best to be of the common phenotype because females are more likely to choose a common male-type. For any male, the best solution to this problem is to be alone with a female and facilitate mating if she will allow it – and coerce her if she will not.

Internal fertilization

With no constraint on the ability to coerce, under internal fertilization, the best strategy for either a high viability male or a low viability male is to be a coercer/cooperator (Figure 1.2). Though the same behavioral phenotype is best in both viability classes, it is the result of selection for those behaviors in different contexts. When in competition against males of equal viability (eg Type I vs Type I), a pure cooperator never wins, and a pure coercer wins against all but a coercer/cooperator. But when in competition against males of the other viability class (Type I vs Type II), pure cooperator Type I males win often while pure cooperator Type II's never win.

With constraints on the ability to coerce, the optimal male phenotype is still a coercer/cooperator. When the constraint is such that high viability males are the most successful coercers, high viability coercer/cooperators should be the sole male phenotype in the population. When low viability males are more adept at coercion though, it is possible to maintain alternative male phenotypes in a population. Such a constraint can balance the reproductive success of male phenotypes if the relative benefits of coercion and cooperation are the same for alternative phenotypes.

External fertilization

Under external fertilization, for males the best strategies are cooperate if high viability, and coerce if low viability (Figure 1.3). However, for high viability males, there is no selection against coercion when it is coupled with cooperation. Unlike internal fertilization, if females control the decision to mate a coercer/cooperator does no better than a pure cooperator. Likewise, for non-preferred low viability males, there is no advantage to being a coercer/cooperator over being a pure coercer (Figure 1.3).

The Cost Avoidance Hypothesis

I suggest that many elaborate sexually selected traits have evolved not in response to female preferences for them, but rather because they effectively limit females' abilities to choose freely. Through the elaboration of cost imposing traits, non-preferred males gain mating success and obtain high fitness. I propose a "Cost Avoidance Hypothesis" of sexual selection, which states that in circumstances where females are confronted with the costs associated with coercion by non-preferred males, they may make the choice to mate with these males and forego paying such costs. In addition, the Hypothesis states that preferred males should exact little cost from females during mating. These males should work with females to facilitate inexpensive reproduction. In either case, an optimally behaving female should act to reduce her costs. As noted above, this mode of sexual selection can result in the evolution of cost imposing strategies in non-preferred male-types. It can also result in the evolution of cost reducing strategies by male-types that are preferred by females based on their success in the face of natural selection.

The possibility for a runaway process in which increased coercion is met with increased cooperation exists. However, such a runaway process is likely to be constrained by two factors 1) the ease of coercion and 2) the coordination of cooperation. For example, if coercing is extremely costly, we should expect to see only high viability males in a population regardless of the ability to cooperate. On the other hand if it is very easy for low viability males to coerce females to mate, high viability preferred males may be lost from the population. Alternative male-types can be maintained in a population if the cost of coercing and the cooperation effort balance such that there is a stable frequency of male-types.

Implications

Males who are successful coercers should be able to control the behavior of females, and limit the ability of females to choose other males. Physically overpowering females is one obvious means by which males can coerce mates. Physical coercion of females by males is common. For example, in the Lake Eyre dragon lizard, *Ctenophorus maculosus*, males press and hold females to the ground while attempting to copulate. For female dragons, resistance leads to wounds and possibly higher predation. Large females are more likely to threaten males attempting to mate with them than small females (Olsson 1995). An interpretation based on the model above is that the cost associated with mate rejection is comparatively lower for large females than for small females and that the overall costs of forced copulation are small for males relative to the associated pay-off in reproductive success. Because large females can sustain more cost, for them, the decision to choose a non-preferred mate should occur at a lower F than for small females. A prediction is that large females are more likely than small females to exhibit mate choice and in fact incur a higher measurable cost by refusing coerced copulation. Small females must avoid the cost associated with forced copulation and allow males capable of imposing such costs to mate without rejection.

Coercion need not be so blatant. In many species, males guard their mate. Mate guarding can be viewed as a means to limit free female choice by preventing access to other males. For example, in the soapberry bug, *Jadera haematoloma*, males from populations with a male biased sex ratio mate guard (Carroll 1993; Carroll and Corneli 1995). Females separated from their mates remate quickly with new males. As much as 72% of the prior male's sperm is displaced upon remating (Carroll 1993). Thus, mate guarding serves to assure fertilization and therefore can be either coercion or cooperation. If the probability of a female obtaining another mate that confers a greater fitness payoff is high, mate guarding is coercion.

Coercion (and cooperation) can also take the form of resource holding. Females need resources to survive and reproduce. In many species males defend resources and females who mate with them gain access to these resources. To establish whether resource holding is coercion or cooperation as described in the above model, it is necessary to determine whether females, if males all had the same value of resources, would choose to mate with males that normally do not acquire the highest value territories. Under these conditions, if females choose to mate with males that are otherwise subdominant, then controlling required resources is a subtle coercion because it limits female choice. Such coercion might be particularly expected in species that require specific nesting conditions. For example, in the pupfish, *Cyprinodon pecosensis*, females favor laying their eggs in exposed rocky substrate to laying them in sand or silt (Kodric-Brown 1977). By controlling territories of the favored rocky substrate, certain males acquire many mates. It is unknown whether, all else being equal, the offspring of territory holders are likely to have higher or lower survival than the offspring of males who do not hold territories. However, adding more exposed rocky substrate to a habitat, results in more males being able to hold territories and a decrease in the variance of their reproductive success (Kodric-Brown 1978). This observation suggests that female choice of mates is confined by the need to acquire good oviposition sites. Those males that acquire good locations mate with females that prefer not to leave their eggs in low quality substrate. The cost that females avoid in this situation is clear. Leaving eggs in low quality habitat reduces the likelihood of those eggs hatching. Pupfish males may thus act as coercers. By placing a high demand on necessary oviposition sites, these males may limit females' ability to choose their preferred mate.

Female mate choice can also be constrained by the behavior of predators. In this light, attracting predators can be a successful means of coercion. In many species, courtship displays draw the attention of predators (Sih 1987; Magurran and Nowak 1991; Fuller and Berglund 1996; Rosenthal et al 2001). Although the probability of being attacked by a predator is likely to be higher for a courting male than for a female being courted, the likelihood of a female being attacked must increase as a result of courtship because males perform courtship displays in close proximity to prospective mates. A cost-avoiding female then will choose to mate with a courting male even if he is a low viability, non-preferred male. This choice is likely to occur particularly if the male is relentless in courtship such that the female has already been able to assess his quality. Thus, when the cost of courtship for females is above that necessary to determine mate quality, courtship is coercion. Cost-avoiding females may mate with courting males who are attracting predator attention or preventing them from performing other behaviors such as feeding. This form of cost avoidance will occur where males either leave females alone after mating, allowing them to return to routine life, or where once mated, males protect females from further harassment. In short, mating with a non-preferred male must reduce the costs of not mating with him. Thus, quickly mating and terminating extended coercion may be a good strategy for a cost-avoiding female.

Cooperation, too, can be quick. The model predicts that, in the face of coercion, cooperation must facilitate mating efficiently to reduce the cost of mating for both females and preferred males. This task is easiest if the time required by females to assess males is short. Assessment time is reduced by honest phenotypes. In this case, an honest phenotype is one that clearly demonstrates the life history trajectory taken by males. The predictions of the above model suggest that the "sneaking" mating tactic used by some small males, may in fact be quick and efficient facilitation of mating in the presence of predators, coercers, or both. Figure 1.4 compares the classic paradigm where the sneaky male is not preferred with those of the cost-avoidance paradigm, where the sneaky male is high viability and preferred. In the figure, the predictions regarding the speed with which mating occurs in different situations are compared.

Females may play a vital role in sneak mating. The model predicts that cooperation to achieve matings should be highly coordinated. In the presence of non-preferred males, drawing attention to preferred males may lead females to lose access to their preferred mate. Instead, females in the presence of preferred males who possess honest phenotypic signals of their viability should do what they can to facilitate quick and efficient mating. Thus, a cost-avoiding female may act in a very subtle manner in order to gain access to the preferred male-type. Indeed, the predictions of the model suggest that a cost-avoiding female should spend very little time in the company of preferred males, and matings with these males should occur quickly and efficiently so as to limit costs. Consequently, assessing female mating preferences is difficult. This difficulty arises because on the one hand females may mate quickly with coercing males to avoid further coercion, and on the other hand females may show no clear tendency to associate with preferred males

Females may also be very un-subtle in their cooperation with preferred males. When coercion is common, females may invest in their own size or in weaponry used to thwart males (Arnqvist and Rowe 2002). The model suggests that females evolve means to satisfy their mate preferences. A large female capable of dominating males should be able to exert mate choice. If females in high coercion populations grow larger to avoid coercion, they may mature later or allocate fewer resources to fecundity than females in low coercion populations. Such differential allocation of resources to growth and fecundity is predicted by life-history theory (Stamps et al 1998), although such work does not explicitly describe the cost of sexual coercion.

If females cannot avoid the costs of coercion, they may develop life history characteristics that limit such costs. For example, if females are unable to avoid coercion and mate frequently with non-preferred males, increased iteroparity may prevent decreased fitness as a result of mating with unwanted partners (e.g. Evans and Magurran 2000). In order for increased iteroparity to be an effective strategy, there must be some probability that a future mating involves the preferred male-type. In this manner, each reproductive event accounts for only a portion of the female's overall reproductive capacity, and avoiding costs and mating with a non-preferred male may afford a female the opportunity to later mate with a preferred male. Alternatively, females may exhibit cryptic choice for preferred males through manipulation of transferred sperm (Eberhard 1991; Pizzari and Birkhead 2000). It must be that cryptic female choice is ineffective in species where females show apparent strong preferences for a particular male-type yet a polymorphism for male-type is still maintained. In these situations it is possible that females invest less in the offspring of non-preferred males. Such investment withholding may take the form of shortened gestation periods (e.g. Evans and Magurran 2000), decreased maternal care or differential investment in developing embryos (e.g. Gil et al 1999; Cunningham and Russell 2000).

Conclusion

When inter- and intra-sexual relationships occur simultaneously, the chosen mate is not necessarily the preferred mate, and interactions with the preferred mate may be very subtle. Subtle cooperation with preferred mates can evolve in response to coercion by non-preferred mates. In this paper I have attempted to develop an alternative theory for the adaptive value of exaggerated sexually selected traits. To do this, I have presented a description of the simultaneous processes of sexual coercion and cooperation.

I have focused on the simple act of attaining a mate to show that simultaneous coercion and cooperation can select for exaggerated male traits that are not preferred by females. Such traits are likely to attract predators or be useful in controlling females or other males. I have suggested that employing such exaggerated traits may be the means by which non-preferred males acquire mates. On the other hand, sexual cooperation should decrease the costs associated with mating for both mates. The model developed here indicates that sexual cooperation is the evolutionary response to the contending of free mate choice by non-preferred mates. Cooperation can also develop because preferred mates can increase their fitness by working together to insure low cost fertilization.

Because coercion and cooperation are responses to each other, there is a constant evolutionary tug of war between the two tactics. Whether this tug of war is pulled to one side depends upon a number of factors including predation risk and resource availability. Other factors include the phenotypes of males and females themselves.

I have suggested that if the phenotypes of males are indicative of heritable life-history trajectories, then females have an honest indicator on which to base their mate choice decisions. Knowledge of the developmental processes that lead to the expression of reproductive phenotypes will be helpful in determining whether observed mate choices are optimal. I have also suggested that if mating systems evolve around female cost avoidance, then life history characteristics of females such as the degree of iteroparity and the age of maturity may be designed to limit costs. In the simple view I have presented here, I have discussed females as the choosy sex. It is obvious that mating systems are more complex and that males too can be choosy. Additional complexity may only make the occurrence of coercion and cooperation more subtle.

Acknowledgements

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Literature Cited

Alonzo, S.H. and R.R. Warner. 2000. Female choice, conflict between the sexes and the evolution of male alternative reproductive behaviours. Evolutionary Ecology Research 2: 149-170.

—, and B. Sinervo. 2001. Mate choice games, context-dependent good genes, and genetic cycles in the side-blotched lizard, Uta stansburiana. Behavioral Ecology and Sociobiology 49:176-186.

Andersson, M.B. 1994. Sexual selection. Princeton University Press, Princeton.

Arnqvist, G., and L. Rowe. 2002. Antagonistic coevolution between the sexes in a group of insects. Nature 415:787-789.

Aspbury, A.S., and A.L. Basolo. 2002. Repeatable female preferences, mating order and mating success in the poeciliid fish *Heterandria aurus*. Behavioral Ecology and Sociobiology 51: 238-244.

Ball, M. A., and G. A. Parker. 1996. Sperm competition games: External fertilization and ‘’adaptive’’ infertility. Journal of Theoretical Biology 180:141-150.

—. 1997. Sperm competition games: Inter- and intra-species results of a continuous external fertilization model. Journal of Theoretical Biology 186:459-466.

Bilton, H.T. 1978. Returns of adult coho salmon in relation to mean size and time at release of juveniles. Canadian Marine Services Technical Report: 73.

Carroll, S. P. 1993. Divergence in male mating tactics between two populations of the soapberry bug: I. Guarding versus nonguarding. Behavioral Ecology 4:156-164.

—, and P.S. Corneli. 1999. The evolution of behavioral reaction norms as a problem in ecological genetics: theory, methods and data. Pages 52-68 *in* S.A. Foster and J.A. Endler eds. Geographic variation in behavior: Perspectives on evolutionary mechanisms. Oxford University Press, Oxford.

Clutton-Brock, T.H., and G.A. Parker. 1995. Punishment in animal societies. Nature (London) 373:209-216.

Cunningham, E.J.A. and A.F. Russell. 2000. Egg investment is influenced by male attractiveness in the mallard. Nature (London) 404:74-77.

Darwin, C. 1871. The descent of man, and selection in relation to sex, with an introduction by John T. Bonner and Robert M. May. Princeton University Press, Princeton. 1981.

Eberhard, W.G. 1991. Copulatory courtship and cryptic female choice in insects. Biological Reviews of the Cambridge Philosophical Society 66:1-32.

Elgar, M. A., J. M. Schneider, and M. E. Herberstein. 2000. Female control of paternity in the sexually cannibalistic spider Argiope keyserlingi. Proceedings of the Royal Society of London Series B-Biological Sciences 267:2439-2443.

Evans, J.P. and A.E. Magurran. 2000. Multiple benefits of multiple mating in guppies. Proceedings of the National Academy of Sciences, USA 97:10074-10076.

Falconer, D.S. and T.F.C. Mackay. 1996. Introduction to quantitative genetics. Prentice Hall, Harlow.

Fuller, R., and A. Berglund. 1996. Behavioral responses of a sex-role reversed pipefish to a gradient of perceived predation risk. Behavioral Ecology 7:69-75.

Gil, D., J. Graves, N. Hazon and N. Wells. 1999. Male attractiveness and differential testosterone investment in zebra finch eggs. Science 286:126-128.

Gowaty, P.A. 1996. Battles of the sexes and origins of monogamy. Pages 21-52 *in* J.M. Black, ed. Oxford Ornithology Series; Partnerships in birds: The study of monogamy. Oxford University Press, Oxford.

. 1997. Principles of females' perspectives in avian behavioral ecology. Journal of Avian Biology 28:95-102.

Greeff, J.M. 1998. Local mate competition, sperm usage and alternative mating strategies. Evolutionary Ecology 12:627-628.

Gross, M.R. 1985. Disruptive selection for alternative life histories in salmon. Nature (London) 313:47-48.

—. 1991. Salmon Breeding-Behavior and Life-History Evolution in Changing Environments. Ecology 72:1180-1186.

.1996. Alternative reproductive strategies and tactics: Diversity within sexes. Trends in Ecology and Evolution 11:92-98.

Gustafsson, L., A. Qvarnstrom, and B. C. Sheldon. 1995. Trade-Offs between Life-History Traits and a Secondary Sexual Character in Male Collared Flycatchers. Nature 375:311-313.

Hager, R. C., and R. E. Noble. 1976. Relation of size at release of hatchery-reared coho salmon to age, size and sex composition of returning adults. Progressive Fish Culture 38: 144-147.

Hamilton, W. D. 1979. Wingless and fighting males in fig wasps and other insects, Pages 167-220 *in* M. S. Blum, and N. A. Blum, eds. Sexual Selection and Reproductive Competition in Insects. New York, Academic Press.

Heisler, I.L., M.B. Andersson, S.J. Arnold, C.R. Boake, G. Borgia, G. Hausfater, M. Kirkpatrick, R. Lande, J. Maynard Smith, P. O'Donald, A.R. Thornhill, and F.J. Weissing. 1987. The evolution of mating preferences and sexually selected traits. Pages 97-118 *in* J.W. Bradbury and M.B. Andersson, eds. Sexual selection: testing the alternatives. Report of the Dahlem Workshop, Berlin, August 31-September 5, 1986. Life Sciences research Report 39. Wiley, Chichester.

Herberstein, M. E., J. M. Schneider, and M. A. Elgar. 2002. Costs of courtship and mating in a sexually cannibalistic orb-web spider: female mating strategies and their consequences for males. Behavioral Ecology and Sociobiology 51:440-446.

Hunt, J., and L. W. Simmons. 2002. Confidence of paternity and paternal care: covariation revealed through the experimental manipulation of the mating system in the beetle Onthophagus aurus. Journal of Evolutionary Biology 15:784-795.

Iwamoto, R.N., Alexander, B.A. and W.K. Hershberger. 1984. Genotypic and environmental effects on the incidence of sexual precocity in coho salmon *Oncorhynchus kisutch*. [Meeting] Aquaculture 43:105-122.

Jaeger, R. G., J. R. Gillette, and R. C. Cooper. 2002. Sexual coercion in a territorial salamander: males punish socially polyandrous female partners. Animal Behaviour 63:871-877.

Kennedy, J.S. 1992. The new anthropomorphism. Cambridge University Press, Cambridge.

Kodric-Brown, A. 1977. reproductive success and the evolution of breeding territories in pupfish *Cyprinodon*. Evolution 31:750-766.

Kodric-Brown, A. 1978. Establishment and defense of breeding territories in a pupfish, Cyprinodontidae, *Cyprinodon*. Animal Behaviour 26:818-834.

, and J.H. Brown. 1984. Truth in advertising: The kinds of traits favored by sexual selection. American Naturalist 124:309-323.

Kokko, H. 2001. Fisherian and good genes benefits of mate choice: how (not) to distinguish between them. Ecology Letters 4:322-326.

Luttbeg, B. 1996. A Comparative Bayes tactic for mate assessment and choice. Behavioral Ecology 7:451-460.

Magurran, A.E. and M.A. Nowak 1991. Another battle of the sexes: The consequences of sexual asymmetry in mating costs and predation risk in the guppy, *Poecilia reticulata*. Proceedings of the Royal Society of London Series B: Biological Sciences 246:31-38.

Maynard-Smith, J. 1982. Evolution and the theory of games. Cambridge University Press, Cambridge.

Morris, M.R., and M.J. Ryan 1990. Age at sexual maturity of male *Xiphophorus nigrensis* in nature. Copeia 1990:747-751.

Olsson, M. 1995. Forced copulation and costly female resistance behavior in the Lake Eyre Dragon, *Ctenophorus maculosus*. Herpetologica 51:19-24.

Parker, G.A. 1979. Sexual selection and sexual conflict. Pages 123-166 *in* M.S. Blum and N.A. Blum eds. Sexual selection and reproductive competition in insects. Symposium, Washington DC, USA 1976. Academic Press, New York.

———, and J. Maynard-Smith 1990. Optimality theory in evolutionary biology. Nature (London) 348:27-33

———, M. A. Ball, P. Stockley, and M. J. G. Gage. 1996. Sperm competition games: Individual assessment of sperm competition intensity by group spawners. Proceedings of the Royal Society of London Series B-Biological Sciences 263:1291-1297.

Pizzari, T., and T.R. Birkhead. 2000. Female feral fowl eject sperm of subdominant males. Nature (London) 405:787-789.

Qvarnstrom, A., and E. Forsgren. 1998. Should females prefer dominant males? Trends in Ecology & Evolution 13:498-501.

Radwan, J. and I. Bogacz. 2000. Comparison of life-history traits of the two male morphs of the bulb mite, *Rhizoglyphus robini*. Experimental and Applied Acarology 24:115-121.

Roff, D.A. 2002. Life history evolution. Sinauer Associates, Sunderland, Mass.

Rosenthal, G.G., T.Y. Flores Martinez, F.J. Garcia deLeon, and M.J. Ryan 2001. Shared preferences by predators and females for male ornaments in swordtails. American Naturalist 158:146-154.

Ryan, M.J. 1980. Female mate choice in a neotropical frog, *Physalaemus pustulosus*. Science 209:523-525.

Sato, T. 1994. Active Accumulation of Spawning Substrate – a Determinant of Extreme Polygyny in a Shell-Brooding Cichlid Fish. Animal Behaviour 48:669-678.

Sih, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. Pages 203-224 *in* W.C. Kerfoot and A. Sih, eds. Predation: Direct and indirect impacts on aquatic communities. University Press of New England, Hanover.

Souroukis, K., and Cade, W.H. 1993. Reproductive competition and selection on male traits at varying sex ratios in the field cricket, *Gryllus pennsylvanicus*. Behaviour 126: 45-62.

Stamps, J.A., M. Mangel, and J.A. Phillips. 1998. A new look at relationships between size at maturity and asymptotic size. American Naturalist 152:470-479.

Thorpe, J. E. 1994. Performance thresholds and life-history flexibility in salmonids. Conservation Biology 8: 877-879.

Trivers, R.L. 1972. Parental investment and sexual slelection. Pages 136-179 *in* B. Campbell, ed. Sexual selection and the descent of man. Aldine, Chicago.

Wagner, W.E. 1998. Measuring female mating preferences. Animal Beahviour 55:1029-1042.

Williams, G.C. 1966. Adaptation and Natural Selection. Princeton University Press, Princeton.

Zahavi, A. 1977. The cost of honesty: Further remarks on the handicap principle. Journal of Theoretical Biology 67:603-606.

Table 1.1:

Payoff matrices: Arrow points to winner. In some cases, arrows point to both opponents. In these cases, the value of the parameters ($F, C_1, C_2, \square_1$, and $\square_2$) will determine the winning male phenotype. For example, when Type II coercers are capable of giving only a very small cost, Type I's who cooperate may win if females can still gain a higher benefit by mating with them.

A: Under internal fertilization, the male-type chosen by the female is the winner.

B: With external fertilization, a female can exhibit no choice. Here, Type I males are considered winners if they are chosen by females and Type II males win if they cause females to exhibit no mate choice. The reason for this "winning rule" is that females will not choose Type II males when Type I's are present. Choosing Type II's means a lower fitness payoff for females because in doing so, less eggs are fertilized by high viability Type I males.

A: Internal Fertilization Matrix (for a given set of parameters)

	TI do nothing	TI cooperator	TI coercer	TI coercer/cooperator	TII do nothing	TII cooperator	TII coercer	TII coercer/cooperator
TI do nothing	----							
TI cooperator	----	----						
TI coercer	☐	☐	----					
TI coercer/ cooperator	☐	☐	☐	----				
TII do nothing	↑	↑	↑	↑	----			
TII cooperator	↑	↑	↑	↑	----	----		
TII coercer	☐	☐ ↑	☐ ↑	☐ ↑	☐	☐	----	
TII coercer/ cooperator	☐	☐ ↑	☐ ↑	☐ ↑	☐	☐	☐	----

B: External Fertilization Matrix (for a given set of parameters)

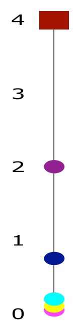
	TI do nothing	TI cooperator	TI coercer	TI coercer/cooperator	TII do nothing	TII cooperator	TII coercer	TII coercer/cooperator
TI do nothing	----	----	----	----				
TI cooperator	----	----	----	----				
TI coercer	----	----	----	----				
TI coercer/ cooperator	----	----	----	----				
TII do nothing	↑	↑	↑	↑	----	----	----	----
TII cooperator	↑	↑	↑	↑	----	----	----	----
TII coercer	▯	▯ ↑	▯	▯ ↑	----	----	----	
TII coercer/ cooperator	▯	▯ ↑	▯	▯ ↑	----	----	----	----

Figure 1.1: Guide to constructing and reading strategy payoff figures.

A: The number of “wins” (represented by the solid square) for a given strategy plotted along with the values of the parameters (solid circles) used in a single run of the model. By looking at the figure, we can determine how many of the encounters with alternative male phenotypes the phenotype of interest wins for the denoted parameter set, in this case 4 wins. Such a plot is produced for each run of the model.

B: Plotting several such parameter sets together gives an impression of how successful a given phenotypic strategy is across a number of situations. By connecting the points on the individual lines to produce a polygon, we can see the overall success of a strategy. For a given strategy, this polygon is produced with a dashed line here while the parameters are connected with a solid line. Comparing graphs of the payoffs to each strategy gives a picture of which strategy is most successful and under which parameter values it succeeds or fails. The strategy that covers the largest area across the range of parameter values is the most successful. Any strategy that fits entirely within the area of another strategy always loses to that strategy and is expected to disappear.

A


4
3
2
1
0

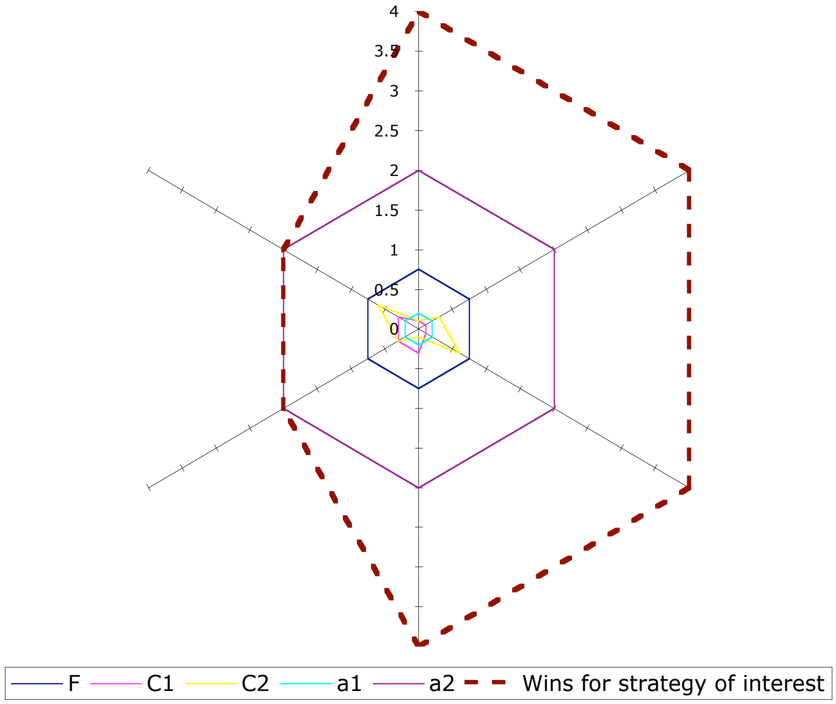
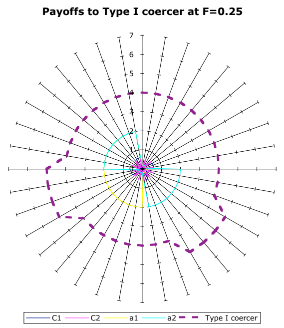
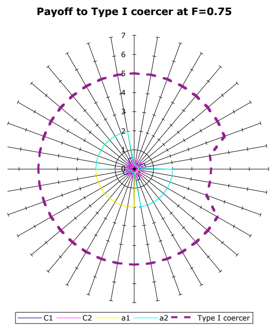

4
3.5
3
2.5
2
1.5
1
0.5
0
F
C1
C2
a1
a2
Wins for strategy of interest

Figure 1.2: Payoff figures for 5 male strategies (Type I coercer, Type I cooperator, Type I coercer/cooperator, Type II coercer, and Type II coercer/cooperator) under internal fertilization. Strategies were evaluated at low (F = 0.25) and high (F = 0.75) frequency under 36 parameter combinations in which the imposed cost of coercion (C) was allowed 3 possible values (0.1, 0.3, and 0.6), and the coefficient of cooperation ($//$) was allowed 2 possible values (2 and 0.2). Thus, the figure represents the model under 72 parameter sets. Each strategy is most successful when at high frequency. For example, the area encompassed by the strategy Type I coercer in B (high frequency of Type I coercers) is larger than in A (low frequency of Type I coercers). Conversely, the strategy Type II coercer does better when it is at high frequency (compare G to H). Under internal fertilization, the best strategy for either Type I or Type II males is a combined coercer/cooperator. For example, the strategy plotted in E, F encompasses those plotted in A, B, and C, D. And the strategy plotted in I, J covers that plotted in G, H. When there are no constraints on the ability to coerce, Type I coercer/ cooperators should prevail.

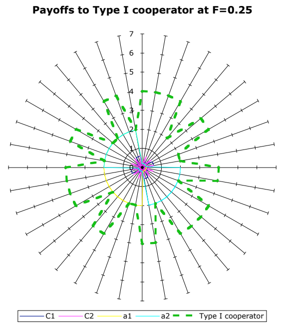
A


Payoffs to Type I coercer at F=0.25

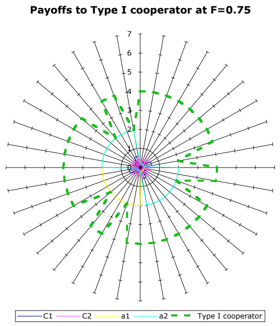
B


Payoff to Type I coercer at F=0.75

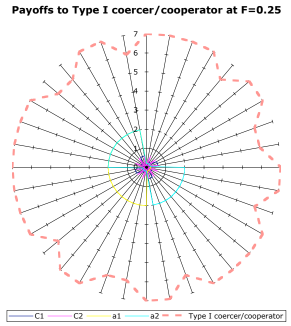
C


Payoffs to Type I cooperator at F=0.25

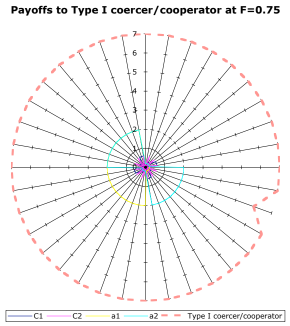
D


Payoffs to Type I cooperator at F=0.75

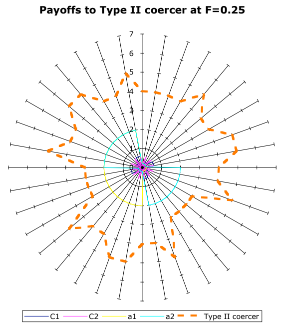
E


Payoffs to Type I coercer/cooperator at F=0.25

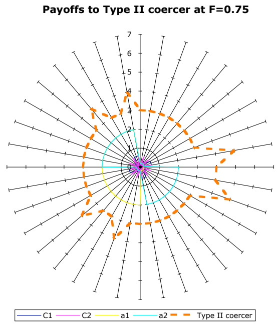
F


Payoffs to Type I coercer/cooperator at F=0.75

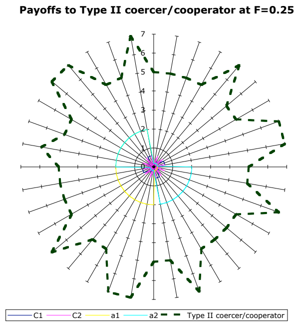
G


Payoffs to Type II coercer at F=0.25

H


Payoffs to Type II coercer at F=0.75

I


Payoffs to Type II coercer/cooperator at F=0.25

J

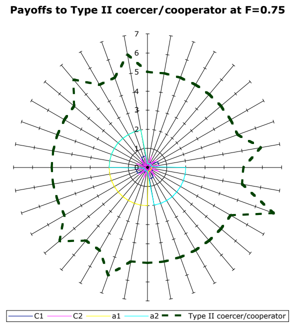
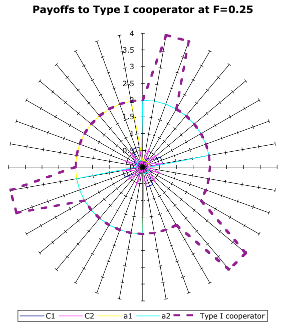
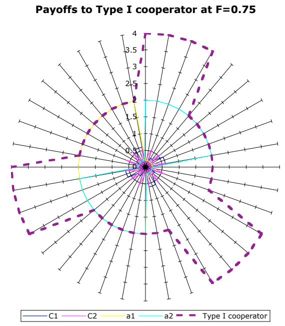

Payoffs to Type II coercer/cooperator at F=0.75

Figure 1.3: Payoff figures for 4 male strategies (Type I cooperator, Type I coercer/cooperator, Type II coercer, and Type II coercer/cooperator) under external fertilization. Strategies were evaluated as in Figure 1.2. Under external fertilization with female control of oviposition, there are two best strategies – cooperate if Type I and coerce if Type II. There is no selection against the combined strategy, coercer/cooperator (C,D and G,H) as it encompasses the best strategy for either male-type.

A


Payoffs to Type I cooperator at F=0.25

B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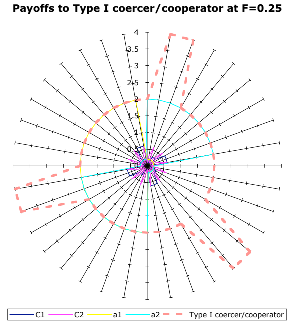
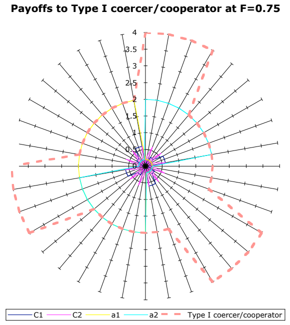
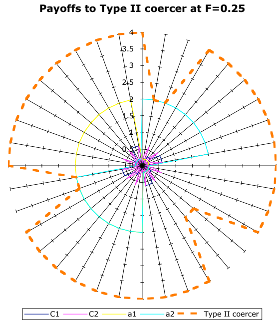
C


Payoffs to Type I coercer/cooperator at F=0.25

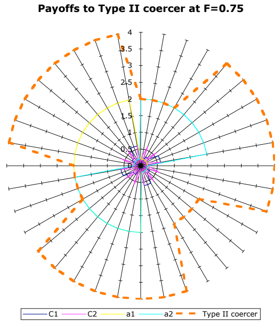
D


Payoffs to Type I coercer/cooperator at F=0.75

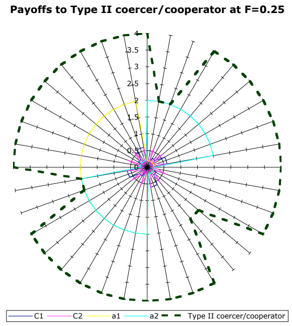
E


Payoffs to Type II coercer at F=0.25

F


Payoffs to Type II coercer at F=0.75

G


Payoffs to Type II coercer/cooperator at F=0.25

H

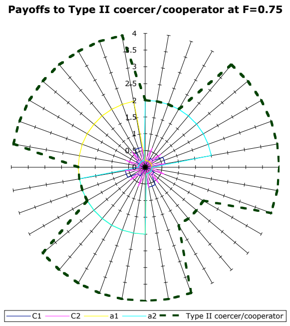
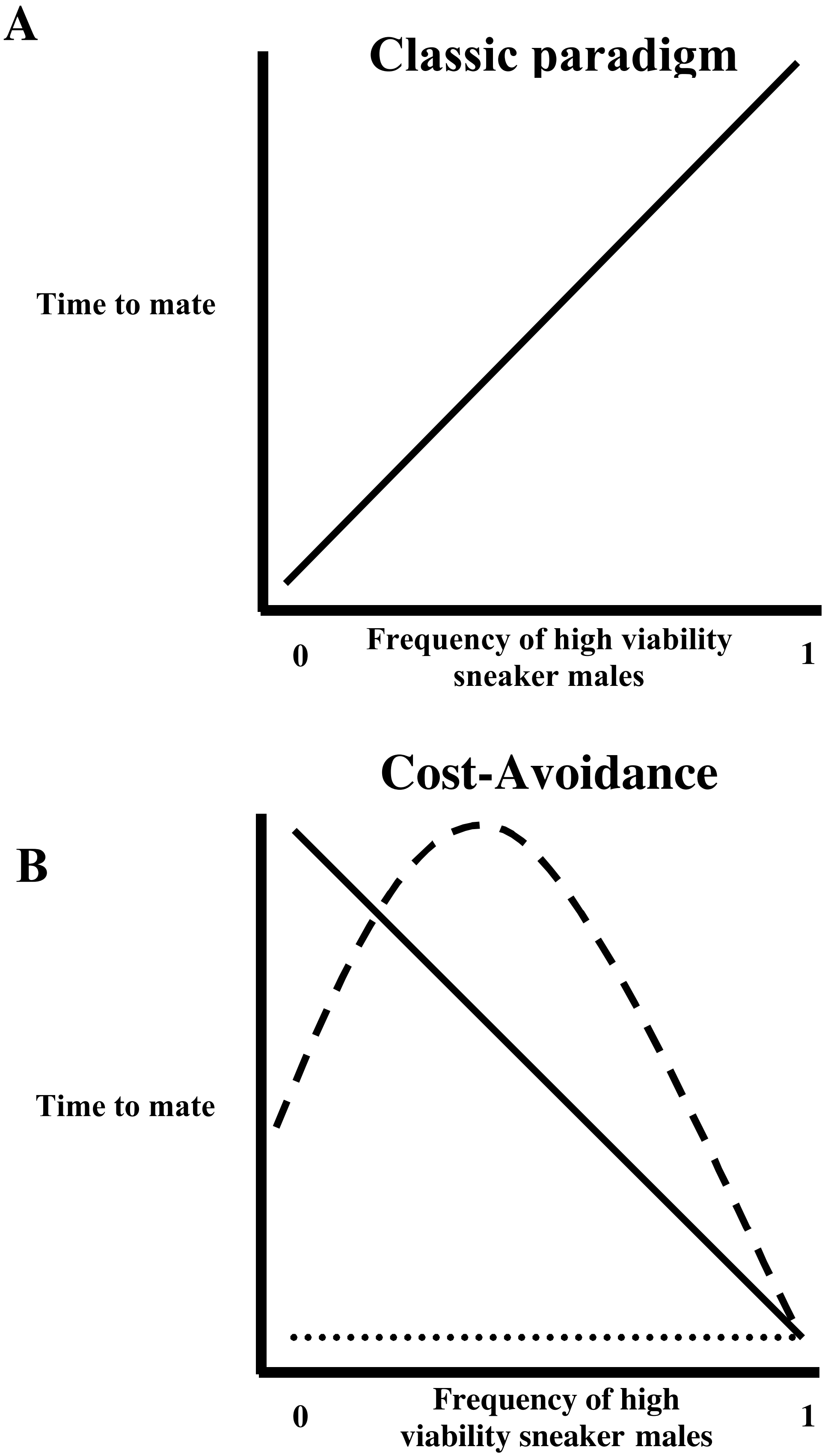

Payoffs to Type II coercer/cooperator at F=0.75

Figure 1.4: Predictions of the speed at which females will mate. Panel A represents the predictions of the “Classic Paradigm” in which sneaker males are considered non-preferred. Panel B shows the predictions of the “Cost-Avoidance Paradigm.” Under cost-avoidance, sneaker males may be higher viability (Type I) and thus preferred by females. When possible, females should mate rapidly with Type I males. The solid line in panel B indicates no coercion or cooperation; females should mate quickly with Type I males. The dashed line represents some coercion and some cooperation, females should mate quickly when alone with Type I males, but should also mate relatively quickly when alone with Type II’s. Mating with Type II’s reduces the cost of coercion. Mating should take longest when females are in mixed company. As Type II males become better coercers, mating should occur quicker (dotted line) under all conditions.


A
Classic paradigm
Time to mate
0
Frequency of high viability sneaker males
1
Cost-Avoidance
B
Time to mate
0
Frequency of high viability sneaker males
1

Chapter 2

Resource Clumping Drives the Development of Alternative Behavioral Phenotypes

Abstract of the chapter

The environment plays a key role in directing development, and drives much individual variation within populations. In many species, development of alternative behavioral phenotypes is a threshold trait contingent on high growth rate. Here, it is investigated how a simple ecological parameter – resource clumping– is likely to shape the distribution of growth rates in a population and affect the expression of alternative reproductive phenotypes. At low population densities clumped resources increase the variance in growth, while evenly spread resources decrease this variance. If expression of an alternative phenotype is under the control of a relatively high size threshold then because habitats with clumped resources produce higher variance in growth rates, they are more likely to produce alternative phenotypes than habitats with evenly spread resources are. For this effect to be in place, it must be that the supply of resources in either habitat is not so ample as to allow all individuals to meet this developmental threshold. This idea is tested empirically using coho salmon (*Oncorhynchus kisutch)*, a species with alternative male phenotypes. The results demonstrate that varying physical attributes of the rearing habitat influences the growth rates of juveniles and the subsequent expression of alternative male phenotypes at maturity.

Introduction

In many species, the development of alternative reproductive phenotypes is condition-dependent (Crespi 1988; Eberhard 1982; Gross 1996; Moczek & Emlen 1999; Radwan 1993). According to this strategy, individuals follow life-history trajectories that will optimize their fitness with respect to some current internal state. A central tenet of conditional strategy theory is that a developing individual must meet a threshold condition in order to express a particular phenotype later in life (Gross 1996; Gross & Repka 1998; Hazel *et al.* 1990; Repka & Gross 1995). For example, in the bulb mite, *Caloglyphus berlessei*, males reared in high density and fed poor diets are less likely to mature as “fighter” males than those reared under reciprocal conditions (Radwan 1995). Radwan’s research suggests that there is some minimum level of body condition that a male must attain to mature as a fighter. A similar situation arises in the Atlantic salmon, *Salmo salar*. In this species, large, fat juvenile males are able to mature at a young age because they meet a threshold body condition. Smaller individuals do not meet this threshold body condition and follow an alternative life history to mature later (Thorpe 1994; Thorpe *et al.* 1998). It is variation in developmental rate that allows some individuals to acquire this threshold condition but not others. For many species, development proceeds at a rate metered by the environment. Differential access to resources resulting from social conditions, features of the habitat, or both, can cause individuals to develop at varying rates. Thus, we must focus on the circumstances surrounding development to study the maintenance of alternative phenotypes (Caro & Bateson 1986; Eberhard 1982; Emlen 1997; Repka & Gross 1995).

An individual’s ability to acquire resources is one factor that may determine whether or not it reaches a threshold condition. Because the ability to defend resources depends on their distribution, both the spatial distribution of resources, and the degree of competition for those resources, should shape a population’s phenotypic distribution. For example, when resources are evenly distributed in a habitat, they are difficult to defend and the allocation of resources to each individual is approximately equal. But when resources are clumped, territorial behavior increases (Brown 1964; Rubinstein 1981; Ryer & Olla 1995). The result is a non-uniform allocation of resources that generates a positive feedback system wherein large individuals can hold resources and grow even larger, thus exaggerating individual variation in a population (Grand & Grant 1994; Maret & Collins 1997; Ryer & Olla 1995).

Resource clumping, growth, and phenotypes

The body condition (as defined by growth rate, size, or other parameters) of an individual depends on its ability to acquire food. Thus, the average condition of individuals in a population will depend on the availability of food in the habitat and the degree of competition for that food, and should be predictable. Here economic defendability theory (Brown 1964) is used to describe the distribution of phenotypes in a population. In doing so, the effects of resource clumping and population density on a single cohort of individuals developing in a closed habitat are considered. In such a system, variation in growth rates and sizes in a single cohort is easy to observe and is at the root of phenotypic divergence.

When resources are clumped, they are easier to defend than when they are evenly spread and superior competitors acquire a disproportionate share (Grand & Grant 1994; Grant & Guha 1993; Hakoyama & Iguchi 1997). When it is profitable for some individuals to defend resources, their uneven allocation will create variation in body condition within a population (Ryer & Olla 1995). Those individuals holding resources are likely to be in better condition than individuals not holding resources. These differences will be more pronounced when there is competition for a single, necessary resource.

Given that alternative phenotypes will occur when members of the population reach the threshold condition for the expression of a particular phenotype, the probability of a rearing environment producing individuals that have reached this threshold is determined by two primary factors: 1) the position of the threshold, and 2) the distribution of resources (Figure 2.1). Although the threshold is likely to vary for each genotype, assume initially that there is only a single genotype in the population (Hazel *et al*. 1990). This assumption avoids complications that may arise from competitive differences in genotypes and allows us to focus on the maintenance rather than on the evolution of alternative phenotypes. Resource clumping causes the phenotypic distribution to expand. Thus, when the threshold is relatively high, individuals reared in habitats with clumped resources will be more likely to express alternative phenotypes than those reared in habitats with evenly distributed resources. Furthermore, variation in resource distribution between cohorts can cause the frequency of alternative phenotypes to fluctuate over time.

Thresholds in Salmonid Life Histories

The natural history of coho salmon (*Oncorhynchus kisutch*) illustrates how a spatially and temporally variable distribution of resources can influence the frequency of alternative phenotypes. Coho salmon follow a conditional strategy for the expression of alternative male phenotypes (Gross 1991). These fish spawn in coastal freshwater streams. After a year of growth in the natal stream, juveniles undergo a parr-smolt transformation that prepares them for life in seawater. Smolts then migrate to the ocean. At maturity, fish return to their natal streams to spawn and die. Males return as either a jack- or a hooknose- phenotype (Gross 1985). Jacks mature after 6 to 12 months in the ocean while hooknoses take longer (18 to 24 months). The largest smolts become jacks whereas smaller smolts become hooknoses (Bilton 1978; Hager & Noble 1976).

In the natal creek, juvenile coho are found in riffles and pools. Riffle habitat is shallow and turbulent whereas water in pools is relatively slow moving across an area of greater depth (Bisson & Montgomery 1996). Observations on wild coho salmon parr describe at least three phenotypes: “territorials,” “floaters,” and “poolers.” These phenotypes make different uses of this habitat structure (Nielsen 1992; Puckett & Dill 1985). Territorial juveniles are the largest and fastest growing phenotype; these fish are found in riffle habitat. Floaters are also found in riffles but are not territorial. They are small and move between occupied sites. Poolers, as their name suggests, are found in pools. These fish, too, are non-territorial and reach an intermediate size. What these observations suggest is that different microhabitats represent different selective pressures to which juveniles inhabiting them must respond.

Presented here is an experiment that examines how habitat structure influences the phenotypic distribution in coho salmon. By following PIT (passive integrated transponder) tagged individuals, we tested whether habitat type directs the growth and development of individuals into different adult phenotypes. We reared these fish in artificial freshwater habitats constructed from round fiberglass tanks. In natural streams, the dynamics of water flow and the structural composition of a stream-reach are not independent factors. Instead, flow dynamics are defined by the structure of the stream-reach (Newbury 1996). Thus, the question arises: Is structural variation in the habitat as important as hydraulic variation in driving the phenotypic differentiation of juvenile salmon? Our treatments de-coupled the effects of structure on water flow dynamics: Pool tanks were structurally complex while at the same time hydraulically simple. By contrast, riffle tanks lacked any structure but were hydraulically complex. Treatments were named according to which natural habitat they most resembled hydraulically. The tanks, like natural habitats, also differed in the way they delivered resources to the fish. In pool tanks, food fanned out evenly and drifted slowly through the tank. In riffle tanks, food was quickly swept toward the bottom by the current and did not fan out. As a result, pool tanks presented the fish with evenly spread resources while the resources in riffle tanks were spatially clumped. Our experimental design had two treatments (riffle and pool) with two independent replicates each, within which individual fish were nested.

Methods

The Animals

We obtained Coho salmon fry of Trinity River Hatchery (California) stock in January of 1999. Hooknosed males sired all animals. The fry had absorbed their yolk sacs and were feeding exogenously by January 15, 1999 (Bio Diet, Bio Products, Warrenton, Oregon). Between January and April of 1999, all animals were housed in a single round fiberglass tank (radius 60 cm, water depth 30 cm). As of April 1, 1999 the fish were feeding on Rangen soft-moist salmon diet (Rangen Inc., Buhl, Idaho), and we considered them hardy enough to move. On April 2, 1999, 200 fish (50 fish for each experimental tank) were captured at random from the stock holding tank, weighed, measured, and transferred to the four experimental tanks.

Habitat Structure

In pool tanks (radius 60cm, water depth 58 cm) water flow as directed into the tank on one side through a polyvinyl chloride (PVC) spray bar (41.9 cm x 1.27 cm diameter). Water then flowed across the tank and drained through a drainpipe (71.1 cm x 5.08 cm diameter) across the surface of the tank opposite to the spray bar. Covering the tank's bottom with sand and adding concrete cinder blocks to one side of the tank added structure. One small (19.1 x 19.1 x 19.1 cm) and 5 large (39.4 x 19.1 x 19.1 cm) cinder blocks were added to each of the two tanks in the same positions.

Riffle tanks (radius 60 cm, water depth 30 cm) were prepared by allowing water to enter the tanks through a PVC spray bar (21.6 cm 1.27 cm diameter). Water circled around the tanks and exited through a central drain.

All four experimental tanks received the same water flow rate at all times (15 ± 1 l/min). Water temperature was maintained at 12° ± 1° C for the freshwater rearing phase of the experiment.

Experimental tanks were divided into a grid consisting of fourteen 30cm squares. Water velocity was measured at 2/3 depth in the center of each quadrant of the grid. Mean water velocity in the pool tanks was 0.01 m/s, with a variance of 0.0001 $(m/s)^2$. Mean water velocity in the riffle tanks was 0.08 m/s, with a variance of 0.002 $(m/s)^2$. All four tanks received the same quantity of food. Fish were fed such that there was always left over food. If it was necessary to increase the food delivered to one tank because it was all consumed, all tanks were increased to the same amount. In all tanks, food was delivered with automated feeders at the surface at the point where water entered.

Measuring Growth and Maturity

Forty days after introduction to the experimental tanks (May 12, 1999) fish were weighed to the nearest 0.1 g, measured to the nearest mm, and implanted with PIT tags (Biomark, Boise, Idaho). Fish were then weighed and measured every 40 days, 7 times prior to smolting. Standard length, fork length and total length were recorded though only standard length measurements are reported here.

On February 28, 2000 all surviving fish (163) were trucked to the Bodega Marine Laboratory and placed in a single concrete raceway containing freshwater. The fish were slowly acclimated to seawater conditions and were in full seawater by April 1, 2000. Fish were then maintained in seawater until January 2001.

From January 1- January 3, 2001 the remaining fish (155) were euthanized with an overdose of anaesthetic (tricaine methane-sulfonate: MS 222) and dissected to determine whether or not they were mature. PIT tags were retrieved at this time. Nine fish did not retain their PIT tags.

Analyses

All analyses were performed using JMP for Windows version 4 (SAS Institute, 1999) or Systat for Windows version 8.0 (SPSS Inc, 1998). To determine if the experimental tanks all received the same distribution of sizes and weights, we compared measurements taken the day fish were placed in the experimental tanks with a one-way ANOVA. We made these measurements on animals taken from the same tank, prior to their experiencing experimental treatments and ran the ANOVA to determine if we distributed the fish to the experimental tanks evenly with respect to size and weight. Consecutive measurements of PIT tagged animals were averaged to obtain freshwater growth rates: We calculated changes in standard length and weight for each fish that retained its PIT tag and survived to the end of the experiment. Seawater growth rate was also calculated. Distributions of the freshwater growth rates of fish reared in the two treatments were compared visually using quantile-quantile plots to determine if the replicates within a treatment were similar. We used a Levene's F test to determine if there was a difference in the variance of the growth rates between treatments. We also compared growth rates between treatments using either a Wilcoxon two sample test (if Levene's test showed a significant variance difference) or a t-test. We used the non-parametric analysis because we designed the experiment explicitly to produce differences in the variance of the phenotypic distributions of fish reared in the alternative treatments. Additionally, the non-parametric analysis evaluates the median, a good measure of the location of a distribution where a few large or small individuals can skew the value of the mean.

Two logistic regression models were produced to calculate the probability of becoming a jack. The first model was based on the effects sex, freshwater rearing treatment, freshwater growth rate (standard length), and seawater growth rate (standard length). The second model included the effects sex, freshwater rearing treatment, freshwater growth rate (weight), and seawater growth rate (weight). Growth in standard length and weight was modeled separately to avoid the confounding effects of these two covariates.

Results

Initial Measurements

Similar distributions of fish size and weight were placed into the experimental tanks at the start of the experiment (One-way ANOVA, on standard length grouped by tank, $F_{3,196} = 1.3064$, $p = 0.2735$; on weight grouped by tank, $F_{3,196} = 0.4240$, $p = 0.7360$). Variation for each measure among subjects was also similar at the start of the experiment (Levene's test, for standard length, $F_{3,196} = 1.9114$, $p = 0.1290$; for weight, $F_{3,196} = 1.5177$, $p = 0.2112$).

Growth

Comparison of treatments

One hundred forty six fish survived the full two years of the experiment and retained their PIT tags (Table 2.1). The sex ratio among the tanks was similar (Pearson $\chi^2 = 1.365$, $p = 0.7137$; Table 2.1).

We visually inspected the distributions of freshwater growth rate as indicated by standard length and weight using quantile-quantile plots and found the replicates of each treatment to be similar. For further analysis then, we grouped the replicates of each treatment. A similar visual comparison of treatments revealed that riffle tanks and pool tanks produced different distributions. The distributions differed with respect to both location (median) and shape (variation).

Sex Comparisons

The median freshwater growth rates of males were similar among the treatments (Wilcoxon two-sample test, for standard length $Z = -0.67$, $p = 0.51$; for weight $Z = -0.32$, $p = 0.75$). However, the variance in freshwater growth rate was lower for males reared in the pool tanks than for males reared in the riffle tanks (Levene's test, for standard length $F_{1,59} = 6.24$, p ,0.02; for weight $F_{1,59} = 9.89$, $p < 0.003$). Riffle tanks produced extremes. Males reared in these tanks showed the highest as well as the lowest freshwater growth rates (Figure 2.2 A,B).

Median growth rate of males once they were transferred to seawater did not differ with respect to the treatment in which they were reared in freshwater (for standard length t-test = 0.60, df = 59, $p = 0.55$; for weight t-test = 0.52, df = 59, $p = 0.61$).

Median freshwater growth rates of females differed between treatments. Females grew faster in pool tanks (Wilcoxon two-sample test, for standard length $Z = 4.04$, p <

0.0001; for weight $Z = 3.89$, $p < 0.0001$). Like males, females in pool tanks had lower variance in freshwater growth rates (Levene's test, for standard length $F_{1,83} = 5.27$, $p = 0.02$; for weight $F_{1,83} = 5.16$, $p = 0.03$) (Figure 2.2 C,D).

Median seawater growth rates did not differ for females reared in the experimental tanks (for standard length t-test = -0.87, df = 83, p = 0.39; for weight t-test = -0.24, df = 83, p = 0.81). There was no difference in variance in seawater growth rate for females (Levene's test, for standard length $F_{1,83} = 0.06$, $p = 0.81$; for weight $F_{1,83} = 0.24$, $p = 0.63$).

Maturity

Of the males reared in riffle tanks, 17.2% (5 of 29) matured as jacks. In comparison, 3.1% (1 of 32) of males reared in pool tanks were mature. A single female matured at two years of age. This female was reared in a riffle tank; representing 2.3% (1 of 44) of females reared in this treatment (Table 2.1).

Logistic regression for probability of jacking

Freshwater growth rate had the largest effect on the jacking rate (standard length, p = 0.01; weight, p = 0.005). Seawater growth rate also influenced jacking rate, but was only marginally significant (standard length, p = 0.10; weight, p = 0.05). Sex had a marginal influence on jacking rate as well (standard length model, p = 0.13; weight model, p = 0.14), while treatment also had a marginal effect (standard length model, p = 0.11; weight model, p = 0.13; Table 2.2).

Discussion

Previous researchers have shown that the distribution of resources affects the competitive behavior of animals. For example, Goldberg et. al (Goldberg *et al*. 2001) demonstrated that, in the Zenaida dove, the spatial and temporal clumping of food results in increased aggression. Presumably, when some doves are fiercely aggressive and control food, the physical condition of members of the population varies. In another example, Ryer and Olla (Ryer & Olla 1995) showed that the physical condition of chum salmon juveniles reared in conditions where food was localized varied more than that of individuals reared with evenly distributed food. Our research adds to this body of work by showing that these simple interactions between habitat and individuals can direct life-history decisions and subsequently effect population demographics. When alternative life-history trajectories are dependent on some high threshold condition, resource clumping will determine the proportion of alternative phenotypes expressed in a population. Accordingly, features of the habitat that drive resource distribution will be important in determining the demographic composition of a population.

Freshwater habitat type plays a major role in directing the growth rate of juvenile coho salmon and the subsequent expression of early maturation. Our simple experimental “riffle” and “pool” treatments represented habitats with clumped and evenly spread resources. The riffle treatment, which provided clumped resources, produced far more jacks than did the pool treatment. We conclude that the freshwater rearing habitat and the response of individuals to that habitat plays a critical role in determining demographics (age of maturity) in populations of coho salmon.

For juvenile coho salmon, an important feature of the habitat is water flow dynamics. Riffles and pools differ with respect to water flow dynamics and the opportunities they provide for resource control and subsequent growth. An energetically profitable position is one with shelter from high flow and easy access to drifting prey (Fausch 1984). In riffles, these refuges represent a patchy resource that can be controlled by a few individuals. These individuals are able to easily acquire food, which is also clumped in space as a result of water flow dynamics. Conversely, in an idealized pool, no one spot is better than another because water flow is uniform, spreading food out as it drifts into the pool. Thus, though the best opportunities for growth occur in riffles in the form of energetically profitable positions, so do the worst. Meanwhile pools represent opportunities for predictable and steady, yet intermediate growth

Because the developmental patterns of individuals in a population are intertwined and dependent on the behavior of other individuals, varied life histories can and do occur. We have suggested that 1) the distribution of resources shapes the phenotypic distribution of a population; 2) the control of resources by some individuals results in non-uniform acquisition of resources by members of a population; and 3) for developing individuals, this non-uniform distribution of resources can result in profound variation in phenotypes. When the variation in physical condition is extreme, competition between individuals on opposite tails of the distribution becomes one sided. It is this situation that sets the stage for the development of alternative phenotypes. Our work provides a suggestion for the manner in which growth rates are controlled ecologically. Further work should examine our predictions in the field as well as the role of population density in determining the economic defendability of clumped resources. At high population densities, it becomes unprofitable to defend even a clumped resource (Warner & Hoffman 1980) and phenotypic variation decreases. Thus, the observed phenotypic distribution is the result of the costs and benefits of resource defense driving the developmental rates of individuals

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Literature Cited

Bilton HT, 1978. Returns of adult coho salmon in relation to mean size and time at release of juveniles. In: Can. Fish. Mar. Serv. Tech. Rep.:73.

Bisson PA, Montgomery DR, 1996. Valley segments, stream reaches, and channel units. In: *Methods in Stream Ecology* (Hauer FR & Lamberti GA, eds), Academic Press; 23-52. Academic Press.

Brown JL, 1964. The evolution of diversity in avian territorial systems. *Wilson Bull* 76:160-169.

Caro TM, Bateson P, 1986. Organization and ontogeny of alternative tactics. *Anim Behav* 34:1483-1499.

Crespi BJ, 1988. Adaptation, compromise and constraint: the development, morphometrics, and behavioral basis of a fighter-flier polymorphism in male *Hoplothrips karni* (Insecta: Thysanoptera). *Behav Ecol Sociobiol* 23:93-104.

Eberhard WG, 1982. Beetle Horn Dimorphism: Making the best of a bad lot. *Am Nat* 119:420-426.

Emlen DJ, 1997. Diet alters male horn allometry in the beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Proc Roy Soc Lond B* 264:567-574.

Fausch KD, 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. *Can J Zool* 62:441-451.

Goldberg JL, Grant JWA, Lefebvre L, 2001. Effects of the temporal predictability and spatial clumping of food on the intensity of competitive aggression in the Zenaida dove. *Behav Ecol* 12:490-495.

Grand TC, Grant JWA, 1994. Spatial Predictability of Food Influences Its Monopolization and Defence By Juvenile Convict Cichlids. *Anim Behav* 47:91-100.

Grant JWA, Guha RT, 1993. Spatial Clumping of Food Increases Its Monopolization and Defense By Convict Cichlids, *Cichlasoma nigrofasciatum*. *Behav Ecol* 4:293-296.

Gross MR, 1985. Disruptive selection for alternative life histories in salmon. *Nature* 313:47-48.

— 1991. Salmon breeding behavior and life history evolution in changing environments. *Ecology* 72:1180-1186.

— 1996. Alternative reproductive strategies and tactics: Diversity within sexes. *Trends Ecol Evol* 11:92-98.

—, Repka J, 1998. Game Theory and Inheritance in the Conditional Strategy. In: *Game Theory & Animal Behavior* (Dugatkin LA, Reeve HK eds). New York: Oxford University Press.

Hager RC, Noble RE, 1976. Relation of size at release of hatchery-reared coho salmon to age, size and sex composition of returning adults. *Prog Fish Cult* 38:144-147.

Hakoyama H, Iguchi K, 1997. Why is competition more intense if food is supplied more slowly? *Behav Ecol Sociobiol* 40:159-168.

Hazel WN, Smock R, Johnson MD, 1990. A Polygenic Model For the Evolution and Maintenance of Conditional Strategies. *Proc Roy Soc Lond B* 242:181-187.

Maret, TJ, Collins JP, 1997. Ecological origin of morphological diversity: A study of alternative trophic phenotypes in larval salamanders. *Evolution* 51:898-905.

Moczek AP, Emlen DJ, 1999. Proximate determination of male horn dimorphism in the beetle Onthophagus taurus (Coleoptera: Scarabaeidae). *J Evol Biol* 12:27-37.

Newbury RW 1996. Dynamics of flow. In *Methods in Stream Ecology* (Hauer FR, Lamberti GA eds). San Diego: Academic Press; 75-92

Nielsen JL, 1992. Microhabitat-Specific Foraging Behavior Diet and Growth of Juvenile Coho Salmon. *Trans Amer Fish Soc* 121:617-634.

Puckett KJ, Dill LM, 1985. The energetics of feeding territoriality in juvenile coho salmon (*Oncorhynchus kisutch*). *Behaviour* 92:97-111.

Radwan J, 1993. The adaptive significance of male polymorphism in the acarid mite *Caloglyphus berlesei*. *Behav Ecol Sociobiol* 33:201-208.

—, 1995. Male morph determination in two species of acarid mites. *Heredity* 74: 669-673.

Repka J, Gross MR, 1995. The Evolutionarily Stable Strategy Under Individual Condition and Tactic Frequency. *J Theor Biol* 176:27-31.

Rubinstein DI, 1981. Population density, resource patterning, and territoriality in the Everglades pygmy sunfish. *Anim Behav* 29:155-172.

Ryer CH, Olla BL, 1995. The influence of food distribution upon the development of aggressive and competitive behaviour in juvenile chum salmon, *Oncorhynchus keta*. *J Fish Biol* 46:264-272.

Thorpe JE, 1994. Performance thresholds and life-history flexibility in salmonids. *Cons Biol* 8:877-879.

—, Mangel M, Metcalfe NB, Huntingford FA, 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. *Evol Ecol* 12:581-599.

Warner RR, Hoffman SG, 1980. Population density and the economics of territorial defense in a coral reef fish. *Ecology* 61:772-780.

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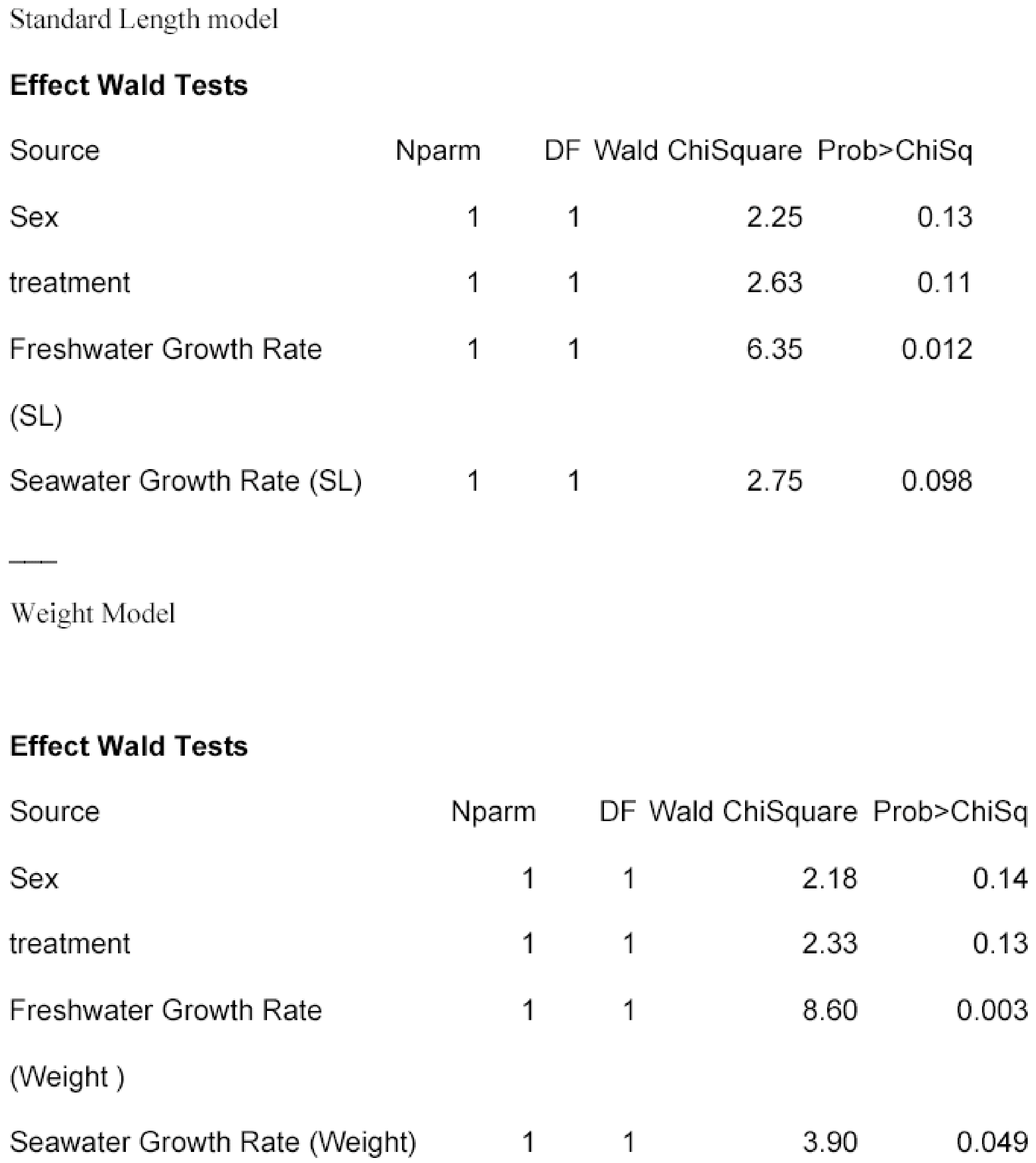
Table 2.1: Number of individuals of each sex surviving to end of experiment and retaining PIT tag, and number of mature individuals at end of experiment.

	Pool Tank #1		Pool Tank #2		Riffle Tank #3		Riffle Tank #4	
	males	females	males	females	males	females	males	females
	14	23	18	18	14	21	15	23
Total	37		36		35		38	
# mature	0	0	1	0	2	1	3	0

Table 2.2: Results of logistic regression models



Standard Length model

Effect Wald Tests

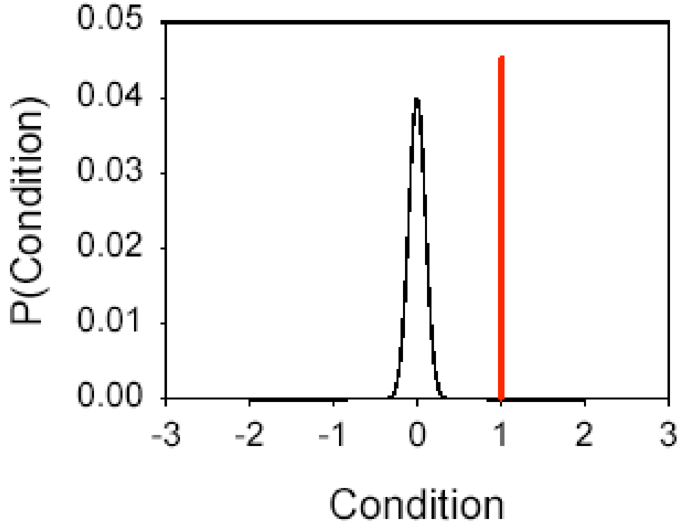
Source	Nparm	DF	Wald ChiSquare	Prob>ChiSq
Sex	1	1	2.25	0.13
treatment	1	1	2.63	0.11
Freshwater Growth Rate (SL)	1	1	6.35	0.012
Seawater Growth Rate (SL)	1	1	2.75	0.098

Weight Model

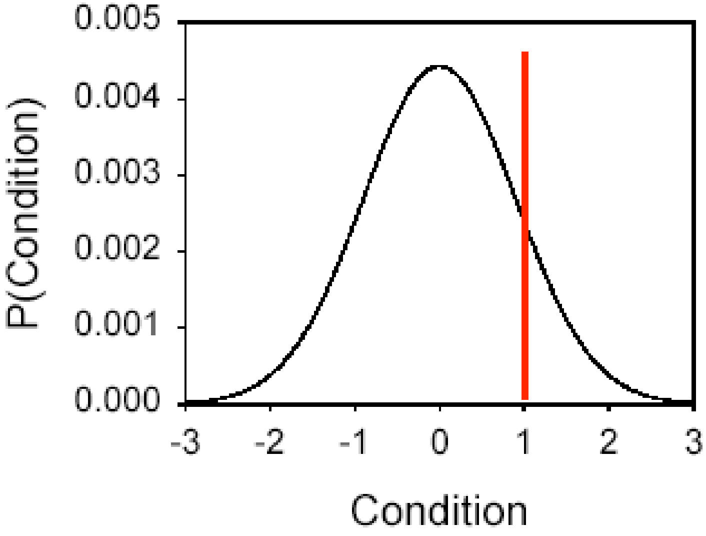
Effect Wald Tests

Source	Nparm	DF	Wald ChiSquare	Prob>ChiSq
Sex	1	1	2.18	0.14
treatment	1	1	2.33	0.13
Freshwater Growth Rate (Weight)	1	1	8.60	0.003
Seawater Growth Rate (Weight)	1	1	3.90	0.049

Figure 2.1: Phenotypic distributions in habitats with evenly spread (A) and highly clumped (B) resources. The variance among phenotypes increases initially with resource clumping. A threshold condition (vertical line) is superimposed on the distribution. Resource clumping increases the likelihood of the expression of alternative phenotypes.

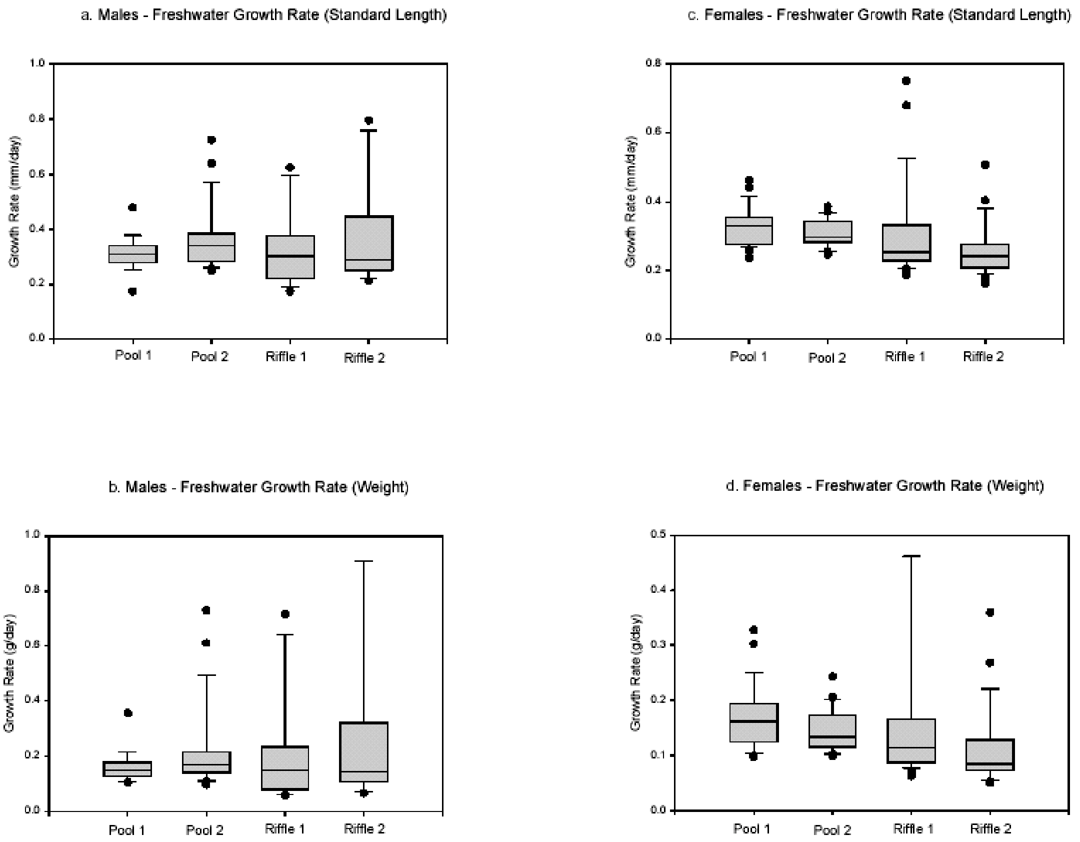


A: Evenly Spread Resources



B: Clumped Resources

Figure 2.2: Box plots of freshwater growth rates for males (A,B) and females (C,D). Growth rates are shown as indicated by changes in standard length (A,C) and weight (B,D). Males grown in riffle tanks varied more with respect to growth rates than those grown in pool tanks. Females reared in riffle tanks grew at lower median rates and had higher variance in growth rates than those reared in pool tanks.



Chapter 3

Mate choice by female coho salmon: Simultaneous coercion and cooperation and cryptic choice

Abstract of the chapter

To gain mates, males of many species coerce females. Females may choose to mate to end the costs of coercion. At the same time, females may have mating preferences for males with certain traits. These males should cooperate with females, making reproduction inexpensive for both parties. With respect to either male, females making mate choices should avoid costs. Cooperation between preferred mates in the presence of concurrent coercion by un-preferred mates may be difficult to observe, yet the occurrence of this simultaneous coercion and cooperation is likely to characterize many mating systems. This paper presents the first study investigating simultaneous coercion and cooperation in the wild. I observed naturally spawning coho salmon (*Oncorhynchus kisutch*). This species is well-known for the occurrence of alternative reproductive phenotypes (sneakers and fighters) in males. I found evidence that females actually prefer to mate with and cooperate with small sneaker males, but regularly mate with large fighting males to avoid the costs of coercion.

Introduction

Sexual conflict occurs as a result of divergence in the evolutionary interests of males and females (Chapman et al. 2003; Parker 1979; Partridge and Hurst 1998). For females, sexual conflict may result in phenotypes that avoid the costs imposed by males either during mating (Arnqvist and Rowe 2002b; Rowe et al. 1994) or in resisting mating (Clutton-Brock and Parker 1995b; Jormalainen et al. 2000). Male phenotypes should then evolve as effective coercers that can overcome female resistance (Arnqvist and Rowe 2002a; Clutton-Brock and Parker 1995a; Jaeger et al. 2002; Johnstone and Keller 2000)).

In contrast to conflict, sexual cooperation is predicted to occur when the evolutionary interests of mates coincide (Andersson et al. 2000). Thus when a female and a male share these interests, it is best for them to ensure that their gametes meet. With this scenario, there should be no appreciable cost of mating, and the phenotypes of males should evolve to indicate their mating value to females. Precisely because the mating value of males varies in most populations, some males are likely to be preferred mates. It is this situation, where both un-preferred and preferred mates vie for reproductive opportunities, that allows for simultaneous coercion and cooperation in mating systems (Chapter 1).

Under simultaneous coercion and cooperation, the un-preferred male should develop a phenotype that imposes a cost on females that are unwilling to mate with him. If females choose to mate with these males rather than pay such costs, coercion is successful. In contrast, the phenotype of the preferred male should readily inform females of his mating value and exact no additional toll from females over that necessary to ensure reproduction. Females confronted simultaneously with preferred and un-preferred males face the trade-off of paying some cost to the un-preferred male to mate with the preferred male. The preferred male thus must work closely with the female to facilitate reproduction in the face of this coercion. The result is that females avoid costs – either by mating with the un-preferred male and ending coercion, or by mating with the preferred male cheaply (Chapter 1).

Though it is possible that the simultaneous occurrence of coercion and cooperation is widespread, certain characteristics of a mating system may make its documentation and analysis more feasible than in others. Species or populations in which males show obvious phenotypic differences that are to some genetically based are likely candidates (Dries et al. 2001; Garant et al. 2002; Hankin et al. 1993; Heath et al. 1994; Iwamoto et al. 1984; Lank et al. 1995; Morris and Ryan 1990; Radwan 1995; Shuster 1989; Sinervo and Lively 1996). When such phenotypic differences reflect life-history variants that differ in their abilities to survive, they may also indicate to females the most evolutionarily sound mate (Andersson 1994).

In addition, females must be observed in situations where their mate choice is not predetermined. The probability of a female's choice of mates may be determined by a number of factors that counter an underlying mating preference. It is precisely because un-preferred males must strive to be chosen mates that mate choices do not always reflect mating preferences. It is easiest for females to express their mating preference when allowed to choose freely among mates. Factors that influence free choice include the frequency of male-types, population density, operational sex ratio, courtship behavior, and an inability to avoid males imposing a cost. Thus mate choice may often occur under conditions where female choice does not reflect female preference.

In this paper I present a study of wild spawning coho salmon. The goals of the study were to determine female mating preference and the relation between coercion and cooperation in the mating system of this species.

The Study System

In California, coho salmon (*Oncorhynchus kisutch*) grow in fresh water for 12 to 18 months before migrating to the ocean as smolts to mature. At maturity, adult coho return to their natal stream to spawn and die (Sandercock 1991). While it is thought that all females of California stocks return to spawn at two and a half to three years of age, males vary in age at maturity. Some males mature as 2 and a half to 3 year old hooknoses, after 18 months to 2 years in the ocean while others return to the spawning grounds as one and a half to 2 year old jacks, after only 6 months to a year at sea (Shapovolov and Taft 1954). Jacks are generally referred to as sneakers who gain mates surreptitiously (Gross 1985). Salmon eggs are fertilized externally; often more than one male sires a clutch of eggs at a single oviposition event (Foote et al. 1997).

In general, sneak mating is viewed as a less successful strategy than fighting for access to mates (Eberhard 1982; Gross 1996), although some evidence exists to the contrary for salmonids (Foote et al. 1997; Jones and Hutchings 2001). Gross (1996) suggested that in coho salmon, jacks may have higher average fitness than hooknoses because jacks grow faster as juveniles and experience lower mortality. If indeed jacks are more fit due to an inherited viability advantage, then it is possible that females prefer to mate with them because producing higher viability sons confers a fitness benefit on females. Thus, for female mate choice, heritability of early maturation is important.

Male phenotypes in salmon are heritable. In a study of chinook salmon (*O. tshawytscha*), approximately one half of the sons of jacks matured to be jacks and approximately one quarter of the sons of hooknoses matured to be jacks (Heath et al., 1994). Iwamoto et. al. (1984) found the heritability of the trait to be much lower in coho salmon, although in their study jack sires produced more jack offspring than did hooknoses. These studies found that jacks are more likely to sire jacks than are hooknoses. Indeed, the ability to mature as a jack appears to be a threshold character (Falconer and Mackay 1996; Roff 2002).

The life-history path taken for a male coho salmon to become a jack or a hooknose is apparently based on juvenile size: large juvenile males become jacks while small individuals become hooknoses (Gross 1991; Hager and Noble 1976). Thorpe (Thorpe 1994a; Thorpe 1994b) proposes that the decision for early maturation in salmon is based on fat stores, which represent some “performance threshold.” Animals above this threshold are capable of maturing when young, whereas animals below the threshold must wait to develop a larger size to support maturation. Thus juvenile growth rate plays a major role in the early maturation of coho salmon (Chapter 2). Growth rate is highly heritable in most species studied (Roff 1992).

In nature, large juveniles are dominant to small juveniles; they are thus more adept at holding territories (Martel and Dill 1995; Nielsen 1992; Puckett and Dill 1985), and can displace small individuals from preferred habitat. Territory acquisition decreases the need to maintain an active search for cover, thereby reducing predation risk (Martel &

Dill, 1995). By gaining an energetically profitable position fish can grow faster because they are not paying the physiological cost of constant swimming (Fausch 1984). In freshwater, larger juveniles experience lower mortality than smaller juveniles (Martel and Dill 1995; Quinn and Peterson 1996). Decreased predation risk along with increased growth rate leads to higher freshwater survival of large juveniles, i.e. those individuals that become jacks. The apparent switch in tactic from large territory holder to small sneaker can be understood by considering the survival benefit of returning to spawn as a jack. Large juvenile males have much to gain by returning to spawn as early as possible, foregoing the increased mortality risk of another year at sea. Whether the behaviors that allow juvenile salmon to accelerate growth to increase the likelihood of early maturation are heritable is open for investigation. It is possible that the jack morphology indicates a complex of heritable traits (i.e. a matrix of correlated traits) (Arnold 1994) that comprise a successful life history.

The hypothesis tested here is

> Given that female coho salmon prefer to mate with jacks, hooknoses apply cost to females to achieve matings. Hooknoses, if not preferred should coerce females to mate while jacks, if preferred, should facilitate mating.

Coho salmon spawning behavior

Upon returning to the natal stream, a female coho salmon prepares a nest in which she will bury her eggs. The female constructs this nest by turning on her side and excavating gravel with her tail (Shapovolov and Taft 1954). Only females prepare nests. After spawning, the female moves upstream and covers the fertilized eggs with gravel in another bout of digging behavior. A female may lay eggs in several closely adjacent nests which are collectively referred to as a redd (Sandercock 1991). Redds are typically located at the upstream or downstream end of riffles where the embryos within are aerated by water moving through the mound of gravel built as a result of the female's digging. To assure aeration, the substrate size must be such that it does not compact and suffocate the embryos but can still be manipulated by the female. Redds are easily found by looking for areas where the substrate contrasts in color with the darker, undisturbed surrounding substrate. Generally, such areas are oval or tear drop shaped. Females defend their nest site from other females and remain on the redd from the end of egg laying until death.

Male coho salmon play no role in nest preparation or defense. Males fight among themselves for access to females (Shapovolov and Taft 1954). When more than one hooknose is vying for a female, a linear hierarchy is formed with the primary male taking the position nearest the female (Gross 1991). Males of lower rank take positions at distances from the female that reflect their rank. Typically, hooknoses "line-up" behind the female with males queued according to their rank order. The primary male performs the majority of the observable behavior, interacting with both the other males and the female. Lower ranked males tend to hold their position until chased by the primary male, until the primary male is away on another foray, or until the female moves into the nest depression.

Jacks do not easily fit in to the dominance order of hooknoses. Often, even when there are multiple hooknoses, a jack is second nearest the female. Jacks gain proximity to the female either by hiding near some structure in the creek (rocks, snags etc.) or by staying just off the redd in the darker area of undisturbed substrate. Water depth is often much shallower off the redd as the female has not excavated here. The small body size of the jack allows it to remain in shallow water. Jacks spend a good deal of their time avoiding the attacks of the primary hooknose, who will bite and kill them if possible. When more than one jack competes for the same location, they may fight vigorously (Gross 1985). Observing a linear dominance hierarchy among jacks is difficult because they do not interact with each other as frequently as hooknoses, and they spend much of their time hiding. Indeed, in spawning situations, jacks interact more with hooknoses than with other jacks. Jacks will move onto the redd and interact with females when opportunities arise. Such opportunities occur when the primary hooknose is off the redd or on the opposite side of the female. Through these behaviors, the jack ensures that he is apparent to the female, and that he is in close proximity when spawning occurs.

The act of spawning occurs quickly. The female drops into the depression in the nest and males rush alongside her. Gametes are expressed in a simultaneous orgasm marked by a prolonged gape and slight bodily quivering (Sandercock 1991). Streamside observers can easily see a cloud of milt, although eggs are difficult to see because they sink into the nest depression. Following oviposition, the female breaks from her position, moves forward, and begins to bury the fertilized eggs. This burial digging indicates that the female has oviposited.

Methods

The study site consisted of portions of the main stem and the Devil’s Gulch area of Lagunitas Creek visible from trails in Samuel P. Taylor State Park, Marin County, California. Lagunitas Creek is home to a population of wild coho salmon that is estimated to be around 500 fish (Brown et al. 1994). The center of the study site is located approximately at the bridge where Sir Francis Drake Boulevard crosses the creek at the Irving Picnic Area (Latitude 38° 01′00″; Longitude 122° 43′19″). Although small by comparison to historic numbers, the contemporary Lagunitas Creek population is the largest remaining in California. Females in this population encounter male-types at varying frequencies and operational sex ratios (OSR’s).

Mature coho salmon return in pulses to their natal watershed to spawn. The fish require sufficient flow to traverse the small coastal creeks. Such water flow increases are typically the result of precipitation that runs into the creek and increases its volume. In Lagunitas Creek, the first pulse of fish usually moves upstream with the rains that mark the entry of winter (typically in the second half of November). Consecutive pulses come with the further rains, usually until the second half of January. During the course of the study, there were no steady rains between November and January and the spawning fish moved upstream in 3 or 4 main pulses. The study was conducted in the spawning seasons of 1999-2000 and 2000-2001.

I walked the study area daily in times when new fish were likely to have arrived. During walks, I looked for female coho salmon that were new to the spawning grounds. I considered a female new to the spawning grounds if she was not seen in the location the previous day and if she had no scarring on her caudal fin that results from digging her redd. Females who have not dug for very long are not scarred.

When I located a female that I estimated to be new to the spawning grounds and it was apparent that she was preparing a redd, I set up a video camera quietly and the scene was recorded. Recordings were made from the bank above the surface of the water and the entire redd area was recorded rather than zooming in on a particular fish. A polarizing filter on the camera lens reduced glare.

I also recorded observations in a field notebook. A simple schematic of the redd (an oval) was drawn, fish present were given numbers, and a description of the fish was written next to the number. At five minute intervals, I recorded the location of each fish present on the redd schematic. I also recorded time of oviposition, if it occurred, and the identities of the males taking part in the oviposition. Behavioral occurrences of interest were noted. Such occurrences included behaviors that may not have appeared in the videotape footage, such as fights happening out of frame. Start and end times of observations were recorded. Occasionally the video camera failed, in which case observations were recorded in the field notebook. Observations ended when an oviposition occurred, when the redd was vacant for 30 minutes or when visibility conditions degraded.

Recording the identities of individual fish in the field notebook made it possible to determine later which males accompanied females most. The total number of males observed during the study was tallied from the notebooks. Males were considered possible mates for the female if they were present for two or more consecutive observations. Males not present for two or more consecutive observations were considered passers-by.

Further observations of male-female and male-male interactions were acquired from the videotapes. Videotapes were watched on a television in the laboratory. Behavioral data were recorded using ViaVoice (dictation software by IBM). Using this software, behaviors of interest are spoken into a microphone as they occur on videotape and speech activates a macro in Microsoft Word that writes the behaviors of interest and time stamps their occurrence.

The behaviors recorded were relevant to the study because they are representative of both intra- and inter-sexual interactions. For example, some of the behaviors (described below) were performed by males toward females and may be direct coercion. Other behaviors performed by males were directed at other males. The behaviors recorded for females were chosen because they are thought to indicate females' preference of mates (e.g. 'dig' described below), may be used to avoid high cost situations, and ultimately indicate females' choice of mates.

The behaviors recorded were as follows:

Male Behaviors

Crossover

Directed movement by the male, in which he swims from one side of the female, over her to the other side and back again (Berejikian et al. 2000). The male often brushes against the female during crossover, and she is sometimes pushed into the substrate. For the human observer, males performing crossover are relatively easy to spot as are the females involved.

Nudge

The male bumps the belly or side of the female with his snout or body (Shapovolov and Taft 1954).

Vibrate

The male approaches side of the female closely (within a few centimeters or less) and quivers (Berejikian et al. 2000; Shapovolov and Taft 1954).

Bite

One fish bites another.

Chase

One fish pursues another. Bites of males by other males were recorded within the context of a chase.

Female Behaviors

Dig

The female turns on one side and uses her caudal fin to excavate gravel (Berejikian et al. 2000). A female must dig to prepare a nest in which to lay her eggs. Females may show their preferences for given male-types by digging more when accompanied by them (Berejikian et al. 2000; de Gaudemar et al. 2000a).

Behaviors recorded for males and females

Leave

An individual swims away from the redd. 'Leaves' were tallied if the individual proceeded to a distance greater than one body length from the redd.

Return

Individual re-enters the redd.

Spawn

Simultaneous oviposition and milt expression. Gametes are expressed in a simultaneous orgasm marked by a prolonged gape and slight bodily quivering. Though it was not possible to observe egg deposition, milt expression was obvious. Additionally, spawns were only tallied if the female performed a "burial dig." The burial dig occurs after oviposition; the female moves upstream of the area where the nest was dug and fills it in with gravel.

Oviposition duration was measured with a hand-held stopwatch for the spawning events that were recorded on videotape. I considered oviposition duration to be the interval of time beginning with the female’s initial gape (see description of spawning behavior above) and ending with the moment at which she moved forward to perform a burial dig. Of a total of 15 ovipositions, three were observed in the field that were not recorded on video. It was not possible to measure the duration of these ovipositions.

One goal of the study was to determine the relative costs imposed on females by males of different types. Behaviors were recorded for the primary acting male and the female. The primary actor was either the male that interacted clearly with the female most and was typically at the top of the dominance hierarchy, or was any male alone with the female. Jacks do not appear to fall clearly into a rank position in the dominance hierarchy. Therefore, a jack was not considered the primary acting male unless he was alone with the female. Thus, for a male to be considered a primary actor, it had to be clearly observed interacting with the female.

I recorded behavioral interactions according to their frequencies (occurrences/minute) and the social situations in which they occurred. These frequencies were calculated from the transcripts of the observations. Social situations varied with the OSR as well as with the composition of the OSR. The composition of the OSR varied with the operational male-type frequency (the proportion of jacks within the OSR). Thus, a social situation denoted (1,1) represents a female accompanied by one hooknose and one jack, while (1,0) is a female alone with a hooknose, and (0,1) a female alone with a jack. It is important to note that many of the females observed in this study experienced more than one social situation.

Analyses

It was sometimes difficult to obtain good video footage. As a result, some observations were not included in all analyses because they were not recorded on videotape or the recording was of poor quality. In these cases, observations recorded in the notebook were used in certain analyses. Analyses were performed on the data using JMP IN 4 (SAS Institute).

Oviposition duration data were placed in one of two categories: oviposition in the presence of hooknoses alone, and oviposition with both hooknoses and jacks. These categories include a number of different social situations. Thus, the category 'oviposition in the presence of hooknoses only' consisted of the social situations (1,0), (2,0) and (4,0). The category 'oviposition in the presence of hooknoses and jacks' included the social situations (1,1), (2,1), and (2,2). The number of males in each group that were involved in spawns was compared with a t-test. Oviposition durations according to these categories were compared using a Mann-Whitney U test. One female spawned in situation (0,1) but was not recorded on videotape. Therefore, oviposition duration was not obtained for this female.

Analyses were performed to determine if female behavior differed with social situation. First, female behavior (digging and leaving) rates were compared for three groups in a one-way ANOVA. The groups were female alone, female with hooknose as primary acting male, and female with jack as primary acting male. Second a standard least-squares multiple regression was run with the independent variables 'number of hooknoses' and 'number of jacks' and the dependent variable 'frequency of female behavior.' The results were blocked by female behavior (i.e. separate models for digging and leaving).

Mating success of the two male-types was analyzed using a chi-square contingency table analysis. In this analysis, the proportions of hooknoses and jacks present as possible mates that spawned were compared. Columns in the table were classified "mated" and "not mated," and rows were classified "jack" and "hooknose".

In addition to determining female behavior in different social situations and with which males females spawned, I wanted to establish if any behaviors predicted whether a female would spawn. To this end, a simple logistic regression was performed on each behavior. The categorical response was whether or not a female spawned, and the effect variable was the frequency of the given behavior. Female behaviors as well as the behaviors of males were entered into this analysis.

The behaviors performed by hooknoses were also compared to those of jacks. The frequencies of behaviors performed by alternative male-types as primary acting males were compared using Mann-Whitney U tests. Because the hypothesis stated that hooknoses would apply more costly behaviors to females, p-values for one-tailed tests are reported.

With respect to the behavior of males in different social situations, jacks were never the primary acting male in the presence of other males. As a result, it was only possible to ask how the behavior of the primary acting hooknose changed when the social situation changed. To approach this question, another standard least-squares model was analyzed. This model determined whether the independent variables 'number of other hooknoses' and 'number of jacks' at the nest site predicted behavior of the primary acting hooknose.

Results

Intensive observations were performed on 23 females during the course of the field study. Of these, 6 were disqualified from the analysis for one of several reasons. These reasons include disturbance of the fish by hikers and rainy weather causing a loss of visibility. In one circumstance, upon examination of the videotape, the female was noted to have extensive caudal fin scarring. Thus she was not new to the spawning grounds and was disqualified from the analysis. Of the remaining females, 13 were videotaped at a quality sufficient for analysis. Over 1200 minutes of videotape were analyzed. Additional data were taken from the field notebooks.

15 females were observed ovipositing. Females spawned in 7 social situations (Table 3.1) including alone with a single hooknose and alone with a jack. No female was observed to spawn with more than 4 males. There was no difference in the number of males involved in spawns between the groups 'with jack' and 'alone with hooknose' (t-test: df=13 p = 0.47, Power = 0.11).

The behavior of females changed with respect to the primary acting male. Females spent more time preparing their nest by digging when the primary actor was a jack than when he was a hooknose (ANOVA: df = 2,33; p = 0.0224). The amount of digging by females when they were alone was intermediate between that done in the presence of hooknoses and jacks, and not significantly different from either (Tukey post hoc comparison) (Figure 3.1). Females did not leave the redd more when accompanied by either male-type than they did when alone (ANOVA: df = 2,32; p = 0.8464).

Female behavior also changed with the overall social situation. Oviposition durations by females were longer when spawning in social situations that included jacks than when alone with hooknoses (Mann-Whitney: p=0.04) (Figure 3.2). Females dug their nests less as the frequency of hooknoses at the nest site increased (standard least squares multiple regression: $R^2 = 0.30$, p = 0.0031). Females were also more likely to leave the redd as the number of hooknoses increased, although this test was marginally insignificant ($R^2 = 0.16$, p = 0.0572).

Although females changed their behavior in different social situations, there was no significant difference in the proportion of jacks and hooknoses that mated (Pearson Chi Square contingency table analysis: Chi Square = 1.418; p = 0.23). Fifty-eight percent (twenty-five of 43) of hooknoses present long enough to be considered possible mates spawned, and 75% (12 of 16) of jacks mated.

The probability that a female spawned increased with the frequencies of certain male behaviors (Figure 3.3). The frequency of crossing over was a good predictor of spawning (logistic regression: $\chi^2_1 = 4.24$, p = 0.0394; Figure 3.3A), as was the frequency of nudging (logistic regression: $\chi^2_1 = 7.28$, p = 0.007; Figure 3.3B). The frequency at which jacks were chased by hooknoses was a very good predictor of spawning (logistic regression: $\chi^2_1 = 14.34$, p = 0.0002; Figure 3.3C). In these cases, the female spawned with both hooknoses and jacks. Conversely, the frequency at which the primary acting hooknose chased other hooknoses did not predict spawning (logistic regression: $\chi^2_1 = 0.306$, p = 0.5801; Figure 3.3D).

Hooknoses engaged in more behavior that was directed at females than did jacks. Hooknosed males were the primary actors for 1089 minutes of observation. Though present for a total of 773 minutes of observation, jacks were primary actors (alone with the female) for only 98 minutes.

Indeed, only 5 jacks were recorded on videotape as the primary acting male while 15 hooknoses were recorded. Many hooknoses were observed as the primary actor in several different social situations. Data on the frequency of behavior performed by the two male-types were analyzed by averaging the frequencies of behavior performed by each primary acting male across social situations. A jack and two hooknoses were observed in the field as primary actors, but not recorded on videotape. For these, behavioral frequencies were difficult to obtain, although the frequency of crossovers was recorded satisfactorily for one of the hooknoses. The Mann-Whitney U test was used to evaluate the hypothesis that hooknoses impose a higher cost on females than jacks do.

With respect to costly behaviors directed at females, only hooknoses chased or bit females. Hooknoses also crossed over females (Mann-Whitney: $p = 0.045$) and nudged females at higher frequencies than jacks (Mann-Whitney: $p = 0.0015$). There was no difference in the frequency of vibratory movement (Mann-Whitney: $p = 0.30$).

Primary acting hooknoses also changed their behavior depending on the social situation. These changes occurred in the frequencies of both male- and female-directed behaviors. Increases in the frequency of hooknoses at the spawning site resulted in increased attacks on other hooknoses (standard least squares multiple regression: $R^2 = 0.65$, $p < 0.0001$). As expected, jacks were also attacked more by hooknoses when the frequency of jacks increased at the spawning site ($R^2 = 0.46$, $p = 0.0009$). Female directed behavior performed by the primary acting hooknose changed more subtly with the social situation. Hooknoses made fewer vibratory movements towards females as the proportion of hooknoses increased ($R^2 = 0.28$, $p = 0.0222$). Otherwise, the occurrence of increased numbers of other males appeared to have no effect on the female directed behaviors performed by the primary acting hooknose.

Discussion

The data gathered in this study consistent with the idea that female coho salmon prefer to mate with early maturing jacks. Although females regularly mate with hooknoses, certain aspects of this study suggest that jacks are welcome mates. These points include the observation that a female readily mated when alone with a jack. Taken alone, this observation suggests that it is not necessary for jacks to rely upon sneaking to mate with unaware females. Additionally, in this circumstance, there were at least two hooknoses very nearby. After mating, the jack moved slightly downstream to join these two hooknoses and another jack who were associated with a different female. This second female then mated (with all four of these males) just a few minutes after the operational male-type frequency changed from 0.33 to 0.5 with the addition of this new jack. Observations on this female had been ongoing for over an hour.

Differential allocation of parental investment is thought to indicate a female's preference for a particular mate. Females of many species invest more in offspring with higher expected fitness than in others (Kolm 2001; Sheldon 2000). In this study, females spent more time preparing their nest when accompanied solely by jacks than when in the company of hooknoses. Coho salmon die shortly after spawning and do not care for their young after they hatch. Thus any investment in the offspring must come before the mother dies. Extra care spent in preparing the nest may provide hatching insurance for the offspring. Because females do not feed when on the spawning grounds, they are limited to how much energy they can expend on nest construction. In a study on Chinook salmon, there was no difference in the amount of digging seen between females paired with large or small males (Berejikian et al. 2000).

Further consistent with the female preference for jacks is the observation that females oviposited for longer durations when jacks were involved in the spawn. It is possible that females are able to expel more eggs in longer ovipositions than in shorter ones. De Gaudemar et al. (de Gaudemar et al. 2000b) have shown that the same female Atlantic salmon laid varying numbers of eggs in different spawnings. Though the trend was that fewer eggs were laid in later spawnings, no work has addressed whether females can vary the number of eggs deposited at a given mating. If females indeed can vary the number of eggs laid when in the presence of different males, they are capable of cryptic mate choice (Birkhead and Moller 1993).

If jacks are indeed preferred by females, then according to the cost avoidance hypothesis, hooknoses should coerce females to mate by increasing their pre-copulatory costs (Chapter 1). When these costs reach some level above which the female suffers unacceptable fitness degradation, she should mate with hooknoses. Several behaviors performed by the males observed in this study appear to be costly for females. Biting and chasing are the behaviors observed that constitute attacks on females. Although these behaviors occur at low frequencies, they must be costly to females. Indeed, I have observed a female who has left the spawning site being dragged back to the redd in the jaws of a hooknose! Other behaviors are subtler in the costs they administer to females.

Some behaviors that increase risk for females are subtler than direct aggression. For example, drawing the attention of predators may be a means for un-preferred males to coerce mates. For these males, the cost associated with increased predation risk must be acceptable. Crossing over, traditionally considered a mate guarding behavior (Shapovolov and Taft 1954), is plainly obvious to the streamside observer – particularly when performed by a brightly colored hooknose. This behavior may serve to increase females' predation risk. The probability that the male performing the behavior will be noticed is likely to increase as well. However, for all coho salmon that have returned from the sea, death is ensuing – and it is better to die having had sex than to die a virgin. Thus, for un-preferred males any increased predation risk associated with crossing over must be acceptable if coercion is to be successful.

While it is possible that crossing over increases predation risk, the behavior also applies a direct cost to females. Often, when the male crosses over the female, he drags his body across her back. During this process, he pushes the female downward and her belly, swollen with ripe eggs, comes into contact with the substrate. Thus there is some pressure placed on her abdomen. Pressure placed on the abdomen of a mature female may represent a direct cost in lost or damaged eggs. The nudging behavior performed by males is another example of direct pressure placed on the female's abdomen. This behavior is described elsewhere as stimulation of the female to mate (Shapovolov and Taft, 1954). Indeed, when the behavior increases in frequency, the female is most likely to mate. If crossing over and nudging are costly for females, the observation that females are more likely to spawn when these behaviors occur at high frequencies suggests that females make mate choice decisions that avoid further costs. The observation that hooknoses perform these behaviors at higher rates than jacks suggests that they coerce females to mate. Additionally, because males usually leave the female after spawning, spawning is a way for females to temporarily prevent the acquisition of further cost. Further work should examine the amount of contact endured before spawning by females in varying physical states or with larger versus smaller complements of eggs. In this way, it is possible to establish the role of female condition in mate choice.

Males apparently use vibratory movements to communicate their condition to females. When a male performs vibratory movements towards a female, he does not usually make contact with her. This behavior is thus not likely to be as costly for females as nudging and crossing over. Vibration may therefore be used as an advertisement by males rather than as coercion. Primary acting hooknoses decrease the frequency of this behavior as the number of other hooknoses increases. Under these conditions male-male competition increases and the primary acting male attempts to drive off additional males. At the same time, he maintains the rate at which he performs behaviors directed at the female to increase the likelihood of spawning.

While males direct some behaviors that appear costly at females, other behaviors are directed at other males and do not appear to be costly for females. Among these, the male-directed behavior of chasing a jack is a very good predictor of whether a female spawns. There are several arguments that may be posited to explain this observation. For example, females may spawn under these conditions because the likelihood of the female being caught in the middle of a fight and injured increases with increased attacks by males on other males. If this is the case, the likelihood of spawning should also increase with attacks by hooknoses on other hooknoses. However, attacks by hooknoses on other hooknoses do not predict spawning. Another argument might suggest that females are spawning readily at these times because the primary hooknose has successfully demonstrated his might to her by attacking the jack. With this argument too it would follow that attacking other hooknoses is an ample demonstration of fighting ability. Additionally, by the same logic, one might suggest that the jack has amply demonstrated to the female his ability to evade the hooknose's attacks. Thus, these arguments do not seem to adequately explain the observation that attacks by hooknoses on other hooknoses do not predict spawning while attacks on jacks do.

I suggest that the observation that females are more likely to spawn when there are increased attacks on jacks can be explained as evidence for cooperation between females and their preferred mate. The cost-avoidance hypothesis says that females and preferred males should work together to decrease the costs for both individuals and facilitate mating (Chapter 1). That females spawn when there are increased attacks on jacks may be the only evidence of cooperation to facilitate reproduction with jacks in the face of coercion by hooknoses. The data showing female preference for jacks additionally supports this interpretation. If mating with jacks is unacceptable for females and they are more likely to spawn following an attack on a jack, then the expectation would be that female oviposition duration would be short when a jack is present. By spawning quickly after an attack on a jack, females might be able to prevent jacks from fertilizing a large portion of eggs. But the opposite is the case. Females oviposit for longer durations when jacks are present – suggesting that females give jacks every opportunity to fertilize their eggs.

Conclusion

The simultaneous occurrence of intra- and inter-sexual relations is likely to place great demands on the individuals involved. For males, these demands arise from the needs to both convince the female to mate and assure one's own reproductive success when she in fact does. In this study I show that coho salmon jacks appear to have solved these problems by developing a phenotype that not only indicates to females their mating value, but also extracts very little pre-copulatory cost from her. Hooknoses resolve these problems with force. For females, mate choice relies on much more than mating preference. It is the outcome of changing costs associated with the number and types of males encountered.

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Literature Cited

Andersson, J., A.-K. Borg-Karlson, and C. Wiklund. 2000. Sexual cooperation and conflict in butterflies: a male-transferred anti-aphrodisiac reduces harrassment of recently mated females. Proceedings of the Royal Society of London Series B-Biological Sciences 267:1271-1275.

Andersson, M. B. 1994, Sexual selection: Monographs in behavior and ecology. Princeton, N.J., Princeton University Press.

Arnold, S. J. 1994. Multivariate inheritance and evolution: A review of concepts, Pages 17-48 *in* C. R. B. Boake, ed. Quantitative Genetic Studies of Behavioral Evolution. Chicago, The University of Chicago Press.

Arnqvist, G., and L. Rowe. 2002a. Antagonistic coevolution between the sexes in a group of insects. Nature 415:787-789.

—. 2002b. Correlated evolution of male and female morphologies in water striders. Evolution 56:936-947.

Berejikian, B. A., E. P. Tezak, and A. L. LaRae. 2000. Female mate choice and spawning behaviour of chinook salmon under experimental conditions. Journal of Fish Biology 57:647-661.

Birkhead, T., and A. Moller. 1993. Female Control of Paternity. Trends in Ecology & Evolution 8:100-104.

Brown, L. R., P. B. Moyle, and R. M. Yoshiyama. 1994. Historical decline and current status of coho salmon in California. North American Journal of Fisheries Management 14:237-261.

Chapman, T., G. Arnqvist, J. Bangham, and L. Rowe. 2003. Sexual conflict. Trends in Ecology & Evolution 18:41-47.

Clutton-Brock, T. H., and G. A. Parker. 1995a. Punishment in animal societies. Nature (London):209-216.

—. 1995b. Sexual coercion in animal societies. Animal Behaviour 49:1345-1365.

de Gaudemar, B., J. M. Bonzom, and E. Beall. 2000a. Effects of courtship and relative mate size on sexual motivation in Atlantic salmon. Journal of Fish Biology 57:502-515.

de Gaudemar, B., S. L. Schroder, and E. P. Beall. 2000b. Nest placement and egg distribution in Atlantic salmon redds. Environmental Biology of Fishes 57:37-47.

Dries, L. A., M. R. Morris, and M. J. Ryan. 2001. Why are some male pygmy swordtails large? Copeia:355-364.

Eberhard, W. G. 1982. Beetle Horn Dimorphism: Making the best of a bad lot. American Naturalist 119:420-426.

Falconer, D. S., and T. F. C. Mackay. 1996, Introduction to quantitative genetics. Essex, England, Longman.

Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology 62:441-451.

Foote, C. J., G. S. Brown, and C. C. Wood. 1997. Spawning success of males using alternative mating tactics in sockeye salmon, Oncorhynchus nerka. Canadian Journal of Fisheries and Aquatic Sciences 54:1785-1795.

Garant, D., P. M. Fontaine, S. P. Good, J. J. Dodson, and L. Bernatchez. 2002. The influence of male parental identity on growth and survival of offspring in Atlantic salmon (Salmo salar). Evolutionary Ecology Research 4:537-549.

Gross, M. R. 1985. Disruptive Selection for Alternative Life Histories in Salmon. Nature 313:47-48.

—. 1991. Salmon Breeding-Behavior and Life-History Evolution in Changing Environments. Ecology 72:1180-1186.

—. 1996. Alternative reproductive strategies and tactics: Diversity within sexes. Trends in Ecology & Evolution 11:A92-A98.

Hager, R. C., and R. E. Noble. 1976. Relation of Size at Release of Hatchery-Reared Coho Salmon to Age, Size, and Sex Composition of Returning Adults. Progressive Fish-Culturist 38:144-147.

Hankin, D. G., J. W. Nicholas, and T. W. Downey. 1993. Evidence for Inheritance of Age of Maturity in Chinook Salmon (Oncorhynchus-Tshawytscha). Canadian Journal of Fisheries and Aquatic Sciences 50:347-358.

Heath, D. D., R. H. Devlin, J. W. Heath, and G. K. Iwama. 1994. Genetic, Environmental and Interaction Effects on the Incidence of Jacking in Oncorhynchus-Tshawytscha (Chinook Salmon). Heredity 72:146-154.

Iwamoto, R. N., B. A. Alexander, and W. K. Hershberger. 1984. Genetic and environmental effects on the incidence of sexual precocity in coho salmon (*Oncorhynchus kisutch*). Aquaculture 43:105-121.

Jaeger, R. G., J. R. Gillette, and R. C. Cooper. 2002. Sexual coercion in a territorial salamander: males punish socially polyandrous female partners. Animal Behaviour 63:871-877.

Johnstone, R., and L. Keller. 2000. How males can gain by harming their mates: Sexual conflict, semianl toxins and the cost of mating. American Naturalist 156:368-377.

Jones, M. W., and J. A. Hutchings. 2001. The influence of male parr body size and mate competition on fertilization success and effective population size in Atlantic salmon. Heredity 86:675-684.

Jormalainen, V., S. Merilaita, and R. Hardling. 2000. Dynamics of intersexual conflict over precopulatory mate guarding in two populations of the isopod Idotea baltica. Animal Behaviour 60:85-93.

Kolm, N. 2001. Females produce larger eggs for large males in a paternal mouthbrooding fish. Proceedings of the Royal Society of London Series B-Biological Sciences 268:2229-2234.

Lank, D. B., C. M. Smith, O. Hanotte, and T. A. C. Burke, F. 1995. genetic polymorphism for alternative mating behavior in lekking male ruff, *Philomachus pugnax*. Nature 378:59-62.

Martel, G., and L. M. Dill. 1995. Influence of Movement of Coho Salmon (Oncorhynchus kisutch) Parr on Their Detection by Common Mergansers (Mergus merganser). Ethology 99:139-149.

Morris, M. R., and M. J. Ryan. 1990. Age at Sexual Maturity of Male Xiphophorus-Nigrensis in Nature. Copeia:747-751.

Nielsen, J. L. 1992. Microhabitat-Specific Foraging Behavior Diet and Growth of Juvenile Coho Salmon. Transactions of the American Fisheries Society 121:617-634.

Parker, G. A. 1979. Sexual selection and sexual conflict *in* M. S. Blum, and N. A. Blum, eds. Sexual selection and reproductive competition in insects. New York, Academic Press.

Partridge, L., and L. D. Hurst. 1998. Sex and conflict. Science 281:2003-2008.

Puckett, K. J., and L. M. Dill. 1985. The energetics of feeding territoriality in juvenile coho salmon (Oncorhynchus kisutch). Behaviour 92:97-111.

Quinn, T. P., and N. P. Peterson. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (Oncorhynchus kisutch) in Big Beef Creek, Washington. Canadian Journal of Fisheries and Aquatic Sciences 53:1555-1564.

Radwan, J. 1995. Male Morph Determination in 2 Species of Acarid Mites. Heredity 74:669-673.

Roff, D. A. 1992, The evolution of life histories : theory and analysis. New York, Chapman & Hall.

—. 2002, Life history evolution. Sunderland, Mass., Sinauer Associates.

Rowe, L., G. Arnqvist, A. Sih, and J. Krupa. 1994. Sexual Conflict and the Evolutionary Ecology of Mating Patterns - Water Striders as a Model System. Trends in Ecology & Evolution 9:289-293.

Sandercock, F. K. 1991. Life history of Coho salmon, Pages 395-445 *in* C. Groot, and L. Margolis, eds. Pacific salmon life histories. Vancouver, B.C, UBC Press.

Shapovolov, L., and A. C. Taft. 1954. Fish Bulletin No. 98: The life histories of the steelhead rainbow trout (Salmo gairdneri gairdneri) and silver salmon (Oncorhynchus kisutch) with special refernce to Waddell Creek, California, and recommendations regarding their management, Pages 375, State of California, Department of Fish and Game.

Sheldon, B. C. 2000. Differential allocation: Tests, mechanisms and implications. Trends in Ecology & Evolution 15:397-402.

Shuster, S. M. 1989. Male Alternative Reproductive Strategies in a Marine Isopod Crustacean (Paracerceis-Sculpta) - the Use of Genetic-Markers to Measure Differences in Fertilization Success among Alpha-Males, Beta-Males and Gamma-Males. Evolution 43:1683-1698.

Sinervo, B., and C. M. Lively. 1996. The rock-paper-scissors game and the evolution of alternative male strategies. Nature 380:240-243.

Thorpe, J. E. 1994a. Performance thresholds and life-history flexibility in salmonids. Conservation Biology 8:877-879.

—. 1994b. Reproductive strategies in Atlantic salmon, Salmo salar L. Aquaculture and Fisheries Management 25:77-87.

Table 3.1: Social situations at which females spawned and oviposition durations. See text for definition of "social situation."

Social situation	Number of females observed spawning	Oviposition durations (seconds)
(1,0)	3	9.5, n/a, n/a
(2,0)	1	13.2
(4,0)	2	8, 10.4
(0,1)	1	n/a
(1,1)	4	13.2, 16.9, 14.5, 16.2
(2,1)	1	15.8
(2,2)	3	12, 10, 15

Figure 3.1: Bar graph of digging frequency when the primary actor is a jack or a hooknose. Mean digging frequency is plotted with standard error bars.

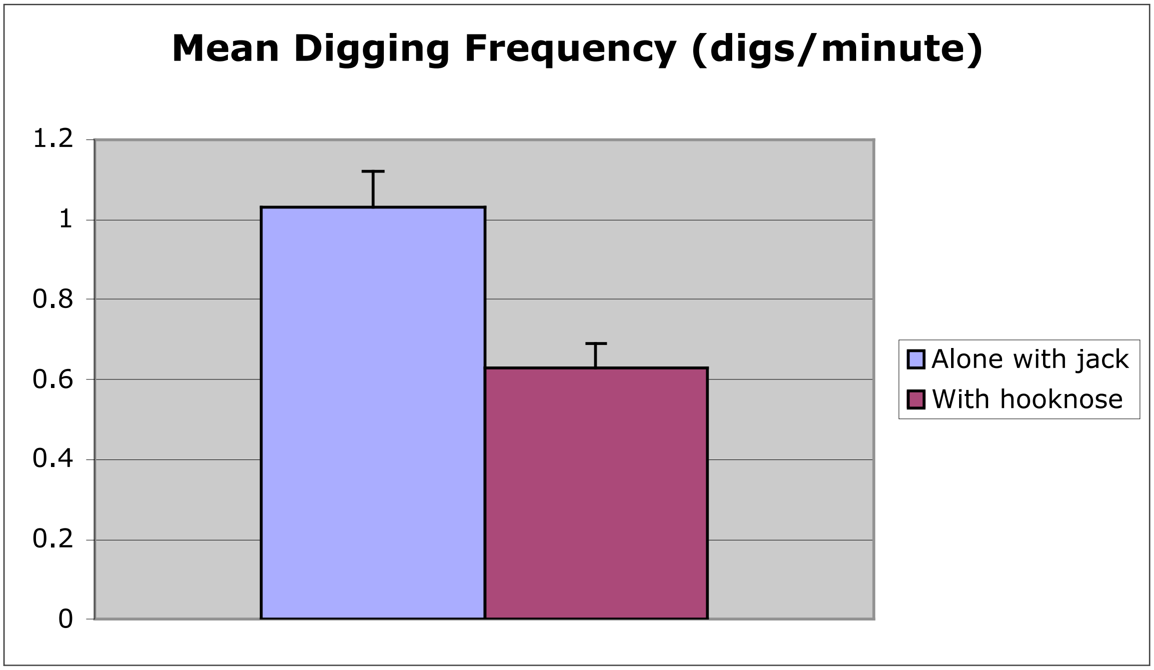


Figure 3.2: Bar graph of oviposition duration as a function of male-type. Mean oviposition duration is plotted with standard error bars.

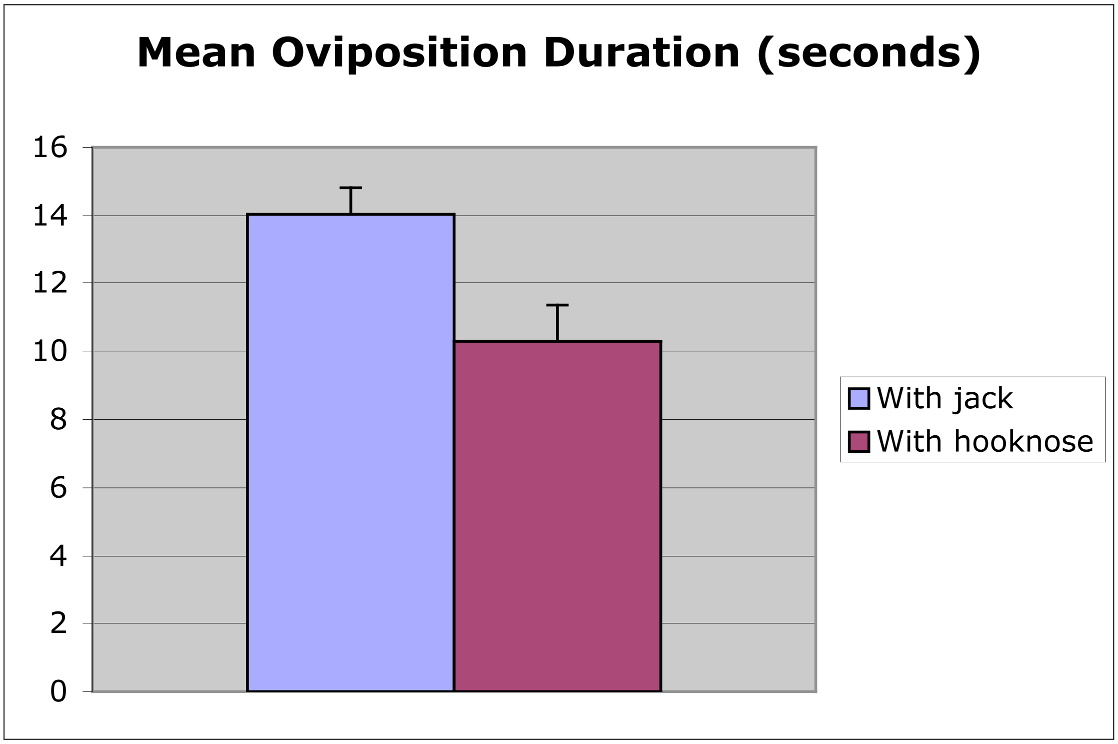
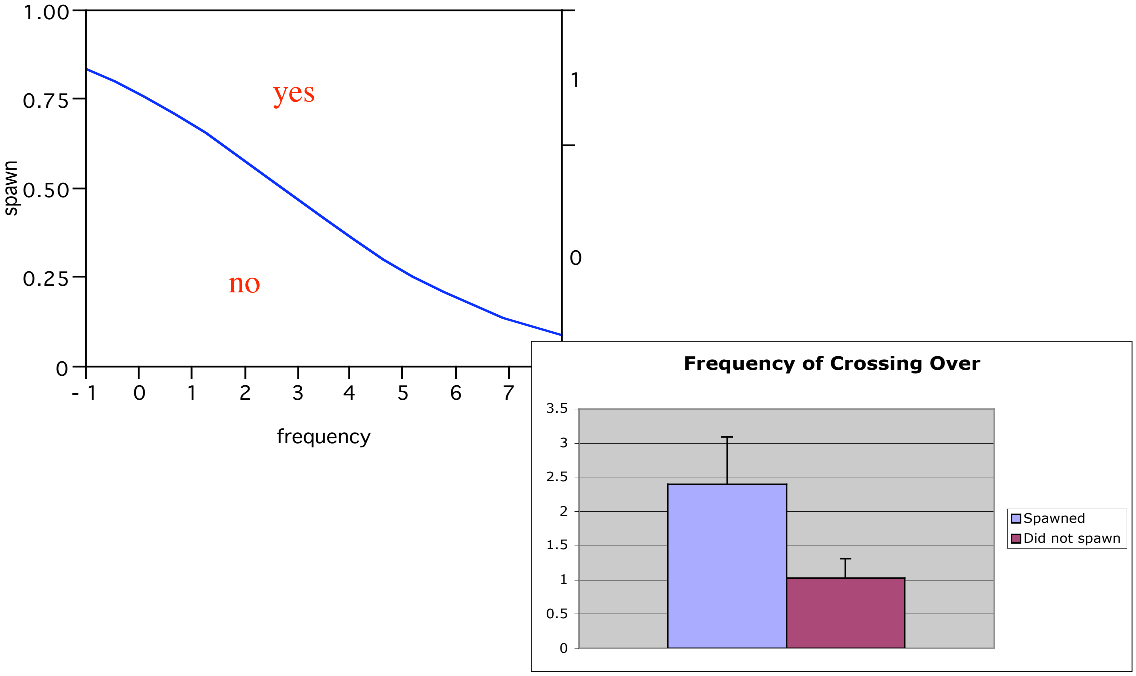
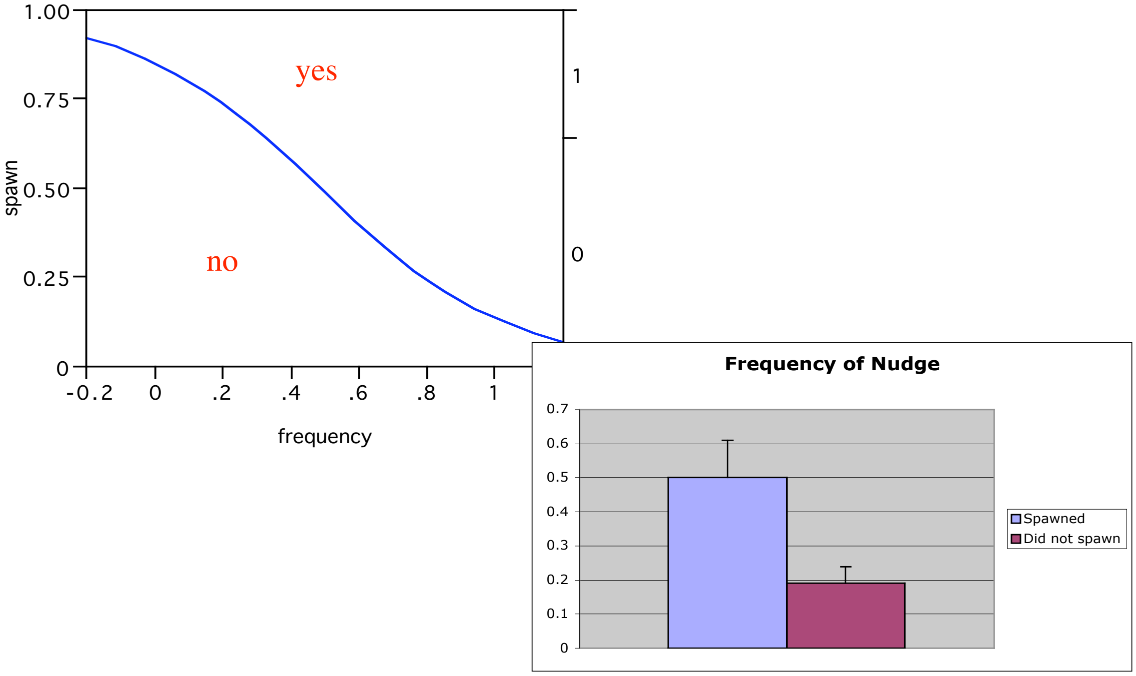


Figure 3.3: Logistic regression plots for predicting the probability of spawning with the frequency of several behaviors. The x-axis is the frequency of the noted behavior. The area above the curve represents the probability of spawning associated with the frequency of behavior while the area below the curve is the probability of not spawning. Bar graphs depict the mean and standard error of frequencies of behaviors experienced when females spawned and did not spawn.

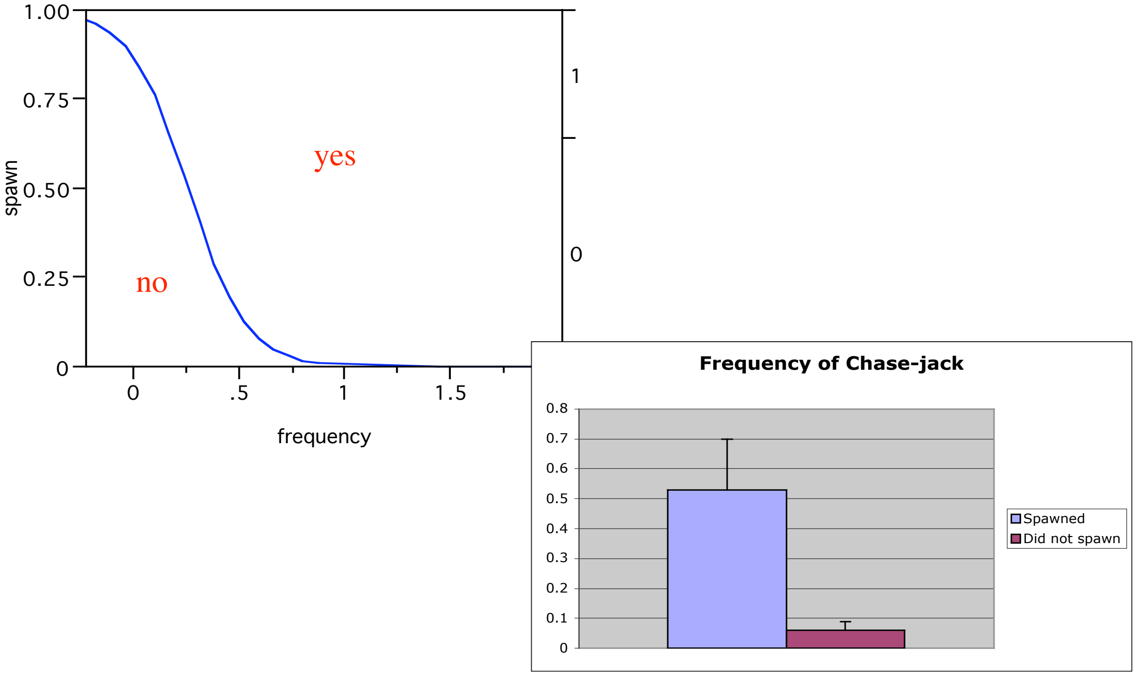
A. Logistic regression on frequency of crossing over



B. Logistic regression on frequency of nudge



C: Logistic regression on frequency of chase-jack



D: Logistic regression on frequency of chase-hook