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POLYGAMY, FEMALE CHOICE, AND THE MOTTLED
SCULPIN, COTTUS BAIRDII,

THE OHIO STATE UNIVERSITY, PH.D., 1978
POLYGAMY, FEMALE CHOICE, AND THE
MOTTLED SCULPIN, COTTUS BAIRDI

DISSERTATION

Presented in Partial Fulfillment of the Requirements for the
Degree Doctor of Philosophy in the Graduate School of The
Ohio State University

By

Luther Park Brown, B.A., M.S.

****

The Ohio State University
1978

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The great question ... which I have not been able to answer, despite my thirty years of research into the feminine soul, is "What does a woman want?"

Sigmund Freud
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INTRODUCTION

The diversity of vertebrate breeding patterns has inspired numerous explanations for the occurrence of various mate selection patterns and mating systems, and these explanations have illustrated a number of correlations between the breeding patterns apparent in a population and other aspects of vertebrate ecology. The distribution and abundance of resources, the costs of reproduction to males and females, and the roles that each sex plays as parents are some of the more obvious correlates of vertebrate breeding patterns. These factors have consequently been the subject of much theoretical and experimental analysis. Less generally recognized factors may have been underestimated, however. The characteristics that determine mate quality, the mechanisms by which prospective mates are located and evaluated, and the consequences of choosing mates of different qualities may well differ from group to group. Such differences may have been obscured by general mating system analyses designed to explain patterns seen in large taxonomic groups. At the same time, these factors may be critical determinants of the breeding patterns apparent in a population.

The mottled sculpin (Cottus bairdi) is a polygamous freshwater fish with a breeding biology that allows experimental analysis of the criteria on which females base their choice of mate, the
mechanisms by which mates are chosen, and the characteristics that make high quality mating situations. Resource quality and male quality can be precisely defined in this organism, and large, high density breeding populations allow direct, manipulative analyses of the patterns, mechanisms, and consequences of mate selection.

Analysis of almost 2,000 individual matings reveals that female sculpins discriminate among available males and that this discrimination is based on male body size: females preferentially mate with large males. Analysis of male paternal abilities reveals that they too are a function of body size: a female's reproductive success is directly proportional to the size of her mate.

Field observations and computer simulations both suggest that female sculpins select a mate after making simple comparisons among available males. Two selective forces apparently favor this type of choice mechanism. On the one hand, large males make better mates since male paternal abilities are proportional to male size. On the other hand, the timing of reproduction in sculpins is critical, such that the success of individual matings declines as the breeding season progresses. Females choosing large mates thus increase their reproductive success, but females delaying reproduction while searching for a larger male may decrease their subsequent reproductive success. Identification of these selective forces allows evaluation of the benefits and costs of female choice
in the mottled sculpin. Various observations suggest that similar selective forces may influence the mechanisms of female choice in other vertebrates, and that these mechanisms may in turn determine both mate selection patterns and mating system structure.

Here I present this analysis of female choice in the mottled sculpin. This dissertation is divided into three parts, each designed as a separate paper and as an integral part of the whole. In the first section, I review recent analyses of vertebrate mating systems, evaluate current arguments concerning the selective forces molding the breeding biologies of vertebrates, and suggest that both the criteria on which females base their choice of mate and the mechanisms by which females locate and evaluate potential mates may have been underevaluated in these studies. In the second section, I describe the patterns and apparent mechanisms of female choice in a breeding population of mottled sculpins, and examine some consequences of these patterns. In the final section, I examine possible selective forces responsible for the observed choice mechanisms, analyze the consequences of some alternate choice mechanisms, and review the implications of these studies for the mottled sculpin and other vertebrates.
MODEL OF MATING SYSTEMS IN VERTEBRATES: 
A REVIEW AND EVALUATION

The diversity of animal mating systems has inspired a number of theoretical explanations for the occurrence of monogamy, polygamy, and promiscuity among vertebrates (see reviews in Orians, 1969; Downhower and Armitage, 1971; Selander, 1972; and Wilson, 1975). While the scopes of published explanations vary from examinations of the breeding systems of single species (e.g., Downhower and Armitage, 1971), to those of higher taxonomic groups (Wynne-Edwards, 1962; Crook, 1963, 1964; Orians, 1969; Ralls, 1977; Emlen and Oring, 1977), each attempts to define those ecological, evolutionary and behavioral factors influencing the structure of mating systems.

What Determines the Structure of Mating Systems?

Recent analyses of vertebrate mating systems have suggested that the relative abundance and distribution of resources may be critical determinants of the type of mating system prevalent in a population. Armstrong (1955) first proposed, and Snow (1963) and Crook (1963, 1964) later elaborated a model describing the occurrence of polygyny as a consequence of seasonally superabundant food supplies that allow males to reduce the assistance given each mate.
when raising young, and subsequently attempt to attract more mates. Less abundant food supplies require parental co-operation and favor monogamy. The "surplus-food" model was originally proposed as an explanation for polygamy in the wren *Troglodytes troglodytes* (Armstrong, 1955), and expanded by Crook (1963, 1964) to account for the diverse mating systems of Old World weaver finches (Ploceidae) and by Snow (1963) to explain lek formation in New World manakins (Pipridae).

Verner (1963, 1964; and Verner and Willson, 1966) observed that many North American birds breed in areas in which resources appear to be spatially or temporally variable and argued that the number of mates attracted by a male might be a function of the quality of resources that the male could offer. As later formalized by Orians (1969), this model argues that mammalian and avian mating systems result from the interaction of female mate selection, the spatial distribution of material resources available to breeding individuals, and the role that males play in caring for young. When resources are distributed evenly, so that all males can offer equal qualities to prospective mates, monogamy results: a female mating with an already mated male decreases her fitness because male parental care is reduced. When resources are limited or patchy, the quality of patches or territories may vary from male to male, and polygyny results: a female mating with an already mated male possessing a high quality territory may increase or maintain her fitness, since abundant resources may offset reduced
male parental care. This "patchy-environment" model has been used to explain mating patterns of long-billed marsh wrens *Telmatheres palustris* (Verner, 1963, 1964; Verner and Engelsen, 1970), red-winged blackbirds *Agelaius phoeniceus* (Holm, 1973), and yellow-headed blackbirds *Xanthocephalus xanthocephalus* (Willson, 1966).

The patchy-environment model was the progenitor of the recent mating system analysis of Emlen and Oring (1977). These analysts argued that the control or monopolization of critical resources by breeding organisms is a more direct determinant of mating system type than the evenness or patchyness of resource distribution. Particular resources, for example nesting holes, may be entirely monopolized by a relatively small number of mature males. If reproduction requires access to this resource, females may be forced to mate with previously mated males, simply because the resource is monopolized by those few males. Conversely, other resources do not lend themselves to monopolization and cannot be controlled, conditions that do not favor the occurrence of polygamy. The type of mating system prevalent in a population is thus determined by the "economic monopolizability" of a resource, which in turn is determined by the ease with which a resource can be controlled and the ability of organisms to maintain control. A number of organisms appear to conform to this model. For example, male orange-rumped honeyguides (*Indicator xanthonotus*) defend honeycomb, a limited resource critical to successful reproduction in this bird (Cronin...
and Sherman, 1976). Male yellow-bellied marmots (*Marmota flaviventris*) defend grassy territories that are necessary for successful reproduction in this mammal (Downhower and Armitage, 1971). Both of these species are polygamous. Unfortunately, no quantitative applications of this mating system analysis to breeding populations have been reported.

Material resources do not appear to be the only determinants of all of the few mating systems that have been examined. Several species of grouse (*Tetraonidae*) for example, breed in habitats having uniformly abundant food resources. Some of these same species are polygamous, but others are not (Wiley, 1974), an observation that is irreconcilable with simple resource based mating system analyses. Furthermore, grouse mating systems cannot be explained as a sole consequence of single parental care, as suggested by the surplus-food model (Wiley, 1974).

Among polygamous grouse, males are not only larger than females, but commence courtship and reproduction much later in life (Wiley, 1974). Observing that polygamy is generally a correlate of sexual bimaturism, specifically delayed maturity in males relative to females, Wiley (1974) proposed that the existence of polygamy may be more complex than suggested by resource based analyses. Predation, metabolic expenses and other costs may favor delayed maturation of males only. When bimaturism occurs, females may be confronted with a relative scarcity of preferred (i.e., older) males. If such conditions are concurrent with reduced male parental
care, polygamy results. Mating systems may thus be determined by the interaction of sex dependent life history phenomena with the role of the male as a parent. Although originally proposed as a descriptor of grouse breeding biology, this bimaturism model also at least partially describes several mating patterns of mammals (Ralls, 1977).

Current explanations for the occurrence of vertebrate mating systems thus identify a number of ecological and behavioral factors as possible determinants of mating system structure. In particular, the abundances, distributions, and monopolizability of breeding related resources; the roles of males as parents; female choice; and sex dependent survivorship patterns appear to be important determinants. Although particular analyses propose common determinants, each explanation results in a unique interpretation of the significance of various mating systems. Although the resulting explanations are not mutually exclusive, neither are they congruent.

Does Consistency Equal Verification?

As evolutionary studies, one goal of mating system analyses is to provide insight to the selective forces influencing vertebrate breeding patterns. One common method employed in the attainment of this goal has been the formulation of verifiable predictions derived from the assumptions and arguments of various analyses (Orians, 1969, 1972; Carey and Nolan, 1975; Wittenberger, 1976). Consistency between these predictions and patterns observed among breeding
vertebrates has been interpreted as verification of various individual mating system analyses, and therefore as a demonstration that particular analyses identify the selective forces operating on mating systems (Orians, 1972; Selander, 1972; Carey and Nolan, 1975; Wittenberger, 1976; Cronin and Sherman, 1976; Emlen and Oring, 1977). Thus Wittenberger (1976) argues "Agreement between the empirical evidence and deductions based on the model would clarify our understanding of the selective factors involved, as well as provide additional confirmation of the model."

Consistency between the expectations of a model and a set of observations does not demonstrate that the model accurately portrays natural processes or phenomena. Particular observations may be consistent with multiple existing models, or with other explanations as yet unproposed. Unfortunately, this relationship between consistency and verification has been ignored in discussions of mating system models. For example, Carey and Nolan (1975) argued that the patchy-environment model correctly predicted that the sexually dimorphic indigo bunting (Passerina cyanea) would be polygynous, and concluded that they had tested and supported this particular model. Likewise, Verner (1963) concluded that the fact that female long-billed marsh wrens mated with polygamous males while bachelors were available demonstrated a tradeoff between male parental care and breeding situation quality. Extending Verner's conclusion, Selander (1972) claimed support for the patchy-environment analysis: "If the model is correct, females should mate with already mated
males, even when unmated males are readily available. This has been demonstrated...." Orians (1972) followed the same lines of argumentation: "If my model (patchy-environment) is correct, it should be true that the breeding success per female does not decline with increasing numbers of females per male. This prediction has been verified...." Although these statements may be true, their implication of support for particular interpretations of mating system structure at the expense of other interpretations is misleading.

The apparently common argument that verification of the predictions derived from an hypothesis verifies the hypothesis is known as the "fallacy of affirming the consequent" and is deductively invalid (Hempel, 1966, p. 7). Although confirmations involving this type of argument may demonstrate that a particular model adequately describes a given set of data, or that the model appears applicable to a given system, they do not necessarily support the contention that the model correctly identifies the processes or selective factors involved in the system, or that the model has general applicability. An example may help illustrate this relationship. The "broken stick" model was proposed by MacArthur (1957) as a predictor of the relative abundances of the different species in a community. This model provided a basis for many investigations of community structure, and was widely accepted as an accurate portrayal of the factors involved in community organization (reviewed by King, 1964). Later work demonstrated that
the predictions attributed to the broken stick model were not unique, but could actually be generated from two other radically different sets of assumptions (Cohen, 1968). Simple comparison of community structure with the expectations of the broken stick model could not confirm any one of the three possible models.

The verification of predictions attributed to various analyses has thus been both widely accepted and possibly misinterpreted. Although emphasis given to the verification of predictions has allowed the synthetic analysis of a wide range of diverse observations, it may have lead to premature conclusions concerning the nature of selective forces acting on vertebrate mating systems.

Applying Models: Assumptions and Resulting Predictions

Analyses of confirmatory predictions pose two problems: predictions attributed to a single analysis may actually be common to multiple analyses, in which case confirmation does not allow discrimination between alternative interpretations or provide additional insight to selective factors and processes, and particular predictions may be confirmed in some breeding populations but not in others of the same species or of different species, making a general interpretation difficult.

Many assumptions and arguments are shared by multiple mating system analyses (Table 1). Particular assumptions are widely shared. For example, natural selection is commonly assumed to be the ultimate determinant of mating system structure. The arguments
derived from common assumptions may be diverse, however. For example, the disproportionate division of reproductive costs between the two sexes is commonly assumed to be an important organizer of breeding systems. The reproductive success of female vertebrates may ultimately be limited by the energy available for the production (in birds), and subsequent care (in mammals) of eggs and young. Male birds and mammals have substantially lower energetic costs because their gametes are vastly smaller and more abundant than those of the female. Especially in mammals, the various costs involved in the production and nourishment of embryos and in lactation mandate higher reproductive costs for females than for males. Although males may increase their reproductive success by mating with more than one female, females are unlikely to increase their production of young by mating with more than one male. The consequences of mate selection are therefore more serious for females than males, and females may thus be expected to exercise more caution in mate selection than do males (see Orians, 1969; Trivers, 1972).

This common assumption that reproduction costs females more than males has lead to a diversity of arguments. The patchy-environment model argues that since female reproductive costs exceed those of males, selection acts to maximize female reproductive success. Females cannot, therefore, choose mating arrangements that decrease their fitness relative to the best possible mating
arrangement (i.e., monogamy). Since females never enter mating arrangements that decrease their fitness, and since a male's fitness is a function of the number of females with which he mates, polygamy must always be advantageous to males.

The economic-monopolization model does not argue that females never enter mating arrangements that decrease their fitness. According to this analysis, males are generally capable of exploiting monopolizable resources more fully than are females, simply because males share a disproportionately small part of the costs of producing and raising young. The sexual-bimaturism model argues only that disproportionate reproductive costs favor female choice. Females choosing mates that have delayed maturation increase their fitness, since their sons will also delay maturation, increasing their survival, and consequently their own reproductive success.

Existing analyses also assume that male parental care must be reduced in polygamous or promiscuous matings. The surplus-food and patchy-environment analyses have commonly been interpreted as arguments against any paternal care in polygamous matings. If, as proposed by these models, paternal care is non-existent, females must base their choice of mate either on the genetic quality of the male or on the quality of the resource patch controlled by the male (Wittenberger, 1977). The patchy-environment interpretation (but not the surplus-food model) extends this argument. Whenever males control resources critical to reproduction, resource quality will determine female choice. Since females cannot enter
mating arrangements that decrease their fitness relative to the best possible arrangement (i.e., monogamy), and since each additional mate obtained by a male requires an additional allotment of resources for her use, quantum differences must exist between the resource qualities of polygynous males. Thus males with resources sufficient to support a single female obtain a single mate, males with an additional quantum of resource quality obtain two mates, etc. The minimum differences in resource qualities necessary for females to choose polygynous pairings have been termed polygyny thresholds (Verner and Willson, 1966; Orians, 1969; Wittenberger, 1977): a monogamy threshold separates those males with resources sufficient for a single mate from those with insufficient resources, a bigamy threshold separates those males with two quanta of resources from those with only one, and so forth.

The resource-monopolization analysis of mating systems argues that any reduction in male parental care, whether resulting from resource superabundance, resource distributions or reproductive physiology (e.g., lactation in mammals) allows males to exploit the monopolizability of critical resources, thus increasing his potential reproductive success. This analysis does not necessarily argue that paternal care is absent in polygamous species, nor does it argue that quantum differences exist between males or the resources they control.
The sexual-determinism interpretation of mating systems assumes that reduced male parental care is a necessary prerequisite for the evolution of polygamy but that uniparental care is not sufficient cause for the occurrence of polygyny (Wiley, 1974). According to this analysis, paternal roles, which may be determined by resource abundances and distributions interact with selection for sex dependent life history patterns to determine mating system structure.

Just as various mating system analyses share common assumptions, so they share common predictions (Table 2). For example, all models sharing the assumptions that reproduction costs females more than males and that polygamy is incompatible with full biparental care predict monogamy whenever two parents can cooperatively raise more young than the female can by working alone. When the contribution of the male is substantially reduced by over-abundance of food during the breeding season, the physiology of reproduction (e.g., nursing in mammals), or the development of precocial young, males may be freed to seek other mates (or monopolize critical resources), and polygyny may result. These predictions were formally attributed to the patchy-environment analysis by Orians (1969): polyandry should be rare among birds and mammals; monogamy should be exceptional among mammals but prevalent among birds; birds with precocial young should be more commonly polygynous than birds with altricial young; and polygyny
or promiscuity should be most common in species in which clutch size is strongly limited by factors other than the number of young that could be supported by the parents. In fact, these predictions are shared by several models.

Similarly, a large number of predictions attributed to particular mating system models are consistent with other existing models. For example, the prediction that the mating patterns seen in a single species might vary if the species lives in habitats having different resource distributions (Orians, 1969, 1972) is shared by all natural selection models that relate mating systems to resource distributions. The prediction that species demonstrating marked sexual dimorphism will be polygynous (Carey and Nolan, 1975) is shared by those models that assume that female choice influences male courtship success and, implicitly, that male fitness is a function of courtship success. The prediction that females may choose polygynous males even when unmated males are available and perceived by females (Orians, 1969) is shared by any analysis that assumes either that males differ in their suitabilities as mates or that there is no disadvantage to a female entering a polygynous mating. Since this last prediction is consistent with random mating, its verification does not even imply the existence of female choice, let alone the verification of any particular mating system analysis.

Not only are published predictions that have been attributed to particular analyses of mating systems common to multiple interpretations (Table 2), but certain predictions have been confirmed
in particular breeding populations but not in others of the same or different species. For example, the patchy-environment model results in the prediction that there should be a non-negative correlation between average female reproductive success and the number of females mated with a male since females presumably never enter mating arrangements that decrease their fitness (Orians, 1969). Several tests of this prediction have been reported. For instance, Holm (1973) found that fledging success of red-winged blackbirds increased with the number of females breeding with each male, but Weatherhead and Robertson (1977) found a significant negative correlation between the number of young fledged per female and harem size in this same species. Willson (1966) found no significant correlation between female reproductive success and harem size in yellow-headed blackbirds, but negative correlations have been reported for the yellow-bellied marmot (Downhower and Armitage, 1972), the finch *Ploceus phillipinus* (Ambedkar, cited in Crook, 1964), the warbler *Acrocephalus arundinaceus* (Peltzer, 1972), and the sparrow *Passerculus princeps* (McLaren, 1972).

Another example of controversy is provided by the prediction that there should be a positive correlation between the number of mates a male attracts and the productivity of the resource patch that he controls (Orians, 1972). This prediction has proven difficult to examine because of the problems inherent in measuring and interpreting territory productivity. Often, estimates of territory area or vegetation cover have been used as indicators of
productivity. Territory size has variously been found to be insignificantly (Verner and Engelsen, 1970) or positively (Verner, 1964) correlated with the mating success of male long-billed marsh wrens, and negatively correlated with mating success of male yellow-headed blackbirds (Willson, 1966). Higher mating success was observed by Willson (1966) in yellow-head territories with large amounts of emergent edge vegetation, but Holm (1973) was unable to demonstrate this correlation in red-winged blackbirds, and Verner and Engelsen (1970) found no correlation between mating success and the area of cattail, the area of bullrush, the area of mixed cattail and bullrush, percent cattail, or percent mixed cattail and bullrush in territories of male marsh wrens. Furthermore, Weatherhead and Robertson (1977) found no correlation between harem size and their multi-dimensional measure of territory quality in red-winged blackbirds, leading these researchers to conclude that female red-wings based their choice of mate on his behavior, not his territory quality (Weatherhead and Robertson, 1977a).

In summary, much attention has recently focused on the verification of predictions derived from various mating system analyses. Recent examinations of numerous predictions have resulted in the conclusion that particular mating system analyses accurately describe the factors influencing natural mating systems (Orians, 1972; Selander, 1972; Carey and Nolan, 1975; Cronin and Sherman, 1976; Wittenberger, 1976; Emlen and Oring, 1977). Two facts suggest that current understanding is incomplete. Since the assumptions
necessary to generate verified predictions are shared by multiple models, simple verification of the predictions does not provide insight to the selective factors affecting mating systems. Furthermore, particular predictions have been verified in some breeding populations only to be refuted in other populations of the same or different species.

**General Models and Differences Among Breeding Vertebrates**

Emphasis on the production of a general model encompassing many taxonomic groups (birds and mammals: Orians, 1969; all vertebrates: Emlen and Oring, 1977) may have fostered neglect of very real differences existing between vertebrate species. The observation that particular predictions have been verified in some species but not in others certainly suggests that current understanding is incomplete. Furthermore, sexual patterns of some large vertebrate groups, for example the mammals, are not adequately described by existing analyses (Ralls, 1977). These observations may not represent fallacies in current analyses as much as they represent differences in the dimensions of the breeding biologies of various organisms, dimensions that define which males make desirable mates, and how females locate and identify their partners.

**Who Makes a Good Mate?**

The criteria on which females may base their choice of mate have been the subject of far more theoretical than experimental analysis. When females raise their young without male parental
assistance, and when males do not control resources critical to successful reproduction, females may base their choice of mate entirely on male phenotype, since the only contribution that the male makes to his offspring is genetic (Orians, 1969). When males control resources used by females during the reproductive process, females may base their choice of mate on the quality of the resources under the male's control (Orians, 1969; Williams, 1975), and, implicitly, on the number of other females with which she would share these resources. Finally, when males care for their young or assist females in caring for their young, females may base their choice of mate on male physical or behavioral attributes related to paternal ability.

Unfortunately, the relationships between resource patterns, paternal duties, and female choice have only recently been quantified. Demonstrations of correlations between resource quality and male courtship success have frequently neglected any measurement of the physical or behavioral attributes of individual males (e.g., Holm, 1973; Cronin and Sherman, 1976; Carey and Nolan, 1977; but see Verner, 1964). Detailed examination of species, like the red-winged blackbird, formerly cited as examples in which females based their choice on territory quality (Holm, 1973; Orians, 1972) have shown that male behavior and age are significant determinants of female choice even when male parental care is very limited (Yasukawa, 1977; Weatherhead and Robertson, 1977, 1977a). In fact, male physical and behavioral attributes have been implicated as
determinants of female choice in a wide variety of species (Table 4, from Downhower and Brown, 1978a), including several in which resource quality may also be important.

The observation that polygyny is generally concurrent with reduced male parental care (Armstrong, 1955; Orians, 1969; Williams, 1975) has been interpreted to mean that polygynous males have no roles as parents (Wittenberger, 1976). But paternal roles are certainly diverse, and may be subtle. Males may indeed provide critical, limited resources. For example, male dickcissel (Spiza americana) provide their mates with territories rich in insects (Harmeson, 1974) and forb cover (Zimmerman, 1966), male honeyguides provide their mates with honeycomb (Cronin and Sherman, 1976), male marmots provide their mates with suitable breeding habitats (Downhower and Armitage, 1971), male sticklebacks (Gasterosteus aculeatus) provide their mates with nests (Wootton, 1976). At the same time, males may perform a number of non-resource based functions, some more obvious than others. Obviously, males may defend their mates and offspring from predators, warn their offspring of danger, or assist their mates in feeding the young, as for example, do male marsh wrens (Verner, 1964). Less obviously, male mammals may socialize their young (Kleiman, 1977). Male marmots may maintain peace among neighboring females (Downhower and Armitage, 1971), and males of numerous species may simply provide a stable social environment conducive to breeding by driving away disrupting males, especially if strange males are
cannibalistic (e.g., Panthera leo: Schaller, 1972) or cause embryo resorption (e.g., Mus musculus: Wilson, 1975). Male fishes may aerate their eggs, and even prevent the spread of disease among them by eating infected eggs (e.g., Bailey, 1959). Male roles may thus be diverse, unobtrusive, and important to successful reproduction. Furthermore, males of different ages, sizes, experience, etc. may differ in their parental abilities and these differences may influence male desirability.

In some cases, males may be less able to perform their functions for multiple females than for single mates. Multiple females obviously require greater food supplies or more nesting sites than do single females. Multiple broods of young may be more difficult to protect than single broods. The number of mates a male already has would then presumably influence female choice. Alternatively, males may be just as able to perform their functions for multiple females as for a single mate. For example, male fishes may be just as capable of maintaining multiple clutches of eggs as single clutches (Perrone, 1975). In this case, the number of females already mated to a male may have no effect on female choice.

The relationships between resources and the males controlling them can be complex. Particular resources may be limited to the extent that some males are excluded from resource possession as suggested by the resource-monopolization analysis. Female choice would then be restricted to that set of males controlling resources.
Alternatively, resources may be abundant, yet still be differentially controlled by males. Thus a resource that is distributed uniformly about a breeding habitat can be divided among males such that the distribution of resources per male is either uniform or strongly clumped (Figure 1). A resource that has a clumped distribution about a breeding habitat can be divided among males such that the distribution per male is either clumped or is actually uniform (Figure 1). Indirect measures of resource quality, for example territory area, may thus be misleading. The observation that territory size and harem size are not correlated in red-winged blackbirds for example (Orians, 1969; Case and Hewitt, 1963; Holm, 1973; Weatherhead and Robertson, 1977, 1977a), does not necessarily imply that resource quality is unimportant in this species.

Since the resource controlled by a male is a function of both the environmental resource distribution and male territoriality, correlations between resource quality and male courtship success may simply reflect correlations between resource quality and male quality. This may be true whenever those male characteristics resulting in the maintenance of high quality territories are the same as those characteristics resulting in courtship success. Alternatively, male characteristics resulting in territory maintenance may be different from those resulting in courtship success. For example, both epaulet color and vocalizations may play important roles in territorial maintenance by male red-winged blackbirds, and play relatively minor roles in courtship success (review in
Weatherhead and Robertson, 1977a). Furthermore, intersexual selection of females for males may actually be an important determinant of male mating success in various mammals which have breeding patterns generally attributed to intrasexual selection (Ralls, 1977). Thus male-male competition for territories or mates may involve very complex interactions that may still be relatively unclear even in well studied species like the red-winged blackbird.

Female choice of mate can thus be based on resource quality, male quality and/or male marital status depending on the importance of resources, the importance of males as parents, and the importance of monopolizing a male as a mate. Since the relative importance of each of these factors may be quite different in different organisms, generalizations between groups of organisms may be difficult. Finally, current understanding of the interactions between males, the resources they control and female choice is limited. General mating system models may lack the resolution necessary for understanding these differences.

How Do Females Pick Their Mates?

The mechanisms by which females locate and identify desirable males may strongly influence the structure of vertebrate mating systems, and may be quite different among different groups of organisms.
The diversity of vertebrate dispersion patterns and locomotory abilities requires a diversity of female sampling abilities. Through flight, female birds and bats can rapidly locate and evaluate large numbers of males before choosing a mate. This is especially true when locally available males aggregate as in lek forming species. Females visiting a lek can locate and evaluate all locally courting males almost instantaneously. For example, female hammer-headed bats (*Hypsignathus monstrosus*) visit leks of dozens of courting males, evaluate each male in turn, and pick a single mate (Bradbury, 1977). Slightly more sampling effort may be required by females that breed colonially or in limited habitats. Thus female indigobirds (*Vidua chalybeata*) visit a number of males before mating (Payne and Payne, 1977), and female whydahs and bishopbirds (*Euplectes sp.*) wander through colonies of males, ultimately picking a single mate (Emlen, 1957).

When potential mates are more dispersed or when female locomotory abilities are more limited, the sampling effort required to locate a suitable mate may increase and the number of males sampled before a mate is chosen may decrease. Female mountain lions (*Felis concolor*), for example, occupy individual home areas and the areas of several females may be encompassed by that of a single male (Seidensticker, et al., 1973). One direct consequence of mountain lion dispersion patterns is that females are unlikely to sample very many males (more than one?) before mating. Equivalent dispersion patterns may be quite common among mammals, having
been reported in groups ranging from rodents to primates (review in Ralls, 1977). In a similar manner, male yellow-bellied marmots defend hospitable territories surrounded by inhospitable terrain (Downhower and Armitage, 1971). When marmot territories are sparse, simple location of potential mates by females may be difficult, and females may be restricted to sampling a limited number of males.

The ability of females to identify desirable males may be a function of the particular qualities that determine mate desirability. Whenever the distribution of available choices is invariable or some quality is absolutely essential to reproduction, females may base their choice on a fixed threshold, or series of thresholds of male desirability. For example, female honeyguides require honeycomb for reproduction (Cronin and Sherman, 1976), and males either control access to honeycomb or they do not. Alternatively, when the distribution of available choices varies between breeding seasons females may base their choice on simple comparisons among those choices available during that particular season. Thus females might mate with a male if he controlled the best available territory, or if he were older than the average male in the population, or if he had fewer mates than the last male she encountered. This is the type of relative comparison apparently determining female choice in *Drosophila* (Speiss and Schwer, 1978), in which females become habituated to the most common courtship patterns present in a population of males, and then choose a mate
demonstrating slightly different patterns.

Whether females base their choice on thresholds of male quality or on relative comparisons, potential mates must be located and evaluated before they can be chosen. If female choice mechanisms reflect the action of natural selection, then they presumably reflect both the benefits of high quality mating and the costs of the search. When females can sample a large number of males rapidly and with little effort, as for example can many birds, females may be able to choose only high quality matings. When, on the other hand, the dispersion patterns of males and female movement abilities make simple location of males difficult and time consuming, females may ultimately increase their reproductive success by settling for a less than optimal mating rather than searching further for a better mate. This possibility is developed further elsewhere (Section III).

Both the qualities that determine male desirability and the mechanisms by which females choose their mates may thus vary among different vertebrate groups. Particular groups, for example birds, may readily assess available males and may have a relatively large number of options from which to choose. Choices may be more limited for less mobile and more dispersed vertebrates.
The Denial of Alternatives

Acceptance of any single analysis of mating systems may result in rationalization or reinterpretation of data conflicting with that analysis. For example, Selander (1972) argued that Crook's (1963, 1964) observations were in fact consistent with the patchy-environment model since "presumably the male must spend a relatively large part of his effort in holding a territory (which reduces his contribution to parental care), while the female must pair with an already mated male if she is to obtain a good nesting site." No analysis of the importance of "good" nesting sites is available to support this presumption. Similarly, Elliott (1975) relied on a series of arguments concerning longevity, predation, and reproductive investment in his attempt to analyze data presented by Downhower and Armitage (1971) in a manner consistent with the patchy-environment model. In yet another reanalysis of these same data, Wittenberger (1976) made assumptions concerning the occurrence of good and poor habitat qualities, even though habitat quality was not measured or discussed by the original authors. Such apologetics for particular mating system models are unnecessary and may obscure real differences among patterns of breeding in vertebrates.
The Experimental Analysis of Vertebrate Mating Systems

Recent mating system analyses have suggested that resource distributions, male paternal duties, female choice and life history patterns may all be important determinants of the reproductive patterns apparent in a vertebrate population. A brief review of differences between vertebrate breeding requirements, dispersion patterns and movement abilities suggests that these factors may also be important. Manipulative experimental analyses of vertebrate populations may provide insight to the selective forces acting on mating systems.

The criteria on which females base their choice of mate may be discovered by simple manipulations of the distributions of available choices. For example, if resource qualities determine female choice, an experimental reduction in the variance of available resource qualities should produce a corresponding reduction in the variance of male mating success. Reciprocally, an increase in the variance of resource qualities should increase the variance in male mating success. Similar experiments could be used to demonstrate the importance of male qualities. For example, if male size determined female choice then an increase in the variance of male sizes in a population should increase the variance in male courtship success and vice versa. This is the approach pioneered by Ballard and Robel (1974) who removed the dominant male prairie chickens (Tympanuchus cupido) from a lek and observed a subsequent decrease in the variance of male mating success.
Experimental examinations of the mechanisms of female choice may also be possible. Manipulations of the shapes and locations of the frequency distributions of available choices should reveal thresholds of mate acceptability. If, for example, females base their choice of mate on a fixed threshold of territory quality, then reduction of the mean but not the variance of territory qualities should increase the number of bachelors in a population and decrease the number of males chosen by females. If females base their choice on relative comparisons between available territories, such manipulation would have no effect on the number of males chosen by females.

Direct determination of the costs and benefits of female choice may also be possible. If female reproductive success varies in different mating situations, whether they are monogamous or polygynous, the female's benefits of remaining in a given situation or of searching further for a better situation can be quantified. Costs associated with leaving a mating situation may be estimated in terms of the time taken to locate a more suitable mate, the area that must be searched to locate a more suitable mate, the probability of locating a more suitable mate, or the increased mortality associated with the search for a more suitable mate.

If, as is suggested by recent mating system analyses, vertebrate mating systems are responsive to experimental manipulation, direct analyses of the importance of resource qualities, male qualities and female choice to the evolution of the mating systems
of single species may be possible. Such analyses may in turn lead to a better understanding of the selective forces generally acting on vertebrate mating systems.
HOW AND WHY FEMALE SCULPINS (COTTUS BAIRD) PICK THEIR MATES

Although female choice has been cited as a primary determinant of mating system structure (e.g., Orians, 1969; Emlen and Oring, 1977), social organization patterns (Ralls, 1977), and parental investment tactics (Burley, 1977), few analyses of the patterns, mechanisms, and consequences of female choice in natural populations are available.

The criteria on which females may base their choice of mate have been the subject of both theoretical (e.g., Orians, 1969; Williams, 1975) and experimental (e.g., Thornhill, 1976; Yasukawa, 1977) analyses. When females raise their young without male assistance, females may base their choice of mate on male phenotype. When males control particular resources that are critical to successful reproduction, females may base their choice of mate on the quality of the resources that he controls. When males perform their parental function better for single females than for multiple mates, females may base their choice of mate on the number of females with which a male has already mated. The attributes of individual males, the attributes of the resources controlled by individual males, and the number of females already mated to a male may all be female choice criteria.
The mechanisms by which females discriminate among available mates determine the patterns of female choice apparent in a population. A number of studies have documented female preference for males having particular physical or behavioral characteristics, or for males controlling particularly critical breeding related resources. For example, female killifish (*Nothobranchius guentheri*; Haas, 1976), guppies (*Poecilia reticulata*; Haskins, et al., 1961) and sticklebacks (*Gasterosteus aculeatus*; Semler, 1971) all preferentially mate with males having particular nuptial colors or patterns. Female preference for these bright colors is documented, but the mechanism of female choice remains elusive. All males that are more brightly colored than some minimum threshold may be equally acceptable as mates, or females may discriminate among degrees of color and mate with those males that are most colorful relative to their competitors. Furthermore patterns of female choice may be dependent on female age: younger females may make different types of choices than do older females (O'Donald, 1977).

In polygynous situations, quantum differences may exist between males such that some are capable of providing for multiple females although others are capable of providing for only one, or even no mates at all (Orians, 1969). The minimum difference in male parental abilities necessary for females to choose polygynous matings has been termed the polygyny threshold (Verner and Willson, 1966; Orians, 1969). If quantum differences do exist between males, then there is a monogamy threshold, a bigamy threshold, a
trigamy threshold, etc. As originally proposed, such quantum differences represent real differences existing between male or breeding situation qualities (Orians, 1969; Wittenberger, 1976), thus selection may favor those females that recognize these differences. Female choice mechanisms based on thresholds of male acceptability might reflect this recognition.

Alternatively, females may choose simply by comparing available males. For example, a female might mate with a male if his territory were larger than that of the last male that she encountered, or if he had fewer mates than the last male she encountered. A female making this type of choice neither searches for the best possible mate, nor bases her choice on a threshold of mate acceptability. Rather, she simply chooses a relatively high quality mate. This is the type of choice mechanism proposed by Mitchell (1975) as an explanation for the oviposition patterns apparent in populations of the beetle Callasobruchus maculatus, and implied by Spiess and Ehrman (1978; also Spiess and Schwer, 1978) in their discussion of female choice in Drosophila.

Both the criteria on which females base their choice of mate, and the mechanisms by which females discriminate among potential mates presumably reflect the action of natural selection. Females may thus be expected to choose their mates via choice mechanisms that increase their reproductive success. Here I describe the patterns of female choice apparent in a breeding population of
mottled sculpins (*Cottus bairdi*), examine possible choice criteria and mechanisms by presenting a simple model of female choice, and evaluate the consequences of the observed choice patterns.

**Breeding Biology of the Mottled Sculpin**

The mottled sculpin is a small (≤ 130 mm) fish that commonly inhabits high gradient north temperate streams. Although sculpin spawning seasons vary geographically (Smith, 1922; Hann, 1927; Ricker, 1934; Simon and Brown, 1943; Zarbock, 1952; Ludwig and Norden, 1969; Savage, 1963), the general pattern of sculpin reproduction remains constant. With the onset of spring, males construct (Hann, 1927) or locate suitable nesting sites. Nests are most commonly cavities beneath natural streambed rocks (Smith, 1922; Hann, 1927; Bailey, 1952; Ludwig and Norden, 1969), but are also found under waterlogged wood and scrap iron (Bailey, 1952), in crayfish burrows (Ludwig and Norden, 1969), and under pieces of slate, bricks, potsherds, concrete blocks, and other miscellaneous rubble (Downhower and Brown, 1977). Males actively defend their nest sites (cf. Ludwig and Norden, 1969; personal observation), but do not defend any of the surrounding area. In fact, naturally occurring nests are occasionally as little as six inches apart, and may share a common rock or piece of wood as a ceiling. Since males are uniformly dispersed with respect to nest sites and since males defend their nest against competitors, the nest site itself can be interpreted as a territory (Downhower and Brown, 1978).
Courtship is initiated by the male at the appearance of a female. Males typically exhibit a cephalic display (Savage, 1963), consisting of rapid shaking and nodding of the head, often accompanied by elevation of the opercula, gaping or yawning, and fanning of the pectoral fins. Receptive females enter the nest, and, after much maneuvering, lay their eggs on the roof of the shelter. Females spawn only once per year (Hann, 1927; Savage, 1963), and deposit all of their eggs in a single hemispherical mass (Smith, 1922; Bailey, 1952; Ludwig and Norden, 1969). Males, on the other hand, are sequentially polygynous, and may mate with as many as twelve females in a single spawning season (Downhower and Brown, 1978a). Polygynous spawnings of two to five females per male are commonly reported (Smith, 1922; Hann, 1927; Ludwig and Norden, 1969; Bailey, 1952; Downhower and Brown, 1977, 1978, 1978a).

After spawning, females are either driven from the nest (Savage, 1963) or leave the nest to avoid predation by the larger male (Downhower and Brown, 1978). Males generally remain at the nest site throughout the entire breeding season, and do not abandon the nest until the eggs have hatched, the fry have absorbed their yolk sacks, and begun to disperse, some six to eight weeks after the onset of spawning (Downhower and Brown, 1978, also unpublished data).

The oviposition period preceeds and does not overlap subsequent hatching of the eggs and maturation of the fry (Downhower and Brown, 1978). Male residence at the nest site after the
oviposition period thus represents a period of paternal care. Attendant males fan their eggs with their pectoral fins (Savage, 1963), a behavior that has been analyzed in detail for C. gobio (Morris, 1955), and that may maintain dissolved oxygen concentrations suitable for egg development. Guardian males may also eliminate fouling organisms from the nest, defend the eggs from predators, and prevent the spread of fungus through the egg masses by eating dead eggs (Bailey, 1952; Downhower and Yost, 1977).

Since nests are constructed beneath streambed rocks, the distribution of available nesting sites remains static throughout the breeding season. Since courting males generally remain at their burrows during the oviposition period, the distribution of males is also essentially static. Gravid, mobile females are thus confronted with a mosaic of nesting sites and associated males, from which they can choose a single mate.

**Experimental Design**

Sets of rectangular slate tiles were placed in a 200 m stretch of Anderson Creek, Champaign County, Ohio at the beginning of the spring spawning seasons in 1975, 1976 and 1977. In 1975, 75 each of three tile sizes were used (14.5 x 7 cm; 14.5 x 14.5 cm; 14.5 x 21.5 cm). In 1976, 50 each of six tile sizes were used (14.5 x 4 cm; 14.5 x 7 cm; 14.5 x 10.5 cm; 14.5 x 14.5 cm; 14.5 x 18 cm; 14.5 x 21.5 cm), and in 1977, 300 square tiles were used (14.5 x 14.5 cm). Tiles were placed in the stream with their upstream edge
resting on the stream bottom, and their downstream edge supported by a steel pin driven into the streambed. The distribution of tiles was such that subsequent univariate and multivariate analyses of variance demonstrated no significant differences between mean depths, distances to closer shore, dissolved oxygen, current velocities, distance to nearest neighboring tile, or distance to nearest larger neighboring tile (Table 4). The only measurable difference between these experimental nesting sites was thus tile size (Downhower and Brown, 1978a).

The experimental breeding sites were rapidly colonized by sculpins. Over 50 percent of the tiles were occupied by adult male sculpins within five days. More than 90 percent of the larger tiles were eventually occupied.

Tiles were sampled at three to four day intervals throughout each spawning period. On each sample date, each tile was isolated from the surrounding stream with a "capture box" that allowed capture of all fish residing beneath the tile (Downhower and Brown, 1977). The numbers, sexes and total lengths of fish resident beneath each tile, and the number of egg masses in each nest were recorded. Since each egg mass represents the total annual reproductive output of a single female, the number of females mating with an individual male could be determined by counting the number of egg masses present in his nest.
Each nest was photographed on each sample date so that the fates of individual egg masses could be determined. Egg masses were subsequently scored either as successes (i.e., at least one egg hatched), or as failures (i.e., the entire egg mass disappeared prior to hatching).

The Pattern of Male Reproductive Success

Previous observations of the dispersion patterns of adult males, gravid females, and spawnings per male suggested that females selected particular mates from a suite of potential mates (Downhower and Brown, 1977, 1978). Adult males were uniformly distributed beneath the tiles. Gravid females captured beneath tiles were randomly distributed, but spawnings per male were significantly clumped, indicating that particular males or breeding sites attracted more females than expected on the basis of chance. The difference between the random distribution of females and the clumped distribution of spawnings suggested that females were not forced to spawn by males (see Morris, 1955) and did not spawn with the first male encountered, but visited more than one male before mating.

Females apparently demonstrated preference for particular males during much of the breeding season. Spawnings with bachelor males occurred less frequently than expected on the basis of chance encounters at the beginning of the breeding season and throughout the period of peak spawning (Figure 2). As bachelors became rarer, late in the season, the proportion of spawnings with bachelors
approached and became insignificantly different from that expected on the basis of chance encounters. This pattern again suggests that females picked particular males from the suite of available males.

Although the total size distribution of males occupying the study site remained constant during the entire breeding season, the distribution of breeding males changed (Figure 3). Early in the spawning season, only very large males succeeded in their courtship. The frequency distribution of mated males thus occupied the upper tail of the frequency distribution of all resident males. As time elapsed, successively smaller males attracted mates, so that at the end of the oviposition period, virtually all of the males resident in the study site had succeeded in mating with at least one female.

Analysis of male size as a function of courtship success reveals that large males not only bred earlier than small males, but also continued to sequentially mate with additional females (Figure 4). The mean sizes of males mating for the first and subsequent times declined throughout the spawning period, yet males with greater courtship successes were always associated with greater mean sizes than were males with lesser courtship successes. Furthermore, the differences between mean sizes of males mating with their first, second, third and subsequent females were constant, thus the mean sizes of males with equivalent courtship successes declined in parallel as the season progressed. Large males thus obtained
their first mates earlier than did small males and moved from the ranks of bachelors to those of singly mated males earlier in the season. By extension, large males obtained their second mates earlier than did smaller males and moved from the ranks of singly mated males to those of multiply mated males earlier in the season. Since the total distribution of males occupying the study site remained constant during this time (Figure 3), this temporal pattern of male size dependent courtship success indicates that smaller males that were unsuccessful in their courtship early in the season became successful as the season progressed.

The mean sizes of both gravid and spawned females also declined throughout the entire spawning period (Figure 5) yet spawned females were consistently associated with greater mean sizes than were gravid females. Both of these observations suggest that larger females bred earlier in the spawning season than did smaller ones, and this in turn suggests that the apparently changing patterns of male reproductive success may be attributable to size or age specific female preferences. Conversely, large females may have made the same types of choices made by small females, and simply made them earlier in the spawning season.

In summary, females appeared to pick particular males from the suite of available males. Large males bred first, and continued to mate with successive females, but smaller males ultimately succeeded in spawning. Since the total distribution of available males remained constant during this time, males that failed in
their courtship early in the season must have succeeded later. These patterns may reflect size dependent breeding readiness by males or may be a direct result of female choice. If reflecting male responsiveness to females, these patterns suggest that large males were capable of breeding earlier in the spawning season than small males. If resulting from female choice, these patterns suggest that choice criteria may have changed as the season progressed, or that larger (older) females made different choices than smaller (younger) females. Alternatively, these patterns may only appear to change and reflect unchanging female choice mechanisms.

Possible Determinants of Female Choice

Since sculpin eggs and fry remain in the nest for relatively long periods of time (approaching eight weeks), and since sculpin males are responsible for maintaining the eggs during that time (Downhower and Yost, 1977), the determinants of female choice might reasonably include both attributes of breeding sites and of individual males. The experimental breeding sites in this study differed only in their size and not in other edaphic characters (Table 4). Males, on the other hand, probably differed in a number of ways (body shape, age, courtship ability), most of which may be related to body size and are here reduced to a single measure of male size: total length.

Male size was a function of tile size. Large males typically occupied large tiles, while smaller males were found under smaller tiles (Figure 6). Larger tiles were also occupied by proportionally
more males earlier in the spawning season than were smaller tiles (Table 5). Since agonistic interactions have been observed between males (cf. Ludwig and Norden, 1969; Downhower and Brown, 1978), this assortment of males beneath the experimental spawning sites can only be interpreted as a demonstration of male preference for larger breeding sites.

Male courtship success was also a function of tile size (Figure 7). Males occupying larger breeding sites tended to mate with greater numbers of females than did males occupying smaller breeding sites. Both male size and breeding site size were thus correlated with male courtship success and may have reflected female choice. Analysis of covariance, in which male size is the covariate and tile size is a classification variable reveals that when the effect of male size on courtship success is removed statistically, the apparent effect due to tile size disappears (Table 6, taken from Downhower and Brown, 1978a; Brown and Downhower, 1977). Thus male size significantly influenced subsequent courtship success but tile size did not. Confirming evidence of the importance of male size is provided by the simple linear regression of number of matings per male on male size for 1977, the year in which only a single tile size was available (Egg Masses per Male = -2.17 + .05 (Male Length), N = 188, r = .32, F = 20.8, P < .001). Female sculpins thus appeared to base their choice of mate primarily on the attributes of individual males and either ignored spawning site size, or used it as a less important choice criterion.
Despite the fact that large females bred earlier than smaller females (Figure 5), female size had no apparent effect on preference for spawning sites or mates. On none of the three dates in 1976 on which testable numbers of females were captured were there any significant differences between mean sizes of gravid females caught beneath the different tile sizes (3/27: F = 2.25, d.f. = 5, 61, P > .10; 4/2: F = 1.77, d.f. = 5, 147, P > .05; 4/6: F = .95, d.f. = 5, 54, P > .05). Furthermore, the April 2, 1976 sample included 150 male-female pairs, and showed no significant correlation between male and female lengths (r = .057, P > .05, b = .073, P > .05). Large females thus did not prefer large males or tiles any more than did small females.

Analyses of the patterns of male reproductive success thus illustrate a number of aspects of sculpin breeding biology, which for the sake of clarity, can be summarized as follows:

1. Females demonstrated preference for particular mates throughout the spawning season.
2. Large males bred first and continued to sequentially accumulate additional mates, but smaller males succeeded in spawning at least once by the end of the season.
3. Males demonstrated preference for larger breeding sites but breeding site size did not influence courtship success.
4. Male courtship success was a function of male size. Although most males ultimately succeeded in spawning, large males attracted more females than did smaller males.
5. Although larger females bred earlier than smaller females, there is no evidence that female size influenced preference for either spawning sites or associated males.

**Simulation of the Patterns of Female Choice**

Females appeared to move among potential nest sites before breeding and may have based their choice of a nest on the attributes of the nest or its owner. Although statistical analyses of the results of female choice may indicate the relative importance of possible choice criteria, they neither indicate the processes involved in choice nor explain the patterns that these processes may have produced (Figures 2, 3, 4).

Sculpins are bottom dwellers that live in an essentially two-dimensional world: the shallow freshwater stream. A female visiting potential mates cannot view the total distribution of spawning sites at once, but only those sites on her own horizontal plane. Since spawning sites are a function of streambed topography they frequently occur in patches of several sites, and do not form a single continuous array. Furthermore, the swimming abilities of gravid females may well be impaired by their greatly distended abdomens. Thus, females probably do not sample the total distributions of potential nest sites and mature males. The nature of the experimental design allowed these distributions to be defined for the sample tiles, however.
Females may select a mate after sampling a small number of potential mates. The simplest possible comparison necessitates a sample of two. After visiting one potential breeding site, the shortest method of making a comparison is by visiting the nearest neighboring site. If the nearest neighboring site is not occupied by a male or is rejected as a nest, the simplest method of continuing the sampling procedure is to continue visiting successive nearest neighbor sites until a suitable mate is located. This pattern of limited movements is consistent with that observed in a natural population (Brown and Downhower, 1978).

This simple comparison routine was incorporated into a computer program designed to simulate spawnings and evaluate possible choice criteria and the patterns that they produced. A typical simulated spawning began with the computer randomly selecting a tile and storing the male size and nearest neighbor tile size associated with that tile. A comparison, based on the possible model criteria, was then made between the first breeding site and its nearest neighbor. If either of the sites involved in the comparison was not occupied by a male, the program proceeded to visit nearest neighbors until two successive sites with males were encountered. Thus the program assumed that female choice is based on comparison of two adjacent males and/or spawning sites and was designed to include the known spatial geometry of tiles and the known distributions of males associated with the tiles. Because of the large sample sizes available and the availability of multiple tile sizes,
simulation analyses were based on data collected in 1976. A
detailed description of the program is provided in the appendix.

The criteria on which comparisons were based varied with
different models (Figure 8). In the model RANDOM, a successful
spawning was recorded for the second male encountered in a se­
quence. This model thus simulated random spawning given the assump­
tion that females visited at least two successive males in the
programmed manner. Since simulated spawnings were restricted to
those tiles occupied by males, and since male occupancy was a func­
tion of tile size, the model RANDOM did not produce patterns iden­
tical to the Poisson distribution: those tile sizes occupied by
large numbers of males necessarily received large numbers of sim­
ulated spawnings. Since comparisons with a Poisson distribution
would have assumed that males at all sample sites were equally
available, such comparisons were considered inappropriate.

The model MALE SIZE recorded a spawning for the second male
in a series if he was larger than or equal in size to the pre­
ceding male. If the second male was smaller than his predecessor,
the program continued to search nearest neighbors until a series
occurred in which a following male was larger than or equal to
the preceding male. The model TILE SIZE followed the same proce­
dures as did MALE SIZE, except spawning successes were based on
the size of the tile occupied by a male.
Two interaction models allowed evaluation of possible joint effects of male and spawning site size. Both male and tile size for the successful breeding site equaled or exceeded those of the preceding site in the model AND. Either male or tile size provided the basis for comparisons in the model OR.

After each modeled spawning, the program randomly selected a new tile and repeated the comparison procedure. When the number of modeled spawnsings equaled that observed in the field, the program reset, drew a new tile, and resumed comparisons. Each run of the model thus recorded the number of spawnsings observed on that date. To minimize chance variations, 100 iterations were accumulated before the model terminated. After the model sequence terminated, the program printed the frequency distributions of spawnsings per male for each tile size, the means and variances of spawnsings per male for each model run and for the entire set of 100 runs, and the mean lengths and variances for males as a function of the number of spawnsings that they had accumulated.

The Analysis of Male Reproductive Success

The known frequency distributions of spawnsings per male for the total set of tiles and for each tile size on each of eight sample dates during the 1976 season were compared with those expected by the five models ($x^2$ test, expected values extrinsic to those observed, K-1 degrees of freedom (Sokal and Rohlf, 1969)). The results of such comparisons can be summarized concisely by examining the cumulative number of significant differences between
the observed distributions and those expected by the various models. Since the distributions observed on each sample date were dependent on those for preceding dates, the cumulative number of significant differences could not be compared to that expected if each test were independent (Binomial distribution).

The models MALE SIZE, TILE SIZE, and OR all accurately duplicated at least 7 of the 8 observed distributions of spawnings per male for pooled tile sizes. The model RANDOM produced more uniform distributions of spawnings per male than were observed, and differed from the observed in five of eight comparisons. This pattern of differences was hardly surprising since direct analyses of the patterns observed in the field suggested that male reproductive success was not a random event (Figures 2, 3, 4). The model AND restricted breeding to the largest males occupying the largest tiles, and produced more clumped distributions of spawnings per male than were observed. This model also differed from the observed in five of eight comparisons.

Restricting analyses of the frequency of spawnings per male to individual tile sizes allowed closer resolution of the accuracy of the various models (Figure 9). The models RANDOM, TILE SIZE, and AND all differed from the observed distributions at constant rates, and accurately described between 43 and 64 percent of the observed distributions. As might be expected, RANDOM always over-estimated the number of spawnings on small tiles and under-estimated the number on large tiles. Conversely, the models AND
and TILE SIZE always under-estimated spawnings on small tiles and over-estimated the number on large tiles.

The interaction model OR was a moderately good descriptor of the observed distributions early in the spawning season, but became progressively less accurate. Like RANDOM, this model assigned too many spawnings to small tiles and too few to large tiles, resulting in a more uniform distribution of spawnings than was observed.

MALE SIZE was by far the best descriptor of the observed distributions, accurately duplicating 32 of 40 distributions tested (Figure 9). The surprisingly good fits between the patterns generated by this model and those observed are illustrated in Figure 10, which plots the frequency distributions of spawnings per male for each tile size on April 10, 1976. None of the six observed distributions differed significantly from those produced by the model (P < .05). Furthermore, no consistent pattern of deviation of observed from expected is evident, despite the fact that the mean number of observed spawnings per male differed between tile sizes by a factor of nine.

Significantly, the majority of prediction errors made by the model MALE SIZE occurred on the last three sample dates of the breeding season, a period during which losses of egg masses exceeded depositions (Figure 11). Patterns of egg mass loss were significantly different from those of oviposition (Maximum Likelihood Test, $X^2 = 18.6$, d.f. = 3, P < .001), and discrepancies between observed and modeled distributions late in the season may have reflected
The Analysis of Male Size

The distribution of matings per male observed in the field population were accurately duplicated by a simple model in which female choice was based entirely on relative male size. This same model provides insight to the processes producing the patterns of size dependent male reproductive success observed in the field (Figure 4).

The model MALE SIZE predicted that larger males spawned first and continued to mate with successive females in a manner virtually identical to that observed in the field (Figure 12). Bachelor males were always smaller than mated males, and the mean sizes of both bachelors and mated males decreased as the season progressed. The mean length of bachelors at the beginning of the spawning season was equivalent to the mean length of males mated with three females at the end of the season. Thus this model expected that males that failed to breed early in the season succeeded later.

That these patterns of size dependent mating success were generated by a model using unvarying choice criteria demonstrates that a single constant choice routine can account for the apparently changing patterns observed in the field (Figure 4). Assumptions concerning male size dependent reproductive capabilities are unnecessary. Furthermore, the observation that males rejected by females early in the season were accepted later on does not
necessarily indicate that female choice criteria changed. Rather, this temporal pattern can be explained as a reflection of limited female sampling abilities and of the intensity of spawning. The probability that a male would be the larger of two sequentially encountered males was proportional to male size: the larger the male, the greater the probability that he would be assigned a spawning. The number of matings assigned to a male of any given size was therefore a function of his size and the number of spawnings observed on that particular date. As a consequence of the limited number of spawnings early in the season, small males were rarely assigned matings. As the number of spawnings increased through the course of the season, small males were more often assigned spawnings simply because the number of comparisons increased. Large males thus bred first and continued to obtain additional simulated matings in exactly the same manner as observed in the field (see Figure 4).

**Relative and Threshold Choice Patterns**

Female choice based on relative male size provides a simple explanation for the choice patterns observed in the study population. Analysis of the consequences of various alternative choice mechanisms reveals that choices based on absolute or threshold responses cannot provide such simple explanations.

In its most basic form, a threshold response requires that subthreshold stimuli fail to elicit a response, while superthreshold stimuli produce a response. In the case of mottled sculpins, males
smaller than the female response threshold would be rejected as mates, but all males larger than the threshold would be equally acceptable as mates (Figure 13, top). Mating within this group of large males would be random. Whenever this type of single threshold response operates, the relationship between male size and male courtship success will be such that males smaller than the female response threshold have a mean courtship success of zero, but males larger than the threshold all have equivalent mean courtship successes.

Multiple thresholds increase the complexity of the system (Figure 13, middle). As in the case of a single threshold, males smaller than the first female response threshold fail to obtain mates. Males large enough to attract one mate, but too small to attract two mates remain monogamists. Males large enough to attract two mates but too small to attract three remain bigamists, and so forth. Some range of male sizes must separate the adjacent thresholds, and this range translates into a step-like relationship between male size and courtship success: males between adjacent thresholds all have equivalent mean courtship successes (Figure 13, middle). The exact nature of the relationship between male size and courtship success depends on the location of the various thresholds, since the height of the steps corresponds to the range of sizes between adjacent thresholds. If higher level thresholds are more closely spaced, then the resulting steps become increasingly shorter. Conversely, if higher level thresholds are more widely
spaced, then steps become increasingly higher.

Regardless of the exact location of choice thresholds, some differences between threshold choices and simple relative comparisons can be recognized. For example, if threshold responses determine female choice, then male courtship success is not a function of male size in a mathematical sense: all males within the range of sizes between adjacent thresholds are equally likely to obtain mates. Relative choice mechanisms may result in patterns in which male courtship success is a simple linear function of size as illustrated by the simulation models in which males were chosen whenever they were larger than or equal to their predecessors. Thus males of any given size had greater probabilities of courtship success than all smaller males.

Male courtship success was observed to be a simple linear function of male size during this study. This relationship is illustrated by data collected on April 16, 1977 (Figure 13, bottom), a sample date chosen both because all experimental tiles were of the same size on that date, and because that date represented peak spawning in 1977. This simple relationship is consistent with threshold response mechanisms only if females vary so greatly in their abilities to recognize male lengths that the step-like relationship between male size and courtship success has been obscured. This argument is inconsistent with the very concept of response thresholds, however, since the thresholds theoretically represent real differences in mating situation qualities (Orians,
1969; Wittenberger, 1976), and selection should strongly favor those females capable of discriminating between mating situations of different qualities.

If the various response thresholds are fixed, then changes in the shape or location of the distribution of available choices should not modify female choice patterns. Thus, if the size distribution of available males in Figure 13 (middle) were shifted to the right, the monogamy threshold would remain fixed at 80 mm, and the male population would include fewer bachelors, and more mated males. If the size distribution of available males were shifted to the left, the male population would include fewer mated males and more bachelors. In any case, if the thresholds are fixed, the mean sizes of monogamists, bigamists, trigamists, etc., will remain constant even though their numbers change. If the thresholds are not fixed but vary when the distribution of available males varies, then the mean sizes of males with differing courtship successes will vary. Importantly, if the thresholds themselves are variable, but are always separated by the same ranges in male size, then a constant relationship between male size and courtship success must result. For example, if the mean sizes of males with various courtship successes are compared for populations composed of large males and of small males, the step-like relationships resulting in the two populations will have equivalent slopes and differing intercepts.
If females base their choice on relative instead of threshold comparisons, then the choice patterns resulting will be entirely determined by the shape and location of the distribution of possible choices and the number of choices being made. For example, the computer simulation predicted different slopes for the function relating male size and courtship success early and late in the breeding season simply as a consequence of the number of choices made.

The distributions of males breeding in Anderson Creek were different in each of the three years of this study (Figure 14). Females were thus confronted with three different distributions of possible choices, and these differences allow discrimination between relative and threshold choice possibilities: if females make threshold choices based on fixed thresholds, then the relationship between male size and courtship success must be constant in all three years. If females make threshold responses based on variable thresholds separated by constant ranges, then the relationships between male size and courtship success must have constant slopes even though their intercepts may differ. If females make relative choices, then the relationships between male size and courtship success will vary as the distribution of available males varies.

In each of the three years of this study, male courtship success was a simple linear function of male size (Figure 15). The individual regression lines show significant slope heterogeneity (F = 9.85,
d.f. = 2, 13, P = .005) and obviously differ in their intercepts. These observations can be simply explained as a reflection of female choice for relatively, not absolutely large males.

**Some Consequences of Various Choices**

Three types of choice criteria were simulated by the various models. Random mating, occurring in the absence of any choice, did not accurately or adequately describe the male reproductive success patterns observed in the study population. Simulated female choice of breeding site characteristics resulted in some of the observed breeding patterns, and simulated choice of male characteristics resulted in the most accurate duplication of both the numbers of matings per male and the male size dependent reproductive success patterns. These observations suggest that the choice of a relatively large mate might increase female reproductive success, although the choice of a relatively large breeding site might not.

Analysis of the proportion of egg masses that successfully hatched as a function of guardian male size suggests one advantage of mating with a large male (Figure 16). Larger males succeeded in hatching a greater proportion of the egg masses in their nests than did smaller males. The probability that an egg mass would produce fry was thus directly proportional to guardian male size. The simplicity of this relationship is beguiling, however. Since larger males generally guarded more egg masses, both harem size and
male size correlated with hatching probability. Furthermore, both the position of an egg mass in a nest and the date of oviposition affected hatching probability (Section III). In any case, large and small males differed in their paternal abilities. Small males were absent from their nests twice as often as were larger males (Table 7, from Downhower and Yost, 1977). Although egg mass mortality was equivalent for both large and small males when males were absent from the nest, the higher absence rate for smaller males resulted in higher mortality rates. Furthermore, egg masses in the nests of small males were five times as likely to fail as those in nests of larger males even when the guardian male was present in his nest. Although the mechanisms by which males increase egg mass survival have yet to be fully investigated (Downhower and Yost, 1977; Staples, in prog.), larger males may forage less frequently than smaller males and thus remain at the nest for a greater proportion of the incubation period, and larger males may defend their eggs against larger egg predators than smaller males. Such defense may be especially critical in protecting egg masses from the encroachments of other adult and juvenile sculpins, which are known to consume large numbers of eggs (personal observation; Downhower and Yost, 1977; see also Bailey, 1952; Simon and Brown, 1943; Koster, 1936).

Females may have benefited from their choice of large mates after as well as before their egg masses hatched. In both 1975 and 1977 (Figure 17), the mean sizes of nesting males increased
during the post-hatching season, suggesting that larger males remained as guardians of their fry for longer periods than did smaller males. Larger males may have begun the spawning season with greater fat reserves than smaller males, and thus be able to remain at the nest site longer following hatching. This possibility is currently under investigation (Pederson, in prog.). Regardless of the mechanism, the extended residence of larger males may have increased fry survival by decreasing losses due to predation. This possibility is also currently under investigation (Staples, in prog.).

Female sculpins thus directly benefited from their choice of a large mate. Larger males successfully hatched a greater proportion of their egg masses than did smaller males, and larger males may have succeeded in raising a greater proportion of those fry that did hatch to the dispersal stage. These observations may reveal the significance of the courtship displays of male sculpins. Payne and Payne (1977) review evidence from a number of polygynous birds supporting their claim that females of polygynous species with no pair bond may select their mates on the basis of their aggressive displays. Thus polygynous males may include strong aggressive elements in their courtship displays. These authors interpret this observation as an indication that ritualized aggressive signals provide females with a clue to the effectiveness of their potential mate in intrasexual competition. The courtship of
male sculpins (Savage, 1963) includes a number of elements apparent in aggressive interactions (personal observation). Thus sculpin males elevate their gill-covers, shake their heads, and erect their pectoral fins during both courtship (Savage, 1963) and aggressive interactions. In each case these activities increase the apparent size of the displaying male. Since male size influences courtship success, males may benefit by increasing their apparent size when confronting females. Since male size presumably influences male aggressive success, males may benefit by increasing their apparent size when confronting other males. But females benefit directly from their choice of a large male. While the courtship display may clue females to the competitive abilities of their mate, it certainly has the direct effect of simply highlighting male size and therefore parental ability. The similarity between courtship and aggressive displays may therefore be coincidental.

Analysis of the proportion of egg masses that successfully hatched as a function of breeding site size reveals that females gained no reproductive advantage by spawning at a larger breeding site (Table 8). No heterogeneity among hatching successes for the various tile sizes was observed in nests occupied by small males ($\chi^2 = 7.3$, d.f. = 4, $P > .05$), and no dependence of hatching success on breeding site size is apparent. While heterogeneity was observed among nests occupied by large males ($\chi^2 = 19.8$, d.f. = 4, $P < .05$), this variation in hatching success resulted from the low success of
the largest breeding sites ($X^2 = 2.92$, d.f. = 3, $P > .05$). Furthermore, hatching success was inversely proportional to breeding site size among large males.

Choice of a relatively large mate therefore directly increased female reproductive success, while choice of a relatively large breeding site would have had no effect on female reproductive success. Yet males preferred large breeding sites: larger breeding sites were occupied earlier in the season (Table 5) and by larger males than were smaller sites (Figure 6). Such preference appears to be inexplicable in terms of male courtship success and female reproductive success. Alternate explanations must be sought. The smallest tile sizes barely covered the guardian males, and left no room for the male to maneuver without exposing himself. Such exposure certainly increased male susceptibility to visually foraging predators like herons (*Ardea cinerea*) and kingfishers (*Megaceryle alcyon*), both of which have been seen foraging at the Anderson Creek study site. Larger tiles allowed greater maneuverability beneath the tile and may have allowed males to avoid aquatic predators like larger sculpins and water snakes (*Natrix sipedon*), both of which have also been observed eating sculpins at this site. The observed male preference for large breeding sites may thus be unrelated to courtship or reproduction per se, but may be related to male maneuverability and possibly survival.
Real Patterns and Potential Artifacts

One potential objection to any experimental manipulation of a natural breeding population is that the breeding patterns observed may represent artifacts of the manipulation rather than natural phenomena. This possibility was investigated by sampling natural nests in the study site at the end of each oviposition period. In none of the three years were there significant differences between the distributions of spawnings per male for natural nests and experimental tiles (Figure 18: Maximum Likelihood Test, 1975: \( X^2 = 2.79, \text{d.f.} = 4, P > .90 \); 1976: \( X^2 = 3.36, \text{d.f.} = 6, P > .50 \); 1977: \( X^2 = 7.40, \text{d.f.} = 4, P > .10 \)). Both types of nesting sites were thus equally attractive to females.

In both 1976 and 1977, guardian males at natural nests were captured. In neither year was there a significant difference between mean sizes of males occupying natural nests and experimental tiles (Table 9). In both years, the population of males occupying the experimental tiles was less variable than the population of males occupying natural nests (Table 9), however. Both types of nesting sites were thus equally attractive to males as well as females. Since male size was a function of breeding site size, the greater variability of naturally nesting males may simply reflect greater variability in the sizes of natural nests.
Implications

Female sculpins chose among available males. Bachelor males mated less frequently than expected on the basis of chance encounters during the early and peak breeding periods. Large males bred first and continued to obtain additional mates, yet smaller males succeeded in spawning as the number of females choosing mates increased. Since the total size distribution of available males remained constant during this period, males that were unsuccessful in obtaining mates early in the breeding season became successful as the season progressed. Simple computer simulations of female choice based on relative, not absolute male qualities provide a parsimonious explanation for these patterns. The fact that the choice patterns observed in the study population could be duplicated by simple invariate choice routines suggests that female choice patterns need not change during the season. The fact that simulated choices based on relative as opposed to absolute choice criteria accurately duplicated the observed choice patterns suggests that female choice among sculpins was not determined by fixed thresholds of acceptable mate quality and that the patterns observed in the field were not a result of male size dependent responsiveness to females. Although simulations based on changing choice routines and thresholds could undoubtedly be derived, such models would necessitate more complex assumptions concerning sculpin comparison abilities and reproductive physiology.
The patterns of male size dependent reproductive success observed in the study population (Figure 4) can thus be explained as the result of a simple invariate choice routine by which females picked a mate who was larger than or equal to his nearest neighbor. This choice routine directly favored large males. The larger the male, the greater the probability that he would be the larger of two sequentially encountered males and would obtain a spawning. Since this probability was independent of whether a male was being encountered by his first female or some additional mate, larger males obtained matings earlier than did smaller males, and continued to sequentially attract additional females. As larger males increased their courtship success by moving from the ranks of singly mated males to those of males with multiple mates, the mean sizes of males with lesser courtship successes declined.

Temporal patterns of age or size dependent male reproductive success in other polygynous vertebrates suggest that similar female choice mechanisms may be common. Among grouse (Tetraonidae), for example, older, more experienced males may breed earlier and more frequently than younger males (Kruijt, et al., 1972; Wiley, 1973). Older red-winged blackbirds breed earlier and acquire more mates than younger males (Yasukawa, 1977). Polygynous male indigo buntings (Passerina cyanea) also breed earlier than monogamists in the same population (Carey, 1977), and reproductive success is related to age in this species (Carey and Nolan, 1975). The pattern of size (or age) dependent reproductive success illustrated by
sculpins may thus reflect a general pattern among polygynous species and suggests that females of other polygynous species may also base their choice of mate on relative, not absolute criteria.

That a simple model assigning female choice on the basis of male size proved the best overall descriptor of the observed patterns is consistent with previous analyses of the relative importance of male size in this fish. Since male and tile size are both related to male reproductive success and are themselves intercorrelated, both appear to be determinants of female choice. Removal of the effect of male size via ANCOVA, however, eliminates the apparent effect of tile size (Downhower and Brown, 1978). Since the model MALE SIZE assigned choice only on the basis of male size but used the actual distribution of males associated with tiles of different size, it resulted in patterns of spawnings per male that were dependent on tile size (Figure 10), despite the fact that tile size was not a choice criterion. Thus this model resulted in patterns paralleling those observed in the study population.

That female sculpins appear to base their choice of mate on the physical attributes of individual males (or on some behavioral correlate of male physical attributes) is not consistent with current mating system theory, however. Theoretical analyses have suggested that when breeding related resources are limited or unevenly distributed among males, such that certain males can offer females better patches than can other males, females should base their choice of mate on the quality of the patch he has to offer.
The only obvious breeding related resource required by sculpins is a breeding site, a resource that is discrete and defended by mature, courting males. Sites used in this study differed in size by a factor of five, and this difference was recognized by male sculpins occupying the sites: large sites were occupied by more and larger males than small sites (Figure 6; Table 5). Yet female sculpins based their choice of mate solely on male size. Furthermore, females benefited directly from their choice of a large male. Large males hatched a greater proportion of their egg masses than did smaller males. Large breeding sites did not show greater hatching success than smaller sites.

That female sculpins are highly selective in their choice of mate is also inconsistent with current sexual selection theory, which maintains that when parental care is limited to a single sex, individuals of that sex should choose mates carefully, but individuals of the opposite sex should mate indiscriminately (Burley, 1977). Parental care in sculpins is limited to males, yet females do not mate indiscriminately, but appear to choose their mates with some care. Male sculpins are sometimes simultaneously confronted by several females and may then choose among them. The degree to which males select individual females is still under investigation (Downhower and Brown, in prog.), but certainly does not negate female choice of males.
Female sculpins are capable of making rather fine distinctions between potential mates, and appear to base their choices on relative male size. Since comparative data for other polygamous species are not available, the generality of this type of mate selection cannot yet be evaluated. The observations that choices based on comparisons between available males accurately and adequately explain male mating success patterns in sculpins, and that similar patterns have been reported for other polygynous species, suggest that such relative choice mechanisms may be more common than previously expected.

Summary

Polygynous male sculpins accounted for a disproportionately large number of spawnings early in the 1976 breeding season, but bachelors eventually mated. Larger males bred first and continued to obtain successive mates, but smaller males succeeded in mating as the season progressed. Since the total distribution of available males remained constant during this period, males that were unsuccessful in their courtship early in the season became successful later.

Examination of sculpin breeding biology indicated that breeding site size and/or male size might be criteria on which females evaluated potential mates and that females might pick their mate after sampling a small number of potential mates. To examine possible choice mechanisms, a simple computer program was designed
to simulate spawning. The program was based on minimal assumptions concerning sculpin movement patterns and comparison abilities, and used the known distributions of nesting sites and associated males on eight sample dates during the spawning season. Modification of the comparison routine incorporated in the program resulted in four models that assigned spawnings on the basis of relative male size, tile size, and/or interactions of the two variables. A fifth model simulated random spawning.

Comparisons of the modeled distributions of spawnings per male with those observed in the field demonstrated that the observed patterns of male courtship success could be accurately duplicated by simulated female choice of relatively, not absolutely large males. Furthermore, simulated choice of relatively large males produced patterns of male size dependent breeding success that were indistinguishable from those observed in the field.

Female choice based on relative male size provides a parsimonious explanation for the breeding patterns observed in the field. The apparently changing male reproductive success patterns observed in this study do not, therefore, require that female choice patterns changed, that males were differentially responsive to females, or that female choice was based on a threshold of mate acceptability. Furthermore, female choice of relatively large males directly increased female reproductive success, since larger males successfully hatched a greater proportion of their egg masses than smaller males.
Breeding patterns of several polygynous birds suggest that females of other polygynous species may also base their choice of mate on relative, not absolute criteria.
Polygyny poses an enigma. When monogamy is prevalent in a population, most males mate with a single female, and male reproductive success may be relatively uniform. When, on the other hand, polygyny predominates, some males mate with many females but other males remain bachelors. Reproductive success varies greatly among males, and selection for those characters that increase male reproductive success must be intense. Thus polygynous mating systems are particularly interesting to students of sexual selection (Darwin, 1871; Fisher, 1930; Huxley, 1938; Selander, 1965, 1972).

Variance in the reproductive success of polygynous males reflects female choice: females preferentially mate with those males possessing particularly favorable qualities. Whenever the consequences of choice affect female reproductive success, poor choices will be disadvantageous relative to good choices, and selection will favor those females that increase their reproductive success by choosing well. In the best of all possible worlds, selection may be expected to produce the best of all possible choices. In the absence of experimental evidence, this has been assumed to occur. Female selection of a particular mate has been
interpreted as choice of the best possible mate (Verner, 1963; Orians, 1969; Elliot, 1975; Wittenberger, 1976; Weatherhead and Robertson, 1977). This interpretation may not accurately describe the world in which all animals reproduce. Here I examine the costs and benefits of female choice in mottled sculpins (Cottus bairdi) and demonstrate that the best available choice may not be the best of all possible choices in this less than best of all worlds.

Experimental Design

The methods by which the data used in this study were collected have been detailed elsewhere (Downhower and Brown, 1976; 1978; 1978a), and are here reviewed and elaborated briefly.

A naturally breeding population of mottled sculpins was provided with sets of experimental spawning sites (3 sizes in 1975, 6 sizes in 1976, and a single size in 1977). These sites differed only in their size, were readily accepted by the breeding sculpins, and were apparently used by the sculpins in exactly the same manner as were natural nests (Downhower and Brown, 1978a). Sites were sampled at three to four day intervals throughout each spawning season, and the total lengths and sexes of all fish resident in each nest, as well as the number of egg masses in each nest were recorded. Each egg mass represents the total annual reproductive output of a single female, hence the number of females mated with each male could be accurately determined by counting the egg masses
present in a male's nest.

A photographic record was kept for each nest from the day that spawning was first observed through the day that hatching terminated. Subsequent analyses of these photographic series allowed evaluation of the fates of individual egg masses. Hatching of sculpin egg masses followed and did not overlap the oviposition period, and predation and other post-spawning factors caused considerable egg mass attrition before hatching occurred. Since losses of entire egg masses were easier to accurately score than losses of individual eggs, the post-spawning fates of egg masses were determined on a per mass basis. Thus, an egg mass either disappeared entirely from the nest, or at least part of the mass remained to produce at least one fry, in which case it was scored as a success. Any nests in which egg mass losses were attributable to the experimenters were excluded from all subsequent analyses.

Tempus Fugit or Time Waits for No Fish

The mere existence of a discrete spawning period suggests that the timing of reproduction might influence the subsequent survival of the young produced. In fact, the probability that an egg mass produced at least a single fry was inversely proportional to the date on which oviposition occurred (Figure 19, Curve A). Almost 80 percent of the egg masses deposited early in the spawning period successfully hatched, while almost all late ovipositions disappeared prior to hatching. The date of spawning thus affected
reproductive success.

Male sculpins are sequentially polygynous and therefore court and mate with a series of females. The first female mating with a male may be the only female in the series, in which case her egg mass remains solitary, or she may be followed by successive matings. Each additional female may in turn be the last female in the series or be followed by further matings. At the end of the oviposition period, each egg mass in a male's nest can be described as solitary, the first in a series, in the middle of a series, or the last in a series. The survival of egg masses in each of these four classes was different (Table 10). Solitary egg masses and those that were last in a series had consistently low hatching probabilities, but those masses that did not end a series (firsts and middles) had consistently high hatching probabilities.

The temporal position of an egg mass with respect to its nest mates is thus critically important to its subsequent survival. Since the number of females breeding in a population is finite, and since each female breeds once, the probability that an egg mass will remain solitary or be the last in a series increases during the course of the breeding season (Figure 19, Curve B). As the probability that a spawning will be the last in a series increases, the probability that the spawning will produce young declines (Figure 19, Curve A).
Hatching probabilities within each class of egg masses varied little during the course of the spawning season (Table 10). The patterns of variation among classes of egg masses and sample dates suggest, however, that the date of oviposition might also influence survival, and analysis of the effect of oviposition date for all position groups reveals this effect (Distribution Free Two-Way Layout, $S = 8.63$, treatments = 4, groups = 4, $P = .019$ (Hollander and Wolfe, 1973)). Both the absolute date of oviposition and the relative position of an egg mass in its nest thus influence hatching success.

That position alone is an overriding factor is suggested by the observation that hatching probabilities were proportional to the number of egg masses in a nest, and were identical to those expected given differences among solitary, first, middle and last egg masses (Figure 20). For example, the observed hatching probability for nests with three egg masses (.68) equaled the average probability for one first, one middle and one last egg mass (.687). The observed hatching probability for nests with four egg masses (.70) equaled the average probability for one first, two middle and one last egg mass (.708), and so forth.

The proximate causes of high mortality among late ovipositions, solitary and last egg masses remain unknown. The decreased success of late ovipositions may represent a compound effect of both timing and male paternal abilities. Early ovipositions tended to be with large males while later spawnings included smaller males. The
mean size of males obtaining their first egg masses thus declined through the season (Figure 4). Since hatching success was an increasing function of male size (Section II), the decreased hatching success of first egg masses late in the season may represent effects of both oviposition date and of guardian male size. Similarly, solitary egg masses tended to be guarded by very small males, hence, their low survival may reflect male parental abilities. Alternatively, clusters of egg masses may be more firmly anchored in the nest than single masses, hence the increased survival of first and middle masses. Finally, since masses frequently overlap in the nest, late egg masses and those last in a series may not adhere fully to the nest, or may be loosened from the nest when earlier ovipositions commence hatching.

In any event, the result of the observed mortality patterns is to favor those females that breed as soon after breeding commences in the population as possible. This selection for early breeding is reflected in the highly skewed frequency distributions of spawnings observed in natural sculpin populations. Large numbers of females breed early in the spawning season, but stragglers continue to breed for many days following peak spawning. For instance, 85 percent of the 891 matings occurring during the 1976 season were observed during the first two weeks of the breeding season, while the remaining 15 percent spanned the second two weeks of the season. Thus the frequency distributions of spawnings throughout each of the study seasons were leptokurtic and skewed to the
right (Table 11).

In summary, the timing of reproduction directly affects the subsequent production of young sculpins. Selection strongly favors those females that spawn as early in the season as possible because any delay in oviposition date decreases the probability that the mass will produce young. Although egg masses laid early in the season have a high probability of producing young, spawnings two or three weeks later in the season rarely succeed.

**The Mate Selection Game**

Female sculpins base their choice of mate on relative male body size (Section II). There is no evidence of a threshold of acceptable male size, and there is no evidence that females change their choice criteria or selection techniques during the course of a spawning season. These observations suggest that the choice of a large male must increase a female's reproductive success, and, in fact, the probability that an egg mass hatched was directly proportional to guardian male size (Figure 16). Large males remained at nest sites longer, abandoned nests less frequently, and protected eggs more effectively than did small males (Downhower and Yost, 1977).

Since the relationship between hatching probability and guardian male size was linear, selection favored those females that chose to mate with the largest males in the population. Since hatching probability was not a decreasing function of harem size
(Figure 20), no obvious selective forces opposed maximization of fitness through choice of the best possible mate. Thus, in the best of all possible worlds, female sculpins should have mated with the best or largest possible males.

As less than omniscient beings, female sculpins are confronted with two obstacles to their maximization of reproductive success through choice of the best possible mate. Before a male can be chosen, he must be located and he must be recognized as the best choice. These obstacles may be as insurmountable as they are obvious.

Sculpins inhabit a two dimensional world: the shallow freshwater stream. As bottom dwellers, female sculpins must search for available males on a horizontal plane, and cannot obtain an overview of the total distribution of males and spawning sites. Since males remain at or near their nests, females are restricted to evaluating one male at a time. The rapid stream currents coupled with the greatly reduced swimming abilities of gravid females hinder simple movements among potential mates. Furthermore, daylight movements among nest sites increase susceptibility to visually foraging predators like herons (Ardea cinerea), kingfishers (Megaceryle alcyon), and rainbow trout (Salmo gairdneri).

Once a prospective mate has been located, his suitability must be determined. Male sculpins occupy their nests before the onset of the breeding period (discussion in Smyly, 1957), making female awareness of both spatial and statistical distributions of available
male sizes unlikely. Furthermore, the size distribution of available males varies greatly between years. For example, less than ten percent of the males breeding in the study site in 1975 exceeded 100 mm total length, while almost thirty percent of the breeding males exceeded 100 mm in 1976 (Figure 14). This extreme variability in available male sizes suggests that genetically fixed thresholds of acceptable male size are inappropriate and that females may evaluate the current population of breeding males prior to picking a mate. If the best male is to be located, all available males must therefore be evaluated and their locations remembered. The search effort required to locate and identify the best mate in a large population would be considerable.

Female sculpins are thus confronted with a dilemma. They must pick a suitable mate without knowing where or who the best possible mate is. At the same time, they must pick a mate quickly since any delay increases the probability that their egg mass will be the last in the nest and suffer a subsequently low hatching probability.

The Benefits and Costs of Female Selectivity

The benefits of female selectivity can thus be quantified as the increase in hatching probability resulting from the selection of a large mate. The more selective a female is, the larger the mate she chooses and the greater the probability that her egg mass will produce young. The costs of female selectivity can be quantified as the time taken to locate and identify a suitable
mate. The longer the search, the greater the delay in oviposition and the smaller the probability that the egg mass will produce young.

Both the benefits and costs of female selectivity can therefore be measured. Benefits in terms of male size, and costs in terms of the number of spawning sites visited before a mate is selected. If breeding occurred in the best of all possible worlds, selection might be expected to favor those females that located, identified and mated with the largest male. Female choice of the largest male is extremely costly however (Figure 21). If females are assumed to sample every male only once and possess total recall of male qualities and locations, the number of spawning sites that must be visited to locate and return to the best possible male is equal to the number of males available plus one. On April 10, 1976, 244 adult males occupied nests in the study area. Females would, therefore, have had to visit an average of 245 nests before picking a mate if they were to locate the best possible mate on this date. If females sample males randomly, the cost of locating the best possible mate is much greater. Before she could be 95 percent confident that she had visited all available mates on April 10, a randomly sampling female would have had to visit 730 nests (Figure 21). If females do not possess total recall of male qualities, location of the best male becomes impossible. The costs involved in locating the best male are thus extremely high.
An alternative to the location of the best possible mate is the location of a male that is best relative to his local competi-
tion. Thus, a female might mate with a male if he were the largest male in her subsample of available mates. The chosen male would thus be large relative to his competitors, but might not be the largest available male. If sampling is limited, a number of simple models of female choice based on relative male size are possible. For example, females might mate with a male if he were larger than the last male that she had encountered. By extension, a female might mate with a male if he were larger than the last male that she encountered, who was in turn larger than his predecessor. According to this model, females choose a mate only if he is the largest of some set of sequentially encountered males. Alternat-
ively, females might mate with a male only if he were larger than the last male that she had encountered by some increment.

The costs and benefits associated with these two types of female choice models can be determined empirically through computer simulation (Figure 22). The simulations used in this analysis were based on the known distributions of spawning sites and males associated with those sites on April 10, 1976, a representative sample date. These simulations were directly analogous to those that I have used previously (Appendix) to accurately duplicate the patterns of oviposition observed in the study population. The only assumptions on which these simulations rest are that females move among nearest neighbors when sampling prospective mates, and
that females retain memory traces of the last male encountered for comparison purposes.

Female choice based on relative male quality rarely results in the selection of the best possible mate (Figure 22). Rather, such choices increase the probability that the chosen male will be large (e.g., larger than or equal to average). If a female simply mated with the first male that she encountered, the probability that the chosen male would be larger than average was empirically found to be .50, a reflection of the normal distribution of available males on April 10. If a female mated with the larger of two sequentially encountered males, however, the probability that the chosen male would be larger than average was found to be .70. But the benefits of increased selectivity are not directly proportional to the degree of selectivity. Extreme selectivity may be counterproductive, an observation that requires explanation. Each of these simulation routines based female choice on sequential encounters between females and successively more desirable males. But the distribution of available males was finite and bell-shaped. Limited selectivity requires a short series of encounters with larger males or a small difference between sequential male sizes, and, on the average, results in the choice of males located in the upper tail of the distribution of available males. Higher degrees of selectivity require many more encounters with larger males or greater differences between sequential male sizes. But very large males were very rare. Since the simulation
assumed that females retained a memory trace only of the last male encountered for comparison purposes, the series of sequentially large males required by high selectivity were rarely completed before very small males were encountered. Once a small male was encountered, completion of the series was possible. But since the distribution of available males was bell-shaped, the required series of sequentially large males tended to be completed by males of average size. Thus extreme selectivity resulted in the choice of average sized males. While a female would benefit greatly by being selective, she would thus benefit very little by being highly selective via sequential choice routines.

At the same time, the costs involved in being selective increase exponentially. Thus selection of the larger of two males required an average of 3 visits to spawning sites, while selection of the largest of a sequence of 4 males required an average of 15 visits. The ratio of the benefits derived from selectivity to the costs required for it therefore decreased with increased selectivity.

The time required to locate and evaluate a prospective mate by a female sculpin is unknown, so the costs involved with various choice mechanisms cannot be directly evaluated in terms of decreased hatching probabilities. The implications of the simulation models are clear, however. Choice of the best possible mate involves intense sampling effort and long search time, and is most profitable when females are equipped with complex memory systems.
and are capable of remembering complex movement patterns. If, as
in sculpins, female sampling abilities are limited, and the costs
of delaying breeding are very high, location of the best of all
possible mates may not be feasible. Females can locate relatively
large males, while sampling far fewer breeding sites if choice is
based on relative, instead of absolute male quality. Choice of
relatively high quality males limits selectivity, however, since
costs associated with high degrees of selectivity increase, while
benefits decline.

How Long is the Search?

Simulation analyses thus suggest that female sculpins can
locate relatively high quality males very quickly by basing their
choice of mate on relative, not absolute criteria. On April 10,
1976, the sample date used in these analyses, females would have
had to sample several hundred nesting sites before picking the
best possible mate, but only a dozen or so nesting sites before
picking a relatively high quality mate. While the number of
nesting sites actually visited by gravid female sculpins is diffi-
cult to measure directly, the spawning behavior of sculpins allows
search time to be estimated indirectly.

Female sculpins only frequent nesting sites when they are
ready to lay their eggs. Gravid females are rarely captured at
nests prior to the oviposition period, and the number of daily
captures of gravid females parallels the intensity of spawning.
Spawned females are even more rarely captured at nests since females leave the nest after spawning and presumably begin foraging. Although gravid females occur in heterosexual pairs more frequently than expected on the basis of random assortment, spawned females avoid mature males, either because males exclude them from their nests, or because males occasionally eat effete females (Downhower and Brown, 1978). The first occurrence of a gravid female in a nest can thus be used as an indicator of the beginning of her search for a mate, and the presence of a spawned female in a nest can be used as an indicator of the search's end.

The mean sizes of both spawned and gravid females captured at the experimental nesting sites declined throughout the spawning season, yet spawned females were associated with greater mean sizes than gravid females on any individual sample date (Figure 5). If females were captured only during their search for a mate, then the delay between the time when a gravid female of a given size was captured and the time when a spawned female of the same size was captured provides an estimate of the search time for a female of that size. The distributions of search times for females of different sizes can therefore be estimated by measuring the delay between cumulative capture probabilities for gravid and spawned females of the same size (Figure 23). Unfortunately, sample sizes limit the sizes of females that can be compared to small (70 mm), medium (70-74 mm), and large (74 mm). Mean delays between the cumulative capture probabilities for gravid and spawned females in
each of these size categories were determined by measuring the delays at .025 probability intervals. In 1976 mean (and variance) delays were 11.3d (1.3d), 7.4d (7.1d), and 7.2d (19.9d) respectively. Small females were thus the least variable in their search time but required the longest search before locating a mate. Large females were the most variable in their search time but required the shortest search before locating a mate. These differences may reflect size dependent differences in female movement abilities or differences in male responsiveness to females of various sizes. Since larger females carry more eggs (Downhower and Brown, unpublished data; Ludwig and Norden, 1969; Patten, 1971; Ludwig and Lange, 1975) and since males are occasionally simultaneously encountered by more than one female, males confronted with both a large and small female might increase their reproductive success by courting the large female and ignoring the small one, thus smaller females would be forced to search longer. Male choice is currently under investigation (Downhower and Brown, in prog.). Regardless of the reasons for size dependent differences in female search times, female sculpins appear to spend an average of 7-11 days searching for a mate.

The amount of time required for a female sculpin to evaluate a single male remains unknown. Laboratory studies are suggestive however. For example, Smyly (1957) found that twenty to thirty hours elapsed between the time that a female *Cottus gobio* entered
a nest and spawning occurred. Females typically spent this time upside down in the stationary spawning position. This same author suggested that this species was nocturnal, implying that females move among nests principally at night. Savage (1963) observed that spawning in C. bairdi was primarily a nocturnal event. He also observed that laboratory females frequently entered nests, were courted, assumed the upside down spawning position, and later left the nest without spawning. The duration of encounters between male and female sculpins ranged from one minute to more than five hours, but only one of the measured encounters resulted in a spawning. Actual spawning maneuvers required as little as twenty minutes, but typically occurred during the night, several hours after a female had first encountered a male.

All of these observations suggest that female sculpins sample a very limited number of potential mates before breeding. If females move among males only at night and spend several hours evaluating each male, as is apparently the case, females could not sample all available males, but only a limited subsample. Choice of the best possible male, which is associated with the longest possible search time, is thus not a viable option for gravid female sculpins. Choice of a relatively large male, which is associated with a short search time, is the alternative.
Female Choice and the Evolution of Polygyny in Sculpins

Mate selection is exercised whenever the choice of one partner precludes acceptance of other partners, and whenever the rejection of one partner is followed by encounters with other partners with virtual certainty (Fisher, 1930). The first of these conditions is obviously met by female sculpins that breed only once per year. The second of these conditions is met only within certain bounds, however. Although the rejection of a potential mate may indeed be followed by encounters with other potential mates, the delay in mating produced by such rejection may offset any benefits obtained by locating a better mate. This relationship will be true whenever the timing of reproduction affects reproductive success.

Female choice presents a problem. The best possible mate must be located and identified, but his location and identification must be completed rapidly enough to offset any decrease in reproductive success resulting from the search. This problem has both complex and simple solutions. Females might begin their search by looking for the best possible mate and change their acceptance criteria as search time elapsed. On the other hand, females might use a single invariable search routine that generally maximizes the benefits of female selectivity while minimizing the associated costs. Sculpins exemplify this simpler alternative.

Polygyny among mottled sculpins reflects the process of female choice. Since hatching probability is proportional to the number of egg masses in a nest (Figure 20), there is no disadvantage in
mating with an already mated male. On the other hand, females are not omniscient and the time spent locating the best of all possible mates results in late, and thus less successful, oviposition. Selection thus favors those females that choose the best available mate in the shortest amount of time, a goal that appears to be readily accomplished simply by mating with the larger of two sequentially encountered males. Polygyny ensues. The movements and comparison abilities of female sculpins mandate that certain males, whether they are the largest males or not, will be the larger sequentially encountered males for multiple females and will therefore be polygynists.

When is the Best Time to Breed?

The courtship success of male sculpins is thus determined by female choice of relatively, not absolutely, high quality mates. Female choice based on relative mate quality is in turn attributable to the cost associated with locating suitable mates, costs which directly reflect the importance of reproductive timing.

The general occurrence of discrete breeding periods suggests that the timing of reproduction may be an important determinant of reproductive success among vertebrates. Darwin (1871) recognized this suggestion when he proposed that the most vigorous members of a population would breed earliest in the season and produce the greatest numbers of young. A brief survey of the effects of reproductive timing among various vertebrate groups reveals both
the generality of this proposal and the critical importance of reproductive timing.

Reproductive timing appears critical to a great variety of bird species (Table 12). Avian breeding seasons generally parallel the environmental cycle in such a way that young are produced as close to the period of maximum food abundance as possible (Thomas, 1950; Moreau, 1950; Skutch, 1950; Perrins, 1970, 1965). Several environmental factors select against late breeding in birds, most notably, juvenile mortality increases throughout the breeding season since late fledgers find insufficient food supplies, late breeding adults are forced to undergo their annual molt immediately following the stresses of reproduction, and late breeding may not allow sufficient time for the accumulation of pre-migratory energy supplies (D. Lack, 1950a).

Birds breeding in unpredictable environments or feeding their young on ephemeral food sources best illustrate the correlation between the onset of reproduction and the abundance of food for both adults and nestlings. For example, breeding of the seed eating finches of the Galapagos Islands is strictly controlled by the occurrence of rain (D. Lack, 1950). Breeding seasons of these birds are short, food supplies ephemeral and close tracking of the rains is crucial (Downhower, 1976). The breeding seasons of the European robin (Erithacus rubecula) and various Parus species coincide with peak caterpillar abundance; that of the crossbeak
Loxia curvirostra coincides with peak pine nut abundance (Thomas, 1950). Breeding seasons within single species may vary with geography, but generally coincide with abundant food resources (Moreau, 1950).

Diverse observations indicate that timing within a breeding season is critical to many bird species. Clutch sizes decline throughout the breeding season in many passerine and non-passerine birds (Table 12; and review in Lack, 1947), and detailed analyses of at least one species (Parus major) have demonstrated that the observed decline cannot be attributed to the various age dependent breeding strategies apparent in a population (Perrins, 1970). Average clutch size in this species may decrease as much as .09 eggs per day for each day later that breeding begins (Perrins, 1965). Birds showing decreasing clutch sizes during the breeding season are likely to show decreased survival of late hatchlings, and small, late clutches may actually produce more offspring than large late clutches (Perrins, 1970).

The frequency distributions of clutch initiations during the course of single breeding seasons are strongly skewed to the right for a number of species (Table 12). Such skewing indicates that late breeding birds, like sculpins, are at some disadvantage relative to earlier breeders, and that whatever factors determine the actual commencement of breeding, selection favors those individuals that breed as close to the commencement as possible.
When multiple clutches are produced by a single female in one breeding season, late clutches are frequently smaller than earlier clutches (Table 12). This pattern presumably reflects the same selective forces that cause the general decline in the sizes of clutches initiated throughout a breeding season.

Most supportive of the argument that the timing of reproduction is critical to avian reproductive success are those studies that relate the date of oviposition or clutch initiation to subsequent juvenile survival (Table 12). For example, sparrowhawk (Accipiter nisus) clutches initiated early in the season produce more young than those started later (Newton, 1976). Late fledging herring gulls (Larus argentatus) may suffer a competitive disadvantage compared to earlier fledgers, and have a higher mortality rate (Parson, et al., 1976). Late fledging bank swallows (Riparia riparia) fledge when food is not easily located and have a higher probability of starving than do earlier fledgers (Emlen and Demong, 1975). Late nesting great tits (Parus major) have great difficulties in feeding their young and produce fewer fledglings per breeding pair than earlier nesters (Perrins, 1965, 1970). Other examples are summarized in Table 12.

The other vertebrate groups have not been as thoroughly studied as have the birds. Some evidence suggests that reproductive timing is important to mammals. For example, juvenile survival may be dependent on birth date in the mouse Peromyscus maniculatus.
Late litters of mountain hares (Lepus timidus) grow more slowly, mature later, and have lower survival rates than do earlier litters (Hewson, 1968, 1976). Water voles (Arvicola terrestris) born early in spring have higher survival rates than later litters (Stoddard, 1971).

Among amphibians, early breeding bullfrogs (Rana catesbiana) may succeed in producing young early enough that they can metamorphos a year earlier than the young of late breeders, thus escaping the competitive and predative hazards of pond life (Emlen, 1977). Mortality rates resulting from unknown environmental factors are apparently lowest during the period of peak oviposition by newts (Triturus vulgaris), suggesting that some narrowly defined optimal spawning date occurs (Bell and Lawton, 1975).

Most tropical ostariophysian fishes breed early in the flood season, lay all of their eggs at a single time, and spawn in main rivers, lateral channels, or on the flood plain itself (Lowe-McConnell, 1975). Eggs typically hatch rapidly (2 days), and young hatch at a time when food is plentiful, predators and competitors are dispersed, and protective cover is available in the flood plain. Timing of reproduction among these fishes is likely to be critical since flood waters may rapidly become anoxic as terrestrial vegetation rots, or water levels may drop rapidly, exposing the developing eggs and fry (Lowe-McConnell, 1975).
Reproductive timing may be most critical in those fishes whose larvae feed on ephemeral planktonic organisms. For example, Lasker (1975) has demonstrated that larval anchovies (Engraulis mordax) must encounter phytoplankton densities of more than 20 cells per ml at or within 60 hours of the onset of larval feeding. Furthermore, the plankton encountered must include particular species and must be composed of cells about 40 um in diameter. These required feeding densities are higher than those usually found in the sea. Feeding conditions are thus extremely transient, suggesting that any delay in breeding date may drastically affect subsequent larval survival.

Larvae feeding on zooplankton may confront similar situations. For example, haddock (Melanogrammus aeglefinus) and cod (Gadus morhua) may time their spawning to coincide with the reproduction of copepods eaten by the larval fishes. Larval fishes thus begin foraging when larval copepods are abundant, and grow as their prey grows. Copepod densities necessary to support newly hatched larval fishes are greater than those generally found in the sea, however. Thus, feeding conditions may be transient or patchy (Jones and Hall, 1974). In general, natural ocean food concentrations are orders of magnitude below the optima for larval survival (May, 1974). Any delay in spawning date by fish whose larvae exploit transient high density food patches may result in catastrophic starvation. The considerable variations observed in year
class strength of fishes feeding on such larval food supplies may reflect differential mortality attributable to such starvation (Hjort, 1926; Bannister, Harding and Lockwood, 1974; May, 1974; Cushing, 1974; Jones and Hall, 1974).

Numerous studies thus indicate that the timing of reproduction may be a critical determinant of reproductive success among vertebrates in general. This is most conclusively demonstrated among birds, an observation that may reflect the relative ease with which laying and hatching dates can be determined in this group. Although not as well documented in other vertebrate groups, reproductive timing may also be important to mammals, amphibians, and especially fishes whose larval stages develop in transient habitats or feed on ephemeral food supplies.

Who Constitutes the Best Mate?

The critical impact of timing on subsequent reproductive success interacts with female choice for large mates to produce polygyny among mottled sculpins. Both timing and the attributes that cause males to be desirable mates can thus be identified as important determinants of this particular mating system.

The factors that determine male desirability can, in turn, be identified as the physical or behavioral attributes of individual males, the quality of the breeding related resources controlled by individual males, and the number of females already mated to
individual males. Much controversy has surrounded the relative importance of each of these types of determinants (reviewed by Williams, 1975; and Wilson, 1975). Unfortunately, virtually no data pertaining to this controversy exist (Downhower and Brown, 1978a). Each of these types of determinants is undoubtedly important to some vertebrates and unimportant to others, the relative role of each type of determinant probably reflecting the role that males play as parents among different species. When males' parental abilities are determined by body size, females may be expected to base their choice of mate on body size. When males' parental abilities are a function of the number of females with whom he is already mated, females may be expected to base their choice of mate on the marital status of potential mates. When males' parental abilities are a function of territorially defensible resources, females may base their choice on resource quality. In many cases, all of these factors may be important. On the other hand, only male size appears important to female sculpins.

Regardless of what factors constitute a desirable mate, females benefit by discriminating among available males and picking males that increase their reproductive success. If, as in sculpins, the probability of successful reproduction decreases as the search for a mate progresses, females may base their choice on relative mating situation (male, resource and/or number of other females) attributes. One consequence of relative female choice patterns is that males may be able to evaluate and even modify their probability
of attracting a mate by evaluating and appropriately modifying their competition. If females preferentially mate with older or larger males, for example, such males might actually benefit from the presence of younger, smaller males as competitors. Such an arrangement may be illustrated by the dueting courtship of the manakin *Chiroxiphia linearis*, in which pairs of males perform a courtship dance, but only the dominant member of the pair actually mates (Foster, 1977). Similar arrangements may be found in the ruff (*Philomachus pugnax*), a lek forming species in which resident territorial males sometimes tolerate the presence of lighter colored, non-territorial satellite males (Shepard, 1975). Although controversy surrounds the conditions under which resident males tolerate satellites (Shepard, 1975; Hogan-Warburg, 1966), resident males with satellites are more successful in their courtship than those without satellites (Shepard, 1975). Similarly, male indigobirds (*Vidua chalybeata*) with nearby neighboring males have greater courtship success than more isolated males (Payne and Payne, 1977).

Alternatively, younger, smaller males certainly suffer a disadvantage when confronting relatively higher quality competition, and selection favors those males that alter their desirability with respect to their competition. This situation is illustrated by several species of poeciliid fishes for which the size of maturation of adult males is controlled by the sizes of mature males in the population. For example, growth of male *Xiphophorus variatus* and *X. maculatus* ceases with sexual maturity. When juveniles are raised in groups, maturation of males is sequential, each male
delaying maturation until he is larger than all previously matured males (Borowsky, 1973; Sohn, 1977). Since size is directly correlated with male courtship success in these species (Borowsky, 1973; McKay, 1971), each successively maturing male becomes relatively larger than all of his competitors and increases his probability of mating.

Selective factors similar to those delaying maturation in *Xiphophorus* may be responsible for sexual bimaturism, a frequent correlate of polygynous mating systems (Wiley, 1974). Whenever attempted reproduction reduces male survival, males can increase their lifetime reproductive success by delaying reproduction when the probability of successful courtship is low, and compensating for this delay with increased early survival or increased fecundity later (Wiley, 1974). If, for example, females based their choice on relative male size, small males may benefit by delaying reproduction when the breeding population is composed of larger males. Since females are not the subject of female choice, they are not subject to the same selective pressure for delayed maturation. Selection thus favors delayed reproduction in males but not in females and bimaturism results. Mottled sculpins exemplify these sex dependent selection pressures. Female sculpins generally mature and breed in their second or third year (Hann, 1927; Bailey, 1952). Males may mature in their second or third year (Hann, 1927; Bailey, 1952), but may not breed until much older. For example, the size ranges of gravid females captured in 1975 and 1976 were
identical, despite the fact that the average sizes of females in 1976 was eight mm larger than the preceding year. The size ranges of males were radically different in these two years, however (Figure 14). In 1975, when the mean size of mated males was small, over 20 percent of the nesting males were less than 85 mm in total length and the smallest male captured at a nest site was only 60 mm long. In 1976, when the mean size of mated males was large, only 4 percent of the nesting males were smaller than 85 mm, the smallest breeding male was 79 mm long and the smallest male captured at a nest site was 70 mm. Thus females of equivalent sizes bred in both years. Small males, however, attempted breeding only when the distribution of available males was composed of small males. In 1976, when many large males were competing for mates, small males did not even occupy potential nesting sites.

The costs of reproduction to male sculpins are still under investigation (Pederson and Downhower, in prog.). Whatever they may be, sexual bimaturism is obvious in sculpins (Figure 14). Although male and female sculpins do grow at slightly different rates (Hann, 1927; Koster, 1936; Ludwig and Norden, 1967), this difference is hardly graphic and may not even be significant (Koster, 1936). The extreme difference in the size distributions of breeding males and females observed during this study can be interpreted only as an indication that male sculpins are generally older than females when they breed. Accurate aging of sculpins is difficult, as age is most reliably determined by examination of otoliths or
vertebral cross sections (Ludwig and Norden, 1967; Zarbock, 1952; Patten, 1971). Otolith age determinations for 37 breeding males indicates that in 1976 the modal age of breeding males in Anderson Creek was 5 years (range: 4-6 years).

In summary, females of different species may be expected to base their choice of mate on a number of different factors, the relative importance of each being determined by her mate's role as a parent. Whenever females make relative, not absolute choices of mates, males may be able to evaluate and even modify their chances of successful courtship by evaluating or modifying their desirability with respect to their competition. Such evaluation by males may be responsible for diverse life history and courtship patterns.

**Expediency, Principles and Compromising Females**

Whenever the timing of reproduction influences subsequent reproductive success, selection favors those females that breed as close to the optimal time as possible. Concurrently, whenever attributes of an individual mating situation (i.e., the male, the number of other females involved, the male's resources, etc.) influence subsequent reproductive success, selection favors those females that choose the best possible mating situation. Since breeding does not occur in the best of all possible worlds, females may not be able to pick the best possible mating situation in the least possible time. Rather, selection may favor those females that choose
a relatively high quality mate in a relatively short time, a compromise situation presumably illustrated by female sculpin choice of relatively large males.

The apparently general importance of reproductive timing among vertebrates suggests that such compromise situations may be quite common, and the diversity of vertebrate mating systems suggests that the form taken by such compromise situations may be highly variable. Slow moving, bottom dwelling female sculpins can evaluate males only very slowly, and are thus restricted to relatively few evaluations before the cost of further search exceeds the benefits. Concurrently, the mating system attributes that influence sculpin reproductive success are entirely summarized in male body size. Females suffer no disadvantage when mating with an already mated male. Different interactions of timing, female sampling abilities, and mating system attributes may produce different compromise situations.

Females of many species are more mobile than female sculpins and may be capable of sampling a greater variety of males before picking a mate. For example, through flight female birds and bats may be able to evaluate many males very quickly and choose the locally best male. When females suffer no disadvantage from mating with an already mated male, and when male quality can be rapidly assessed, this ability may lead to extreme polygyny as it has in lek forming species. In these species, females can evaluate all
mature males in a locality almost simultaneously. Thus, in the hammer-headed bat (Hypsignathus monstrosus) "... the female appears to visit each male at least once, then returns to two or three for repeated and alternating visits over a 3-5 minute period, and finally concentrates on repeated hovering before a single male. An observer certainly gains an impression of direct comparisons of males by the female until she has chosen one for mating. Once a female has landed, copulation is rapid (Bradbury, 1977)." In this species, 5 of 85 lek displaying males accounted for almost 80 percent of the observed copulations. Similar patterns are apparent in other lek formers. For example, Ballard and Robel (1974) report that two lekking male prairie chickens (Tympanuchus cupido) accounted for almost 90 percent of all observed copulations, despite the presence of other courting males. Shepard (1975) discusses a lek of ruffs (Philomachus pugnax) at which three males accounted for 97 percent of the observed female solicitations, despite the presence of six other territorial males. The observation that a single male does not mate with all females may simply reflect individual differences in female perception of male qualities.

When female reproductive success is a decreasing function of the number of females already mated to an individual male, selection may favor those females that enter monogamous mating situations. When the time taken to locate a bachelor male is extremely long, however, females may increase their reproductive success by entering a polygynous mating even if polygyny is disadvantageous relative
to monogamy. If males are irregularly scattered over great distances, or if breeding related resources are so limited that simple location of a bachelor male is unlikely, females may realize a greater net benefit by entering a polygynous situation than by searching further for another mate. For example, male yellow-bellied marmots (*Marmota flaviventris*) defend grassy territories separated by wide areas of inhospitable breeding habitat. Monogamous female marmots realize the greatest reproductive success, yet polygyny is common. The observation that female fitness declines with harem size in this species (Dowhower and Armitage, 1971) suggests that although certain selective pressures favor monogamy, the benefits of remaining in a harem may exceed those of searching for a bachelor male.

If, on the other hand, potential mates are regularly and predictably spaced or are abundant, so that location of a better mating situation is very likely, females may realize a greater net profit by shunning potential polygynists and searching for another mate. The occurrence of monogamy or polygyny may thus be strongly influenced by the costs experienced by females when searching for a mate. For example, many seabirds form large breeding colonies in which females could assess male qualities rapidly. For at least one well studied species, the kittiwake (*Rissa tridactyla*), both parents care for the young suggesting that monogamy is advantageous to females (Coulson and White, 1958a). Yet the timing of reproduction in this species is critical, the number of young
fledged per pair declining by almost .10 per day for each day after the date of first laying (Perrins, 1970). The prevalence of monogamy among kittiwakes indicates that the advantages of searching for a previously unmated male outweigh the costs of delayed reproduction, even though those costs are high. Importantly, kittiwakes are long-lived, with as great as 97 percent survival between reproductive periods (Coulson and White, 1959; Coulson and Wooler, 1976). The costs associated with locating a mate in this species may be offset by the fact that up to 75 percent of breeding kittiwakes remain mated for subsequent reproductive periods (Coulson, 1966). Those individuals breeding for the first time or breeding with a new mate breed later in the season and lay fewer eggs (Coulson and White, 1958; Coulson, 1966), reflecting the costs of locating and adjusting to a new mate. Birds retaining mates from previous years breed earlier in the season, show less variation in the date of clutch initiation, and realize a greater reproductive success (Coulson and White, 1958; Coulson, 1966). Importantly, those birds that changed mates between breeding seasons generally did so after their previous mate had died or after an unsuccessful breeding season (Coulson, 1966). Similar patterns are known in other long-lived monogamous seabirds. For example, in the skua (Stercorarius parasiticus) experienced pairs breed earlier and have higher reproductive success rates than pairs breeding together for the first time (Davis, 1976). Red-billed gulls (Larus
*novaehollandiae*, show up to 95 percent retention of mates between breeding seasons. Mate switching generally follows unsuccessful breeding, and females retaining mates breed sooner after arrival at the breeding colony, breed an average of 10.4 days earlier in the season, and lay larger clutches than females changing mates.

If reproductive timing is so critical that any delay in mating results in decreased breeding success, the costs of any degree of female choice may outweigh the benefits, and more or less random mating may result. Interestingly, the herrings (*Clupeidae*) apparently form spawning aggregations in which many individuals mate simultaneously (Breeder and Rosen, 1966). For example, the Pacific herring (*Clupea arengus*) spawns en mass and no distinct pairing occurs (Schaefer, 1937). Many of the Gadoids, apparently including the cod also form such promiscuous spawning clusters (Breeder and Rosen, 1966). Since the larval stages of these fish feed on extremely temporal planktonic foods, reproductive timing may be extremely important. The role of female choice has yet to be evaluated in these organisms, however.

**Discussion**

Much of the recent work on vertebrate mating systems has been grounded on the argument that female choice is always possible. Since "it should never make sense for an individual to choose a mating arrangement that lowers its fitness," the mating arrangement realizing the greatest fitness should be chosen by a female (Elliott,
1975). For example, when monogamous pairings realize the greatest female reproductive success, monogamy should be the rule (e.g., Elliott, 1975). Extending this argument to sculpins, when the largest available males produce the greatest numbers of young, females should mate with the largest possible males.

These arguments neglect the fact that the strategy of leaving the most surviving young may in fact be realized through tactics other than choice of the best possible mate. Mate selection takes time, and time, for many vertebrates costs. Choice of the best possible mating arrangement may take the longest possible time and may therefore decrease reproductive success. Under these conditions natural selection may favor those females that pick a relatively good mate in a relatively short time over those that delay reproduction while searching for the best possible mate.

Female sculpins exemplify this type of selection: they can pick a relatively high quality male in a very short time by mating with the larger of two sequentially encountered males. Although this type of mate selection generally results in choice of a large male in a short time, it rarely results in choice of the best possible male. Female choice as illustrated by sculpins thus represents a compromise between selection for mate quality and selection for early breeding. Polygyny among sculpins reflects this compromise.
The apparent importance of reproductive timing to various vertebrate groups, suggest that such compromise situations may be common. The diversity of vertebrate mating systems suggests that the type of compromise reached may vary, and may be determined by such factors as the cost of delaying reproduction while searching for a mate, the abilities of females to sample potential mates, and the benefits of choosing a mate possessing particular qualities. These factors are very different from those suggested by interpretations that have ignored constraints on female choice and dealt only with relationships between resources and mating system structure (e.g., Orians, 1969; Holm, 1973; Wittenberger, 1976; Elliott, 1975; Emlen and Oring, 1977).
Table 1. The assumptions and arguments of various mating system analyses. Arguments derived from each assumption are individually numbered, and appear beneath the assumption from which they are derived. An (X) denotes that the argument or assumption is important to a particular analysis.

<table>
<thead>
<tr>
<th>Natural selection determines mating system type</th>
<th>Surplus-Food</th>
<th>Patchy-Environment</th>
<th>Resource-Monopolization</th>
<th>Sexual Bimaturism</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reproduction costs more for females than for males</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>1. Female choice determines mating system type</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2. Females never enter disadvantageous arrangements</td>
<td></td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3. Females are less able to monopolize critical resources</td>
<td></td>
<td></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>4. Females discriminate more than males</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Resource distributions determine paternal roles</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Polygyny is incompatible with full biparental care</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>1. Polygyny is incompatible with male care</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 1 (Continued).

<table>
<thead>
<tr>
<th>Surplus-Food</th>
<th>Patchy-Environment</th>
<th>Resource-Monopolization</th>
<th>Sexual Bimaturism</th>
</tr>
</thead>
</table>

2. Polygyny is compatible with reduced male care

|              |                    | X                       | X                 |
Table 2. Published verifiable predictions that are consistent with multiple mating system analyses. An (X) denotes that the prediction can be derived from a given mating system analysis, while a (+) denotes that the patterns expected by the prediction can be explained by an analysis.

<table>
<thead>
<tr>
<th></th>
<th>Sur - Food</th>
<th>Patchy- Environment</th>
<th>Resource- Monopolization</th>
<th>Sexual Bimaturism</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Polyandry should be rare among mammals and birds (Orians, 1969).</td>
<td>X</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>2. Monogamy should be exceptional among mammals, but prevalent among birds (Orians, 1969).</td>
<td>X</td>
<td>X</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>3. Birds with precocial young should be more commonly polygynous than birds with altricial young (Orians, 1969).</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>4. Polygyny or promiscuity should be most common in species in which brood size is strongly limited by factors other than the number of young that could be supported by the parents (Orians, 1969).</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>5. Mating systems of a single species should vary if that species breeds in habitats having different resource distributions (Orians, 1969).</td>
<td>X</td>
<td>X</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>6. Species demonstrating a high degree of sexual dimorphism should be polygynous (Carey and Nolan, 1975).</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
</tbody>
</table>
Table 2 (Continued).

<table>
<thead>
<tr>
<th></th>
<th>Surplus-Food</th>
<th>Patchy-Environment</th>
<th>Resource-Monopolization</th>
<th>Sexual Bimaturism</th>
</tr>
</thead>
<tbody>
<tr>
<td>7.</td>
<td>There should be a non-negative correlation between average female reproductive success and the number of females mated to a male (Orians, 1969).</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>8.</td>
<td>Females should mate with already mated males even when unmated males are available and perceived by the females (Orians, 1969).</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>9.</td>
<td>Unmated males should not be observed in polygynous systems that evolved in response to physiognomic differences between habitats (Wittenberger, 1976).</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>10.</td>
<td>Unmated males should be observed in polygynous systems that evolved in response to the differential availability of food in different habitats (Wittenberger, 1976).</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>11.</td>
<td>Polygyny should be common in species having widespread feeding areas but restricted nest sites (Orians, 1969).</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>12.</td>
<td>Polygyny should be most common in areas having unevenly distributed food supplies, like marshes and early successional seres (Orians, 1969, 1972).</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
</tbody>
</table>
Table 2 (Continued).

<table>
<thead>
<tr>
<th>Surplus-Food</th>
<th>Patchy-Environment</th>
<th>Resource-Monopolization</th>
<th>Sexual Bimaturism</th>
</tr>
</thead>
<tbody>
<tr>
<td>X</td>
<td>X</td>
<td>X</td>
<td>+</td>
</tr>
</tbody>
</table>

13. There should be a positive correlation between the number of mates a male attracts and the productivity of his territory (Orians, 1972).
Table 3. A partial summary of vertebrates in which physical or behavioral characteristics of reproductively mature males influence mating success. Modified from Downhower and Brown (1978a).

<table>
<thead>
<tr>
<th>ORGANISM</th>
<th>ATTRIBUTES</th>
<th>SOURCE</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>BIRDS</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Agelaius phoeniceus</em></td>
<td>Experience (age)</td>
<td>Yasukawa, 1977; Weatherhead and Robertson, 1977, 1977a</td>
</tr>
<tr>
<td><em>Troglodytes aedon</em></td>
<td>Age</td>
<td>Kendeigh, 1941</td>
</tr>
<tr>
<td><em>Acrocephalus arundinaceus</em></td>
<td>Age</td>
<td>Peltzer, 1972</td>
</tr>
<tr>
<td><em>Centrocercus urophasianus</em></td>
<td>Age, strength, body size</td>
<td>Scott, 1942; Wiley, 1973</td>
</tr>
<tr>
<td><strong>Lyrurus mlokosiewiczi</strong></td>
<td>Experience (age)</td>
<td>Kruijt, et al., 1972</td>
</tr>
<tr>
<td><em>Tympanuchus cupido</em></td>
<td>Aggression (age)</td>
<td>Robel, 1966</td>
</tr>
<tr>
<td><em>Columba livia</em></td>
<td>Color, dominance</td>
<td>Kerfoot, 1964</td>
</tr>
<tr>
<td><em>Passerina cyanea</em></td>
<td>Age</td>
<td>Carey and Nolan, 1975</td>
</tr>
<tr>
<td><strong>Gallus domesticus</strong></td>
<td>Dominance, weight, strength, experience</td>
<td>Guhl and Warren, 1946</td>
</tr>
<tr>
<td><em>Euplectes sp.</em></td>
<td>Display</td>
<td>Emlen, 1957</td>
</tr>
<tr>
<td><strong>Telmatodytes palustris</strong></td>
<td>Nest construction (age?)</td>
<td>Verner and Engelsen, 1970</td>
</tr>
<tr>
<td><strong>REPTILES AND AMPHIBIANS</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Anolis garmani</em></td>
<td>Size (age)</td>
<td>Trivers, 1972</td>
</tr>
<tr>
<td><em>A. lineatopus</em></td>
<td>Size, age</td>
<td>Rand, 1967</td>
</tr>
<tr>
<td><em>Bufo americanus</em></td>
<td>Vocalization</td>
<td>Licht, 1976</td>
</tr>
<tr>
<td><strong>MAMMALS</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ovis sp.</em></td>
<td>Age, size (dominance)</td>
<td>Geist, 1971</td>
</tr>
<tr>
<td><em>Mirounga angustirostris</em></td>
<td>Dominance, age</td>
<td>Le Boeuf, 1974</td>
</tr>
<tr>
<td><em>Papio sp.</em></td>
<td>Age, dominance</td>
<td>DeVore, 1965</td>
</tr>
<tr>
<td><em>Mus musculus</em></td>
<td>Dominance, body size</td>
<td>DeFries and McClearn, 1970</td>
</tr>
<tr>
<td><strong>Antilocapra americana</strong></td>
<td>Territory (age, body size)</td>
<td>Kitchen, 1974</td>
</tr>
</tbody>
</table>
Table 3 (Continued).

<table>
<thead>
<tr>
<th>ORGANISM</th>
<th>ATTRIBUTES</th>
<th>SOURCE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cervus elaphus</td>
<td>Size, strength (age)</td>
<td>McCullough, 1969</td>
</tr>
<tr>
<td>Odocoileus virginianus</td>
<td>Size, age, dominance</td>
<td>Hirth, 1977</td>
</tr>
<tr>
<td>FISH</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nothobranchius guentheri</td>
<td>Color</td>
<td>Haas, 1976</td>
</tr>
<tr>
<td>Poecilia reticulata</td>
<td>Color</td>
<td>Haskins, et al., 1961</td>
</tr>
<tr>
<td>P. latipinna</td>
<td>Size (age)</td>
<td>Baird, 1974</td>
</tr>
<tr>
<td>Ettheostoma caeruleum</td>
<td>Color (size and age)</td>
<td>Reeves, 1907</td>
</tr>
<tr>
<td>Salmo salar</td>
<td>Size</td>
<td>Belding, 1934</td>
</tr>
<tr>
<td>Onchorynchus nerka</td>
<td>Size, age</td>
<td>Hanson and Smith, 1967</td>
</tr>
<tr>
<td>Lepomis sp.</td>
<td>Size, age, tubercule number</td>
<td>Gross, 1978</td>
</tr>
<tr>
<td>Semotilus atromaculatus</td>
<td>Dominance, weight</td>
<td>Ross, 1975</td>
</tr>
<tr>
<td>Xiphophorus sp.</td>
<td>Size</td>
<td>Nobel and Bourne, 1938</td>
</tr>
<tr>
<td>X. variatus</td>
<td>Size</td>
<td>Borowsky, 1973</td>
</tr>
<tr>
<td>X. maculatus</td>
<td>Size</td>
<td>Sohn, 1977</td>
</tr>
<tr>
<td>Tilapia melanchorheron</td>
<td>Size</td>
<td>Barlow and Green, 1969</td>
</tr>
<tr>
<td>Etroplus maculatus</td>
<td>Size</td>
<td>Barlow, 1968</td>
</tr>
<tr>
<td>Cichlasoma maculiacaudata</td>
<td>Size</td>
<td>Perrone, 1975</td>
</tr>
<tr>
<td>Gasterosteus aculeatus</td>
<td>Color</td>
<td>Semler, 1971</td>
</tr>
<tr>
<td>Hemichromis bimaculatus</td>
<td>Color</td>
<td>Nobel, 1938</td>
</tr>
</tbody>
</table>
Table 4. Mean values (and Standard Deviations) of various location variables measured in Anderson Creek on 5/23/75, 6/12/76, and 5/20/77. Tile sizes are ranked from smallest to largest within each year.

<table>
<thead>
<tr>
<th>Year</th>
<th>Tile Designation</th>
<th>Tile Area (cm²)</th>
<th>N</th>
<th>Distance to Closer Shore (M)</th>
<th>Depth (M)</th>
<th>Distance to Nearest Neighbor (M)</th>
<th>Distance to nearest equal sized neighbor (M)</th>
<th>DO (ppm)</th>
<th>Current (m/s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1975</td>
<td>S</td>
<td>90</td>
<td>74</td>
<td>1.57(.95)</td>
<td>.18(.08)</td>
<td>2.98(1.45)</td>
<td>8.2(.30)</td>
<td>.25(.20)</td>
<td>.53(.40)</td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>195</td>
<td>75</td>
<td>1.53(.91)</td>
<td>.16(.07)</td>
<td>2.78(1.33)</td>
<td>8.2(.31)</td>
<td>.20(.18)</td>
<td>.65(.53)</td>
</tr>
<tr>
<td></td>
<td>L</td>
<td>302</td>
<td>74</td>
<td>1.61(.94)</td>
<td>.17(.08)</td>
<td>2.99(1.52)</td>
<td>8.2(.30)</td>
<td>.22(.18)</td>
<td>.69(.63)</td>
</tr>
<tr>
<td>1976</td>
<td>U</td>
<td>53</td>
<td>42</td>
<td>1.90(.92)</td>
<td>.22(.10)</td>
<td>.69(.22)</td>
<td>2.98(1.45)</td>
<td>8.2(.30)</td>
<td>.25(.20)</td>
</tr>
<tr>
<td></td>
<td>V</td>
<td>90</td>
<td>45</td>
<td>1.88(.80)</td>
<td>.21(.09)</td>
<td>.63(.24)</td>
<td>2.78(1.33)</td>
<td>8.2(.31)</td>
<td>.20(.18)</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td>140</td>
<td>49</td>
<td>1.98(.92)</td>
<td>.21(.09)</td>
<td>.64(.31)</td>
<td>2.99(1.52)</td>
<td>8.2(.30)</td>
<td>.22(.18)</td>
</tr>
<tr>
<td></td>
<td>X</td>
<td>196</td>
<td>42</td>
<td>1.99(.98)</td>
<td>.21(.09)</td>
<td>.64(.30)</td>
<td>2.85(1.38)</td>
<td>8.2(.30)</td>
<td>.20(.19)</td>
</tr>
<tr>
<td></td>
<td>Y</td>
<td>250</td>
<td>43</td>
<td>1.89(.87)</td>
<td>.21(.08)</td>
<td>.67(.22)</td>
<td>2.99(1.68)</td>
<td>8.2(.30)</td>
<td>.17(.19)</td>
</tr>
<tr>
<td></td>
<td>Z</td>
<td>302</td>
<td>44</td>
<td>2.10(.78)</td>
<td>.21(.09)</td>
<td>.68(.21)</td>
<td>2.81(1.13)</td>
<td>8.2(.28)</td>
<td>.18(.26)</td>
</tr>
<tr>
<td>1977</td>
<td>-</td>
<td>196</td>
<td>293</td>
<td>2.07(.75)</td>
<td>.16(.07)</td>
<td>.88(.19)</td>
<td>4.9(1.62)</td>
<td>.24(.19)</td>
<td>.89(.41)</td>
</tr>
</tbody>
</table>
Table 5. Proportions of experimental tiles occupied by adult males during the 1976 breeding season in Anderson Creek. Sample sizes are given in parenthesis for each sample date. Tile sizes are as in Table 4.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>U</td>
<td>.06(47)</td>
<td>.29(49)</td>
<td>.35(48)</td>
<td>.43(49)</td>
<td>.48(48)</td>
<td>.28(50)</td>
<td>.26(50)</td>
<td>.22(50)</td>
</tr>
<tr>
<td>V</td>
<td>.16(50)</td>
<td>.69(49)</td>
<td>.84(50)</td>
<td>.85(48)</td>
<td>.88(50)</td>
<td>.82(50)</td>
<td>.80(50)</td>
<td>.84(50)</td>
</tr>
<tr>
<td>W</td>
<td>.56(48)</td>
<td>.86(50)</td>
<td>.86(49)</td>
<td>.94(50)</td>
<td>.96(49)</td>
<td>.92(50)</td>
<td>.92(50)</td>
<td>.88(50)</td>
</tr>
<tr>
<td>X</td>
<td>.69(49)</td>
<td>.96(49)</td>
<td>.96(48)</td>
<td>.98(49)</td>
<td>.96(49)</td>
<td>.96(49)</td>
<td>.90(49)</td>
<td>.86(49)</td>
</tr>
<tr>
<td>Y</td>
<td>.75(48)</td>
<td>.96(47)</td>
<td>.94(47)</td>
<td>.96(48)</td>
<td>.94(48)</td>
<td>.94(47)</td>
<td>.85(48)</td>
<td>.88(48)</td>
</tr>
<tr>
<td>Z</td>
<td>.78(49)</td>
<td>.98(49)</td>
<td>.96(48)</td>
<td>.98(49)</td>
<td>.96(49)</td>
<td>.98(48)</td>
<td>.96(49)</td>
<td>.90(49)</td>
</tr>
<tr>
<td>Total</td>
<td>.50(291)</td>
<td>.79(293)</td>
<td>.82(290)</td>
<td>.86(293)</td>
<td>.86(293)</td>
<td>.81(293)</td>
<td>.78(295)</td>
<td>.76(295)</td>
</tr>
</tbody>
</table>
Table 6. The Analysis of Covariance Table. Male courtship success was the dependent variable, male total length the covariate, and tile size the classification variable. The maximum number of egg masses present at each site was used to estimate the number of spawnings per male. Sites at which the loss of an egg mass could be attributed to the experimenters activities were excluded from the analysis. Regression coefficients were similar for all six tile size classes ($F = 2.07$, d.f. = 5, 373, $P > .05$). Data from those years in which multiple tile sizes were used (1975 and 1976) were combined in this analysis.

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>S.S.</th>
<th>M.S.</th>
<th>F</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>6</td>
<td>278.8</td>
<td>46.46</td>
<td>12.26</td>
<td>.163</td>
</tr>
<tr>
<td>Error</td>
<td>378</td>
<td>1432.2</td>
<td>3.79</td>
<td>(P &lt; .0001)</td>
<td></td>
</tr>
<tr>
<td>Corrected total</td>
<td>384</td>
<td>1711.0</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Partial Sum of Squares Source:

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>S.S.</th>
<th>$F$</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tile Size</td>
<td>5</td>
<td>28.03</td>
<td>1.48</td>
<td>(P &lt; .20)</td>
</tr>
<tr>
<td>Male Size</td>
<td>1</td>
<td>154.23</td>
<td>40.71</td>
<td>(P &lt; .0001)</td>
</tr>
</tbody>
</table>
Table 7. Male size and survival of egg masses. In 1976 the average length of breeding males was 95 mm. All sites were checked at 2-3 day intervals and all losses are tabulated on a per interval basis.

<table>
<thead>
<tr>
<th>Male Length</th>
<th>Less than 95 mm</th>
<th>Greater than 95 mm</th>
<th>$X^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Failure Rate When Male Absent</td>
<td>.47 (N = 34)</td>
<td>.45 (N = 22)</td>
<td>n.s.</td>
</tr>
<tr>
<td>Failure Rate When Male Present</td>
<td>.016 (N = 511)</td>
<td>.003 (N = 694)</td>
<td>6.72</td>
</tr>
<tr>
<td>Frequency of Abandonment</td>
<td>.062 (N = 545)</td>
<td>.031 (N = 716)</td>
<td>7.29</td>
</tr>
</tbody>
</table>
Table 8. The probability that at least part of an egg mass survived to hatching as a function of breeding site size during the 1976 spawning period in Anderson Creek. The average length of breeding males was 95 mm. Tile designations are as in Table 4.

<table>
<thead>
<tr>
<th>Tile Size</th>
<th>Males &lt;95 mm</th>
<th>Males &gt;95 mm</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P(Hatch) (N)</td>
<td>P(Hatch) (N)</td>
</tr>
<tr>
<td>U + V</td>
<td>.64 (76)</td>
<td>.85 (20)</td>
</tr>
<tr>
<td>W</td>
<td>.64 (59)</td>
<td>.78 (104)</td>
</tr>
<tr>
<td>X</td>
<td>.48 (40)</td>
<td>.73 (142)</td>
</tr>
<tr>
<td>Y</td>
<td>.63 (35)</td>
<td>.71 (130)</td>
</tr>
<tr>
<td>Z</td>
<td>.80 (20)</td>
<td>.55 (147)</td>
</tr>
<tr>
<td>X^2 (d.f.)</td>
<td>7.3 (4)</td>
<td>19.8 (4)</td>
</tr>
<tr>
<td></td>
<td>P .05</td>
<td>P .05</td>
</tr>
</tbody>
</table>
Table 9. Descriptive statistics for males breeding in natural nests and males breeding under the experimental tiles in the Anderson Creek study site during the 1976 and 1977 breeding seasons.

<table>
<thead>
<tr>
<th>Year</th>
<th>Natural Sites</th>
<th>Mean Total Length (mm)</th>
<th>Std. Dev.</th>
<th>Sample Size</th>
</tr>
</thead>
<tbody>
<tr>
<td>1976</td>
<td>Natural Sites</td>
<td>95.2</td>
<td>9.60</td>
<td>44</td>
</tr>
<tr>
<td></td>
<td>Experimental Sites</td>
<td>95.2</td>
<td>5.72</td>
<td>201</td>
</tr>
<tr>
<td>1977</td>
<td>Natural Sites</td>
<td>87.0</td>
<td>9.75</td>
<td>56</td>
</tr>
<tr>
<td></td>
<td>Experimental Sites</td>
<td>84.0</td>
<td>7.75</td>
<td>192</td>
</tr>
</tbody>
</table>
Table 10. Hatching successes of egg masses deposited on different dates during the 1976 spawning season. Sample sizes are given in parentheses.

<table>
<thead>
<tr>
<th>Position</th>
<th>3/28-4/2</th>
<th>4/7</th>
<th>4/10</th>
<th>4/13*</th>
<th>Overall Success</th>
<th>X²(d.f.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>First in Series</td>
<td>.76(92)</td>
<td>.79(33)</td>
<td>.65(26)</td>
<td>.58(12)</td>
<td>.74(163)</td>
<td>3.40(3) n.s.</td>
</tr>
<tr>
<td>Middle in Series</td>
<td>.79(72)</td>
<td>.80(146)</td>
<td>.71(110)</td>
<td>.64(22)</td>
<td>.77(350)</td>
<td>5.94(3) n.s.</td>
</tr>
<tr>
<td>Last in Series</td>
<td>.50(12)</td>
<td>.77(30)</td>
<td>.55(66)</td>
<td>.45(55)</td>
<td>.55(163)</td>
<td>5.57(3) n.s.</td>
</tr>
<tr>
<td>Solitary Egg Masses</td>
<td>.33(18)</td>
<td>.38(8)</td>
<td>.36(11)</td>
<td>.36(11)</td>
<td>.35(48)</td>
<td>.00(3) n.s.</td>
</tr>
</tbody>
</table>

*includes samples taken on 4/17, 4/20 and 4/24
Table 11. Descriptive statistics for the frequency distributions of spawnings in the Anderson Creek study site during the 1975, 1976, and 1977 spawning seasons.

<table>
<thead>
<tr>
<th></th>
<th>1975</th>
<th>1976</th>
<th>1977</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of Spawnings</td>
<td>540</td>
<td>891</td>
<td>430</td>
</tr>
<tr>
<td>Mean date of Spawning</td>
<td>April 22</td>
<td>April 8</td>
<td>April 14</td>
</tr>
<tr>
<td>Standard Deviation (days)</td>
<td>5.2</td>
<td>4.7</td>
<td>3.0</td>
</tr>
<tr>
<td>G₁</td>
<td>.845</td>
<td>.543</td>
<td>2.313</td>
</tr>
<tr>
<td>t</td>
<td>8.012</td>
<td>6.618</td>
<td>19.583</td>
</tr>
<tr>
<td>P</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>Interpretation</td>
<td>Skewed to right</td>
<td>Skewed to right</td>
<td>Skewed to right</td>
</tr>
<tr>
<td>G₂</td>
<td>.517</td>
<td>.328</td>
<td>22.803</td>
</tr>
<tr>
<td>t</td>
<td>2.453</td>
<td>2.059</td>
<td>96.508</td>
</tr>
<tr>
<td>P</td>
<td>&lt;.02</td>
<td>&lt;.05</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>Interpretation</td>
<td>Leptokurtic</td>
<td>Leptokurtic</td>
<td>Leptokurtic</td>
</tr>
</tbody>
</table>
Table 12. Some bird species for which reproductive timing is an important determinant of reproductive success.

<table>
<thead>
<tr>
<th>Species in which clutch size declines during the course of the breeding season.</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Passerulus sandwichensis</em></td>
<td>Welsh, 1975</td>
</tr>
<tr>
<td><em>Larus argentatus</em></td>
<td>Haycock and Threlfall, 1975</td>
</tr>
<tr>
<td><em>Sterna dougallii</em></td>
<td>Langham, 1975</td>
</tr>
<tr>
<td><em>S. hirundo</em></td>
<td>Langham, 1975</td>
</tr>
<tr>
<td><em>S. paradisaea</em></td>
<td>Langham, 1975</td>
</tr>
<tr>
<td><em>Thalasseus sandvicensis</em></td>
<td>Langham, 1975</td>
</tr>
<tr>
<td><em>Larus novaehollandiae</em></td>
<td>Mills, 1973</td>
</tr>
<tr>
<td><em>Parus major</em></td>
<td>Perrins, 1970; 1965</td>
</tr>
<tr>
<td><em>Rissa tridactyla</em></td>
<td>Perrins, 1970; Coulson and White, 1958a</td>
</tr>
<tr>
<td><em>Haematopus ostralegus</em></td>
<td>Perrins, 1970; Harris, 1967</td>
</tr>
<tr>
<td><em>Ficedula hypoleuca</em></td>
<td>Perrins, 1970</td>
</tr>
<tr>
<td><em>Lagopus lagopus</em></td>
<td>Jenkins, et al., 1963</td>
</tr>
<tr>
<td><em>Phylloscopus sibilatrix</em></td>
<td>E. Lack, 1950</td>
</tr>
<tr>
<td><em>Hirundo rustica</em></td>
<td>Boyd, 1936</td>
</tr>
<tr>
<td><em>Erithacus rubecula</em></td>
<td>Lack, 1946</td>
</tr>
<tr>
<td><em>Emberiza citrinella</em></td>
<td>Parkhurst and Lack, 1946</td>
</tr>
<tr>
<td><em>Troglodytes aedon</em></td>
<td>Kendeigh, 1941a</td>
</tr>
<tr>
<td><em>Anser anser</em></td>
<td>Newton and Kerbes, 1974</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Species in which the frequency distributions of clutch initiations are skewed to the right.</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Sterna dougallii</em></td>
<td>Langham, 1975</td>
</tr>
<tr>
<td><em>S. hirundo</em></td>
<td>Langham, 1975</td>
</tr>
<tr>
<td><em>S. paradisaea</em></td>
<td>Langham, 1975</td>
</tr>
<tr>
<td><em>Thalasseus sandvicensis</em></td>
<td>Langham, 1975</td>
</tr>
<tr>
<td><em>Sturnus vulgaris</em></td>
<td>Erskln and McLaren, 1976</td>
</tr>
<tr>
<td><em>Stilta currucoidea</em></td>
<td>Erskln and McLaren, 1976</td>
</tr>
<tr>
<td><em>Colaptes auratus</em></td>
<td>Erskln and McLaren, 1976</td>
</tr>
<tr>
<td><em>Turdus bicolor</em></td>
<td>Erskln and McLaren, 1976</td>
</tr>
<tr>
<td><em>Larus delawarensis</em></td>
<td>Ryder, 1975</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Species in which renesting attempts or second clutches are smaller than first clutches.</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Phasianus colchicus</em></td>
<td>Lack, 1947</td>
</tr>
<tr>
<td><em>Tympanuchus cupido</em></td>
<td>Lack, 1947</td>
</tr>
<tr>
<td><em>Colinus virginianus</em></td>
<td>Lack, 1947</td>
</tr>
<tr>
<td><em>Perdix perdix</em></td>
<td>Lack, 1947</td>
</tr>
<tr>
<td><em>Mycroca americana</em></td>
<td>Lack, 1947</td>
</tr>
<tr>
<td><em>Lanius collurio</em></td>
<td>Lack, 1947</td>
</tr>
</tbody>
</table>
Table 12 (Continued).

Species in which fledging success declines among late nesters.

<table>
<thead>
<tr>
<th>Species</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Agelaius phoeniceus</em></td>
<td>Dolbeer, 1976</td>
</tr>
<tr>
<td><em>Thalasseus sandvicencis</em></td>
<td>Langham, 1975</td>
</tr>
<tr>
<td><em>Riparia riparia</em></td>
<td>Emlen and Demong, 1975</td>
</tr>
<tr>
<td><em>Rissa tridactyla</em></td>
<td>Perrins, 1970</td>
</tr>
<tr>
<td><em>Parus major</em></td>
<td>Perrins, 1965; 1970</td>
</tr>
<tr>
<td><em>Haematopus ostralegus</em></td>
<td>Perrins, 1970; Harris, 1967</td>
</tr>
<tr>
<td><em>Ficedula hypoleuca</em></td>
<td>Perrins, 1970</td>
</tr>
<tr>
<td><em>Accipiter nisus</em></td>
<td>Newton, 1976</td>
</tr>
<tr>
<td><em>Larus argentatus</em></td>
<td>Parsons, 1975; Parsons, et al., 1976; Nesbit and Drury, 1972</td>
</tr>
<tr>
<td><em>Stercorarius parasiticus</em></td>
<td>O'Donald, 1977</td>
</tr>
<tr>
<td><em>Sula capensis</em></td>
<td>Jarvis, 1974</td>
</tr>
<tr>
<td><em>Anser anser</em></td>
<td>Newton and Kerbes, 1974</td>
</tr>
<tr>
<td><em>Puffinus puffinus</em></td>
<td>Perrins, 1966</td>
</tr>
</tbody>
</table>
Male Territoriality

UNIFORM

PATCHY

Environmental Resource Distribution

UNIFORM

PATCHY

Figure 1. Some possible interactions between environmental resource distributions and male territoriality. Resource quality is illustrated by the intensity of shading. Male territories are illustrated by the rectangular patches within each example. Whether resources in the environment are distributed in a uniform or patchy manner, male territoriality may result in resource redistribution.
Figure 2. The proportions of female sculpins mating with bachelor males and of tiles occupied by bachelor males in Anderson Creek during the 1976 spawning season. 95 percent confidence limits for each sample proportion are given (Dixon and Massey, 1969), along with the sample size. Spawnings with bachelors occurred significantly less often than expected on the basis of chance encounters ($X^2$ test, $P < .05$) on all dates except those noted as insignificant (NS) and those for which small sample sizes prohibited testing (NT). The shaded area reflects the intensity of spawning during the breeding season.
Figure 3. Size distributions of the total population and breeding population of male sculpins residing beneath sample tiles in Anderson Creek during the 1976 spawning season. On each sample date, the larger, unshaded curve represents the frequency distribution of total lengths for the entire population of males, while the smaller shaded curve includes only those males that had mated at least once. Sample sizes for the entire population are given in parentheses for each date. Mean lengths for both populations are represented by a dashed line.
Figure 3:
Figure 4. Mean lengths of male sculpins breeding with 0-5+ females in Anderson Creek during the 1976 spawning season. Each point represents the mean size of males remaining unmated or of males mating with their first through fifth females during a particular sample interval. Mean sizes for males mating with equivalent numbers of females are joined by diagonal lines, and mean values insignificantly different from each other on any sample date are joined by vertical bars (Student-Newman-Keuls Test, P = .05). Sample sizes are given for each point. A + adjacent to a mean value indicates that males breeding with more than the given number of females were included in that particular mean.
Figure 5. Mean sizes of gravid and spawned females throughout the 1976 breeding season. Means are bounded by two standard errors and sample sizes are adjacent to each mean. The shaded curve refers to the intensity of spawning observed on each sample date. Equivalent patterns were observed in 1975 and 1977.
Figure 6. Mean sizes of males captured beneath the experimental tiles in Anderson Creek during the 1975, 1976 and 1977 breeding seasons. Tile sizes and designations are as in Table 4. Sample sizes are adjacent to each mean. Means insignificantly different from each other are joined by a common vertical bar (Student-Newman-Keuls Test, $P = .05$). The shaded curves refer to the intensity of spawning observed on each sample date during each breeding period.
Figure 6.
Figure 6 (Continued).
Figure 6 (Continued).
Figure 7. Male size and courtship success in 1975 (tile designations: S, M, L), and 1976 (tile designations: U, V, W, X, Y, Z), the two years in which multiple tile sizes were used. Sample sizes are given as subscripts for each tile designation and means are bounded by two standard errors. (Figure 3 of Downhower and Brown, 1978a).
Figure 8. The general schema by which successive males and/or spawning sites were compared by the various models. Each rectangular box represents possible model choice criteria. Thus the illustrated model, MALE SIZE, assigned spawnings solely on the basis of male size. Other models can be illustrated by substituting the criteria 'tile size', 'tile size and male size', 'tile size or male size' for 'male size'. The model RANDOM always assigned spawnings to the second successive male. The distributions of tile sizes, male sizes, and nearest neighbor tile sizes used for each model run were those observed in the field on the date corresponding to that run. A more detailed explanation of the model is provided in the appendix.
Figure 9. The cumulative number of significant differences ($X^2$, $P < .05$) between the distributions of spawnings per male observed in the field and those generated by each of the five models. The number of tests involved is given with the name of each model. Models are described in the text and appendix. Model distributions did not always include enough spawnings to allow comparison to observed patterns, hence the differences in comparison sample sizes. The shaded area reflects the intensity of spawning during the breeding season.
Figure 10. Comparisons of observed frequencies of spawnings per male for each of the six tile sizes with those generated by the model MALE SIZE for 4/10/76. Tile sizes are ranked alphabetically from smallest to largest and tile designations are as in Table 4. The mean numbers of spawnings per male are given as subscripts for each tile size.
Figure 10.
Figure 11. Frequencies and patterns of oviposition (additions) and egg mass mortality (losses) observed in the Anderson Creek study site during the 1976 breeding season. Late in the season losses were far more frequent than additions. Furthermore, the frequency distribution of losses per interval was significantly different from that of ovipositions per interval.
Figure 12. Mean lengths of males mated with 0-5+ females, as predicted by the model based solely on male size. Mean sizes of males with equivalent courtship successes are joined by diagonal lines and the courtship success of each class of males is given to the right of each curve. A + adjacent to a mean value indicates that males breeding with more than the given number of females were included in that sample point.
Figure 13. Properties of single threshold, multiple threshold, and relative female choice mechanisms. See text for details.
Figure 14. Frequency histograms of total length for all breeding sculpins captured in Anderson Creek during the 1975, 1976 and 1977 spawning seasons. Females are represented by the shaded curves, males by the unshaded curves. Means and sample sizes for each distribution are given.
Figure 14.
Figure 15. Mean male length as a function of the maximum number of spawnings obtained by a male occupying Anderson Creek during each of the three years of this study. Sample sizes are adjacent to each mean.
Figure 16. The probability that at least part of an egg mass survived to hatching as a function of guardian male size during the 1976 spawning season in Anderson Creek.

\[ Y = -0.36 + 0.01X \]  
\[ r = 0.91^* \]
Figure 17. Mean sizes of nesting males in Anderson Creek during the 1975, 1976, and 1977 spawning seasons. Sample sizes are given and means are bounded by one standard error. Shaded curves refer to the intensity of spawning, guarding and hatching of egg masses. Percent spawning refers to the total number of spawnings observed. Percent hatching and guarding refer to the number of nests at which these activities were observed on each date.
Figure 17.
Figure 17 (Continued).
Figure 17 (Continued).
Figure 18. Frequency distributions of egg masses per male for natural nests and experimental tiles in the Anderson Creek study site during the 1975, 1976 and 1977 breeding seasons. Sample sizes (N) and mean number of egg masses per male (X) are given for natural nests (subscript n) and experimental tiles (subscript e) in each year.
Figure 19. Hatching success, egg mass position and oviposition date. Curve A (open circles) represents the proportion of egg masses that successfully hatched during the 1976 spawning season as a function of the date of oviposition. Curve B (solid circles) represents the proportion of egg masses that remained solitary or were the last in a series as a function of oviposition date.
Figure 20. The probability that at least part of an egg mass survived to hatching as a function of the number of egg masses present on the nest. Solid circles represent observed probabilities. Open squares represent those expected from differences in the hatching successes of solitary, first, middle and last egg masses (see Table 10 and text). The number of egg masses associated with each point is given and observed proportions are bounded by 95 percent confidence limits. Nests containing 6-10 egg masses are pooled and plotted as though they contained seven masses, the median and modal size for this combined group.
Figure 21. The relationships between the number of sites a female must visit before locating and returning to the best of all possible mates and the number of suitors in a population. Line A was generated under the assumption that females sample males randomly with replacement and are 95 percent confident that they have visited all available males before picking their mate. Thus:

\[(1-.95) = (1 - \frac{1}{\text{males available}})^{\text{sites visited}}\]

Line B was generated under the assumption that females sample each male only once. Both lines assume that females possess total recall of male qualities and that all visited breeding sites are occupied by mature males.
Figure 22. The benefits (solid lines) and costs (dashed lines) of female selectivity for two types of relative choice mechanisms. Benefits are given in terms of the probability that the male selected as a mate will be larger than or equal to the average sized male in the population. Costs are given in terms of the number of breeding sites that must be visited by a female before choosing a mate. Costs and benefits for each degree of female selectivity were determined empirically by computer simulation using the known distributions of spawning sites and associated males in the Anderson Creek study site on April 10, 1976 and based on the assumption that females move among nearest neighboring nest sites when searching for a mate (see text). In the first set of models, the degree of female selectivity was determined by the number of sequentially larger males compared by a female. Thus a female might have mated with the first male encountered (males compared = 1). By extension, she might have mated with a male only if he were larger than or equal to the last male that she had encountered, i.e., his nearest neighbor (males compared = 2), or if he were larger than or equal to the last male who was in turn larger than or equal to his nearest neighbor (males compared = 3). In the second set of models, females mated with a male only if he were larger than his predecessor by some fixed amount (0, 1, 2, 5 or 10 mm).
Figure 22.
Figure 23. Cumulative capture probabilities for small (< 70 mm), medium (70-74 mm), and large (> 74 mm) females during the 1976 spawning season in Anderson Creek.
APPENDIX

The program used to simulate spawnings was written in Fortran and was composed of 407 statement cards. Random numbers were generated using the UNI subroutine of the pseudo-random number package "Super-Duper" (McGill University School of Computer Science). The program was run on an IBM 370/168, with funds provided by the Instruction and Research Computer Center, The Ohio State University. Crucial steps are outlined in Figure 24. Each of the five models was derived by substituting one of the possible comparison statements for the black-box labeled "Compare." The distributions of tiles and experimental breeding sites used in all simulations were those observed in the Anderson Creek study site during the 1976 breeding season.
Figure 24. Flow chart of simulated female choice routines.
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