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An Examination of the Ecological Correlates and Evolution of Polygyny in Marsh Wrens in Delta, British Columbia

by

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Abstract

In this study, I examined the occurrence of polygyny in marsh wrens (*Cistothorus palustris)* in Delta, B.C. Using four field seasons of data, I found in this population that males were moderately (19%) to highly (66%) polygynous, that in three years of the study (1979, 1992, 1993) polygynous males fledged more young than did monogamous males, and that the breeding sex ratio was female biased in three out of the four years of the study (1979, 1982, 1993).

In order to examine if the observed male reproductive success was an accurate measure of male fecundity, I used DNA fingerprinting to assess paternity and therefore male realized reproductive success for the 1992 and 1993 breeding seasons.

In In order to ascertain the importance of predation of breeding nests on female choice of a breeding situation and male and female reproductive success, I compared predation rates on polygynous and monogamous nests.

In order to test all of the possible reasons for polygyny occurring simultaneously I used a multi-modeled approach. I found that the skewed sex ratio model explained the occurrence of polygyny in 1979, 1982, and 1993. Additionally in 1979, 1982, and 1992, the polygyny threshold model also explained polygyny in the Delta population. In 1993, I found that the random settlement model was also supported by the results of this study. Overall in this population of marsh wrens the largest factors affecting the occurrence of polygyny was the skewed sex ratio of the breeding population in favor of females. Secondly, determination of which males became polygynous was most likely affected by female choice of a breeding situation, with females apparently preferring males whose territories were further from the upland edge of the marsh.

Keywords: polygyny, DNA fingerprinting, evolution, extra-pair fertilizations, intraspecific brood parasitism, predation, polygyny models, mating system, marsh wrens, *Cistothorus palustris*

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General Introduction

Among sexually reproducing species, a number of mating systems have evolved including monogamy, polygyny, polyandry and promiscuity. In avian species, polygyny is a rare mating system in which one male maintains pair bonds simultaneously with several females. Overall, polygyny has been found to occur regularly in about 5% of avian species (Verner 1964, Verner and Willson 1966, Lack 1968). Possible explanations as to why such a rare mating system may have evolved have included both the possible benefits for males and the possible benefits and/or costs to females. In sexually reproducing species, males mating polygynously may benefit by an increased reproductive success (Lightbody and Weatherhead 1987). For females, the benefits of mating polygynously may include access to territory resources (e.g., nest sites, food), cooperative nest defense, and/or male parental care. The costs which females may incur as a result of mating polygynously may include reduced parental contribution from a male and/or increased competition due to sharing of territory resources with other females. The generally accepted theory for the evolution of polygyny is that polygyny has evolved as the result of the benefits outweighing the costs (in a given breeding situation) for females mating polygynously (Verner 1964, Orians 1969).

One explanation as to why females mate polygynously may be explained by the parental investment theory. According to the parental investment theory, the initial parental investment through gamete production is larger for females than males. Therefore, it follows that females should be the choosier sex in order to protect their greater investment (Trivers 1972). The polygyny threshold model represents perhaps the most influential theory which has been proposed to explain why females should mate polygynously. The polygyny threshold model assumes that polygyny may occur in a population when females choose to mate with an already mated male despite the fact that there are unmated males available in the same population. This choice may be made in order to increase the females' reproductive success through access to better resources, such as male parental care, high quality males or territories (Verner 1964, Orians 1969, Altmann et al. 1977). When choosing a mate, females may be assessing factors such as fitness of the male, his ability to protect the female and nestlings, the quality of food resources, and/or the availability of high quality nest sites on the territory. It has been proposed that female reproductive success may be affected by these male and territory qualities if highly fit males (i.e., larger, heavier males) sired highly fit offspring (Searcy and Yasukawa 1983). For example, territorial features, such as the degree of emergent vegetation as well as territory size, have been found to be related to male pairing success. In these cases, polygynous males were found to have larger territories and territories with higher degrees of emergent vegetation (Welter 1935, Verner 1965, Leonard and Picman 1988).

However, Searcy and Yasukawa (1989) suggested that polygyny may also occur in the absence of female choice. In this situation, females may be forced to mate with already mated males. This situation may arise due to limited breeding opportunities resulting from few nest sites, a short breeding season or life span, or a skewed sex ratio in favor of females (Skutch 1935, Verner 1964, Emlen and Oring 1977).

The occurrence of polygyny may also be affected by ecological factors such as the clumped distribution of resources, such as nest sites or food, which are important to females for breeding and which the male can defend (Emlen and Oring 1977). The quality of territories may be greatly affected by the pattern of distribution of resources (e.g., mates, food, and nest sites). This may in turn affect the frequency of occurrence and the degree of polygyny in a population (Emlen and Oring 1977). The likelihood that polygyny will occur may be higher when such resources are economically defendable and unevenly distributed, over space or time, since some individuals will be able to obtain and defend more of these resources than others (Emlen and Oring 1977). Therefore, habitat type may greatly influence the type of mating system observed, as seen in the prevalence of polygyny in passerines nesting in marshes, where food is highly abundant and heterogeneously distributed (Verner 1964, Greenlaw 1989).

Reproductive success in avian species may be greatly affected by factors such as predation, starvation, abandonment, infertility, and severe weather (Ricklefs 1969). Among North American passerines, marsh-nesters have been found to suffer the highest rates of nesting failure, mostly due to predation of nestlings (Ricklefs 1969). These high mortality rates have been observed in several studies of red-winged blackbirds (Orians 1980, Holm 1973, Robertson 1972, Weatherhead and Robertson 1977, Searcy 1979). As well, in several studies predation has been found to be an important factor affecting the ability of several marsh-nesting passerines to reproduce and survive. These marsh-nesting species include the marsh wren, *Cistothorus palustris*, (e.g., Kale 1965), yellow-headed blackbird, *Xanthocephalus xanthocephalus* (e.g., Willson 1966), and red-winged blackbird, *Agelaius phoeniceus* (e.g., Robertson 1972).

Several researchers have proposed a number of explanations for the evolution of polygyny in territorial birds, in the form of theoretical models (for review, see Searcy and Yasukawa 1989). These models include: unbalanced (skewed) sex ratio hypothesis (see Skutch 1935); polygyny threshold model, PTM (Verner 1964, Orians 1969); cooperative female choice model (Altmann et al. 1977); female deception (polyterritoriality) model (Alatalo et al. 1981); neutral mate choice model (Lightbody and Weatherhead 1988); random settlement model (Lightbody and Weatherhead 1988) ; sexy son hypothesis (Weatherhead and Robertson 1979); and asynchronous-settlement model (Leonard 1990).

A hierarchy of the theoretical polygyny models based on their assumptions has been proposed by Searcy and Yasukawa (1989), as a way in which all of the models could be tested simultaneously. By testing between the alternative hypotheses using this approach, it may be possible to determine which hypothesis (-es) best explains the occurrence of polygyny in a given species (Searcy and Yasukawa 1989). To date few polygynous passerine species have been studied using the Searcy and Yasukawa's (1989) approach for testing between all of the polygyny models (see Johnson et al. 1993).

In order to examine why polygyny occurs, it is essential that reproductive success of males be examined. In recent years male reproductive success has been examined more closely with the use of DNA fingerprinting. A number of studies using DNA fingerprinting have discovered that matings outside the social pair, resulting in extra-pair fertilizations, are occurring in a wide variety of passerine species (Westneat et al. 1990, Burke et al. 1991, Hartley et al. 1993). As a result of the prevalence of extra-pair matings in many passerines, analyses of reproductive success using DNA fingerprinting is needed to accurately determine male reproductive success and female choice of a breeding partner. Individual reproductive success, traditional measures of reproductive success, and/or parental investment by the male may be strongly affected by the occurrence of extra-pair fertilizations (Trivers 1972, Mock 1983, Gowaty 1985, Birkhead et al. 1990, Gibbs et al. 1990). The proportion of extra-pair matings which result in extra-pair fertilizations may, in turn, be affected by the female's ability to retain sperm after mating. Among avian species, the length of time sperm is stored in female's sperm storage tubules has been found to vary, between 6 and 17 days (see Birkhead et al. 1989, for review). The number of extra-pair young resulting from an extra-pair mating were affected in one study of the zebra finch when a female mated with her social partner shortly after an extra-pair copulation occurred. In this study, the percent of zebra finch young sired by the extra-pair male was greatly reduced (Birkhead et al. 1989).

In this study I examined factors which may have led to the occurrence of polygyny in a population of marsh wrens in Delta, British Columbia, Canada. Marsh wrens, are a small, monomorphic species, which breed in freshwater and tidal marshes throughout North America (Welter 1935, Bent 1948, Verner 1965). Adult marsh wrens have a short life span of approximately two years and usually breed for only one season as a result of the high over winter mortality (Welter 1935, Kale 1965, Verner and Engelsen 1970, Leonard 1986). Males of this species are highly territorial and have been known to have up to four mates simultaneously, although harems of two are most common (Welter 1935, Verner 1965, Leonard 1986). Despite the large number of young sired by a male marsh wren within a breeding season, males in different populations of marsh wrens have been found to provide little or no parental care of their young (Leonard and Picman 1988, Leonard 1990). This reduced male parental care in marsh wrens may not strongly impact the number of young which are able to fledge, contrary to the situation in other species, since food resources are highly abundant on males' territories where female marsh wrens primarily forage (Verner 1965, Leonard and Picman 1988). Marsh wrens have been observed to feed on a variety of marsh invertebrates such as dipterans, coleopterans, hymenopterans, homopterans, and arachnids (Welter 1935, Bent 1948, Leonard 1986).

Multiple nest building has been observed in several avian species (Lack 1935, Welter 1935, Collias and Victoria 1978). Within the family Troglodytidae a number of species have been found to build multiple nests. These include house wrens (*Troglodytes aedon*; Kendeigh 1941), winter wrens (*Troglodytes troglodytes*; Armstrong 1955; Garson 1980), sedge wrens (*Cistrothorus platensis*; Bent 1948; Crawford 1977) and marsh wrens (Welter 1935; Bent 1948; Kale 1965; Berner 1965).

Several theories have been proposed to explain this phenomenon in marsh wrens. It has been proposed that the large number of nests built by males may be used to (1) attract females, (2) as roosts for adults or fledglings, (3) as an indicator of a male's vigor, or (4) to confuse predators (Schufeldt 1926, Welter 1935, Verner 1965, Verner and Engelsen 1970, Metz 1991).

Male marsh wrens defend territories in which they build multiple domed nests, attract mates, breed, and forage. Throughout the breeding season, male marsh wrens build nests in concentrated areas called courtship centres. Upon her settlement, a female lines one of the complete nests (Welter 1935, Verner 1965, Kale 1965). A courtship centre, by definition, is the area which includes courting nests in a male's territory where he sings and displays (Welter 1935). Soon after the first female lays a clutch and is incubating, the male leaves the courtship area and builds new nests in a second courtship centre in an attempt to attract a second mate (Picman and Belles-Isles 1987). Nests of marsh wrens are closed, domed structures measuring approximately 15 cm high and 10 cm wide, with a small, well concealed opening near the top (Welter 1935, Verner 1965). These nests are most often built in moderately dense cattail stands and occasionally also in bulrushes. The outside shell of the nest is constructed with wet, interlaced strips of dead cattail leaves taken from the floor of the marsh. White down taken from cattail heads is incorporated in to the outer shell (Verner 1965).

The breeding biology of marsh wrens has been investigated previously by Welter (1935), Verner (1964), Kale (1965), and Leonard and Picman (1988) using traditional observational techniques. The degree of polygyny in marsh wrens has been found to vary greatly among populations: 2.4 % in Georgia salt marshes (Kale 1965), 12.5% in Washington State (Verner 1965), and 44 % in Delta, Manitoba (Leonard 1986). Predation rates of breeding nests have also been found to vary greatly among populations of marsh wrens: 18.5 % (Verner 1965) in Washington State, 40.2% (Leonard and Picman 1987) in Delta, Manitoba, and between 58.4% and 93.2% during a four year study (Kale 1965) in Georgia.

The structure of the mating system in marsh wrens has been previously examined by several authors (Verner 1964, Kale 1965, Verner 1965, Leonard 1990), with varying conclusions as to which model explains why polygyny has evolved in this species (Verner 1964, Leonard 1990). As a result of the body of information previously collected on marsh wrens in conjunction with the inclusive state of previous work regarding polygyny models, marsh wrens are an excellent species for this type of study (Searcy and Yasukawa 1989). In one of the earliest marsh wren mating system studies, Verner (1964) found that the variation between already mated (polygynous) and unmated (monogamous) males in the levels of emergent vegetation on their territories was large enough that females who mated with already mated males had higher reproductive success at the end of the breeding season than females who mated with previously unmated males. These findings led to the development of the polygyny threshold model (Verner 1964). In a subsequent study of the marsh wren mating system, Leonard (1990) found that polygyny occurred not as the result of the polygyny threshold model explanation, but rather as the result of the high degree of asynchronous settlement between marsh wren females. The asynchronous settlement model was then developed from these findings (Leonard 1990).

The goals of this study were: (1) to determine the realized reproductive success of males by determining paternity of nestlings; (2) to examine the mating structure of the breeding population in order to determine if polygyny is beneficial for both male and female marsh wrens; (3) to evaluate factors which should affect mating choices, such as predation, male traits and territory characteristics; and (4) to determine the factors which have led to the occurrence of polygyny in marsh wrens by simultaneously testing eight of the currently held polygyny models. These goals are examined in the following four chapters. In Chapter 1 (DNA Fingerprinting in Marsh Wrens: alternative reproductive strategies examined) I determined paternity of nestlings. In Chapter 2 (Breeding Ecology of Marsh Wrens: is polygyny beneficial for individuals of both sexes?) I determined males' realized reproductive success, examined the structure of the breeding population, and determined if polygyny was beneficial to males and females. In Chapter 3 (Importance of Predation in a Marsh Wren Population in Delta, British Columbia) I examined predation rates and the effect of predation on mate choice. Finally, in Chapter 4 (Polygyny in Marsh Wrens: Tests of Alternative Evolutionary Models) I examined factors affecting mate and territory choice and their role in the occurrence of polygyny in this population. In this Chapter, I also evaluated the key assumptions and predictions of eight polygyny models to establish which model(s) offers the most plausible explanation for the occurrence of polygyny in a Delta, B.C. population of marsh wrens.

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Chapter 1:

DNA Fingerprinting in Marsh Wrens: alternative reproductive strategies examined

Abstract

DNA fingerprinting was used to assess paternity of 110 nestling (32 broods) marsh wrens (*Cistothorus palustris*) from Delta, British Columbia, Canada. The proportion of young fathered through extra-pair fertilizations was high. Over the two years of the study (1992 and 1993), 15 % of the nestlings tested were extra-pair young. These young were found in 12 (38 %) of the broods tested. In both years, extra-pair young occurred most often in nests of polygynous males (76% of extra-pair young). In 1992, monogamous males fathered all (N=9) of the extra-pair young. Of these fertilizations, 78% (7/9) were assigned to males which were not the nearest neighbors of the cuckolded male. In 1993, polygynous males fathered all (N=7) of the extra-pair young and the nearest neighbors of the cuckolded males sired 86% (6/7) of the extra-pair young. DNA analysis also revealed three cases of intraspecific brood parasitism in two broods of marsh wrens (29% of broods tested), one in each year of the study. In this population of marsh wrens, extra-pair fertilizations appear to play an important role in marsh wrens' alternative reproductive strategies and may have important consequences for the reproductive success of some individuals. The extent of these mixed strategies may confound earlier theories on the structure of the marsh wrens' mating system as well as traditional measures of reproductive success.

Key words: DNA fingerprinting, polygyny, evolution, mixed reproductive strategy, extra-pair fertilizations, intraspecific brood parasitism, marsh wrens, *Cistothorus palustris*.

Résumé

La technique de empreintes génétiques fingerprinting a été utilisée afin de déterminer la paternité de 110 oisillons troglodytes des marécages (*Cistothorus palustris*) nichant dans un marécage de Delta, en Colombie Britannique, Canada. Le nombre de jeunes produits suite à une fertilisation extra-paire était élevée. Pendant les deux années d'étude (1992 et 1993), 15% des oisillons testés étaient des jeunes extra-paires. Ces jeunes ont été retrouvés dans 12 (38%) des nichées vérifiées. Pour les deux années, les jeunes extra-paires ont été trouvés plus fréquemment (76%) dans les nids de mâles polygynes. En 1992, les mâles monogames ont engendré tous les jeunes extra-paires (N=9). De ces fertilisations, 78% (7/9) ont été assignées à des mâles n'étant pas parmi les proches voisins des mâles cocus. En 1993, les mâles polygynes ont produit tous les jeunes extra-paires (N=7). En 1993, les proches voisins des mâles cocus ont produit 86% (6/7) des jeunes extra-paires. L'analyse d'ADN a également révélé trois cas de parasitisme intraspécifique dans deux nichées de troglodytes des marécages (29% des nichées testées) (une nichée par année d'étude). Dans cette population de troglodytes des marécages, les fertilisations extra-paires semblent jouer un rôle important au niveau des stratégies alternatives de reproduction. Ceci peut peut avoir des conséquences importantes sur le succès reproducteur chez certains individus. L'ampleur de ces stratégies mixtes peut confondre les théories concernant la structure du système de reproduction chez les troglodytes des marais ainsi que les mesures traditionnelles du succès reproducteur.

Introduction

With the advent of molecular tools, such as DNA fingerprinting, several studies have found that nestlings in a number of species are not always the genetic offspring of one or both of their social parents (Westneat 1990). Excluded (not genetically related) nestlings in a male's nest have been found to have a strong impact on the understanding of avian mating systems (Westneat 1987 a, b , Birkhead et al. 1990, Gibbs et al. 1990, Morton et al. 1990, Rabenold et al. 1990, Smith et al. 1991), and may strongly influence individual reproductive success, traditional measures of reproductive success, and/or parental investment by the male (Trivers 1972, Mock 1983, Gowaty 1985, Birkhead et al. 1990, Gibbs et al. 1990). These excluded nestlings may have resulted from extra-pair copulations resulting in extra-pair fertilizations (EPFs), egg-dumping (intraspecific brood parasitism, IBP) (Yom-Tov 1980, Andersson 1984, Birkhead et al. 1987, MacWhirter 1989, Rohwer and Freeman 1989, Westneat et al 1990), or rapid-mate switching (Moller 1985, Quinn et al. 1987).

Extra-pair copulations and intraspecific brood parasitism, as breeding strategies in avian species, are considered an important component of a bird's mixed reproductive strategy (Yom-Tov 1980, Birkhead et al. 1987, MacWhirter 1989). A mixed reproductive strategy, as defined by Trivers (1972), is a strategy in which an individual optimizes its potential reproductive success through both siring or mothering young and raising young in its own nest(s) as well as by siring young or dumping eggs in other individuals' nests. Therefore, a mixed reproductive strategy, including extra-pair fertilizations and intraspecific brood parasitism, which would allow individuals to produce as many young as possible in the limited time available should be favored by natural selection. The occurrence of mixed strategies in avian species has been well documented (see Birkhead 1987, Westneat et al. 1990, Birkhead and Moller 1992, for reviews). Extra-pair fertilizations have been found to occur in a wide variety of polygynous species, with the extent of extra-pair matings varying considerably among polygynous passerines (Westneat et al. 1990, Burke et al. 1991, Hartley et al. 1993). In two red-winged blackbird (*Agelaius phoeniceus*) studies, 28% and 24% of young were found to be excluded young, resulting from extra-pair fertilizations (Gibbs et al. 1990, Westneat 1993, respectively). Extra-pair fertilizations appear less common in two other polygynous species; in the bobolink (*Dolichonyx oryzivorus*), 14.6% of young were extra-pair young (Bollinger and Gavin 1991), and in the pied flycatcher (*Ficedula hypoleuca*), only 4% of young resulted from extra-pair fertilizations (Lifjeld et al. 1991). Extra-pair copulations have also been observed in some South and North American wren species, including the stripe-backed wren (10% of young were extra-pair young) (*Campylorhynchus nuchalis*; Rabenold et al. 1990), winter wren (*Troglodytes troglodytes* ; Armstrong 1955), and house wren (*Troglodytes aedon*; Johnson and Kermott 1989).

Inter- and intra-specific brood parasitism are relatively rare reproductive strategies which have been documented in less than 2% of the approximately 8600 avian species (Hamilton and Orians 1965, Payne 1977, Yom-Tov 1980). Intraspecific brood parasitism occurs when a female from outside of a male's territory lays an egg in another female's nest of the same species (Yom-Tov 1980, Gowaty 1985). Intraspecific brood parasitism may occur when a neighboring female's nest has been depredated or destroyed at a time when the female is about to lay her next egg or when a female mates but does not have a nest. As an alternative reproductive strategy, intraspecific brood parasitism may be an important component of a females reproductive success. This behaviour may be an attempt by females to increase their reproductive success if they are unable to care for their own eggs rather than discarding the eggs or laying them in an incomplete, unlined nest (Yom-Tov 1980, Picman and Belles-Isles 1988, Price et al. 1989). Although intraspecific brood parasitism is believed to occur rarely in most passerines, it has been found to occur in over 100 avian species (Yom-Tov 1980, MacWhirter 1989, Rohwer and Freeman 1989). The degree of intraspecific brood parasitism has been found to vary greatly in monogamous species. In the zebra finch (*Taeniopygia guttata*),10.9% of chicks in 36% of broods tested were the result of intraspecific brood parasitism (Birkhead et al. 1990), whereas in the Eastern Bluebirds (*Sialia sialis*) only 2.4 % of nestlings in 9.5% of broods tested were the result of intraspecific brood parasitism (Meek et al. 1994). In polygynous species, several studies have found either no instances (Gyllensten et al. 1990, Gibbs et al. 1990, Lifjeld et al. 1991) or only a very few cases of intraspecific brood parasitism in their study populations (Price et al. 1989). For example, in house wrens (*Troglodytes aedon*) only 2.1% of chicks in 5.6% of broods tested resulted from intraspecific brood parasitism (Price et al. 1989).

The benefits of pursuing extra-pair copulations for a male are straightforward. The male is attempting to increase his reproductive success through siring additional young while, at the same time, avoiding costs such as increased parental care of these additional young (Westneat et al. 1990). There may also be inherent costs for males seeking extra-pair matings, especially for polygynous males. As a result of polygynous males dividing their time between their primary female and seeking additional mates, polygynous males may be less efficient at guarding their mates, especially their primary females, during their fertile period (mate guarding hypothesis; Beecher and Beecher 1979, Birkhead 1979). This may, in turn, lead to an increased risk of cuckoldry (Arak 1984, Alatalo et al. 1987) for polygynous males as the result of a trade-off between acquiring more than one mate (being polygynous) (Alatalo et al. 1987, Birkhead et al. 1987) and/or pursuing extra-pair copulations themselves while at the same time guarding their mates against extra-pair copulations (Arak 1984, Alatalo et al. 1987, Westneat et al. 1990, Hasselquist and Bensch 1991). Some polygynous males may do quite well with this trade-off, while other males may suffer a loss of reproductive success (Gibbs et al. 1990). The possibility of increasing one's reproductive success despite the demands of being polygynous in at least some individuals may have allowed this mixed strategy to evolve.

Male marsh wrens (*Cistothorus palustris*) are known to provide little or no parental care (Verner 1965, Leonard 1986). As a result, males should have opportunities to pursue extra-pair matings since they are devoting little or no time to feeding their young. Consequently, extra-pair fertilizations may be an important component of a male marsh wren's reproductive success (Gibbs et al. 1990). For males, an individual's observed reproductive success (number of young fledged on a male's territory) may differ greatly from their realized reproductive success (fledglings fathered by the male on his territory plus on other male's territories) (Gibbs et al. 1990). The extent of extra-pair fertilizations in a population is measured by the percent of nestlings which result from extra-pair fertilizations and the percent of broods which contain at least one extra-pair young.

A female may participate in extra-pair fertilizations for several reasons. It has been suggested that in a polygynous mating system where female choice is based on territory quality (Verner 1964), a female may participate in extra-pair fertilizations as a way of choosing a higher quality male while nesting on a high quality territory (Birkhead and Moller 1992). During the breeding season a female may be making two separate decisions, that is, separately choosing which male to nest with (social partner) and choosing which male to mate with (genetic partner) (Westneat et al. 1990). Females may benefit from a mixed reproductive strategy by gaining "good" genes for their young (Moller 1988, Smith 1988, Kempenaers et al. 1992), by increasing the genetic diversity (Westneat et al. 1990) of their offspring, or by insuring the fertility of their eggs (Gibson and Jewel 1982). However, females participating in extra-pair matings may also suffer costs such as reduced parental care (Westneat et al. 1990, Birkhead and Moller 1992).

The goals of this study were to determine: (1) the frequency of occurrence of extra-pair fertilizations and intraspecific brood parasitism in a population of marsh wrens through DNA fingerprinting; (2) how mixed reproductive strategies affect the realized reproductive success of males in the population; and (3) why monogamous and polygynous individuals participate in extra-pair copulations and intraspecific brood parasitism. I also examined the possible benefits and costs to males and females as a result of their participation in these reproductive behaviours.

Methods

Study Area and Field Work

I conducted field work at the George C. Reifel Migratory Bird Sanctuary in Delta, British Columbia between April and July of 1992 and 1993. Additionally, data were collected at this field site in 1979 and 1982 by Dr. J. Picman (unpublished data). I have analyzed these two additional years of data and included them in this study. The DNA fingerprinting portion of this study only involved the 1992 and 1993 years of data. The study site consisted of a 600 x 200 m area of an extensive, homogeneous tidal marsh. Cattail (*Typha latifolia*) dominated the marsh early in the season. Bulrush (*Scirpus* sp.) and sedge (*Carex* sp.) become more prevalent late in the summer in the wetter areas which are farthest from the upland edge of the marsh (Picman 1977). Details of the field work can be found elsewhere (Chapter 2).

Within the first month of the breeding season, I attempted to capture and band all adults in the population. My efforts concentrated on those individuals which were mated. I captured adult marsh wrens with mist nets set up near a breeding nest on the male's territory. Upon capture, I individually color marked males and females with a unique combination of color bands, attached a numbered metal band, weighed them (to the nearest tenth of a gram) , measured their wing length (to the nearest millimeter), and took a blood sample. Unfortunately, I was unable to capture some of the males (29/68, 42.6%) in the population. The majority of these males were unsuccessful in fledging their young or in some cases (five males) in acquiring mates. I was also unable to capture the majority of females, as they became less active in the territory once nesting commenced. I removed the ten-day old nestlings from their nests prior to their primary feathers coming out of pin (day 10-12 post-hatching), then banded, weighed, and took a blood sample from each nestling, then returned them to their nests. Nestlings were taken from their nests to be banded prior to their primary feathers coming fully out of pin, in order to avoid their premature fledging (Welter 1935).

The small blood samples, taken from the brachial vein of the wing, were used for DNA fingerprinting analysis (Hoysak and Weatherhead 1991). To obtain the blood samples, I made a small puncture in the vein using a 26 gauge needle. I collected approximately 50 microlitres of blood from each individual, according to guidelines from the American Ornithologists' Union (1988). The collected blood was then placed in 1 ml of prepared "Queen's" lysis buffer (10 mM Tris, 10 mM NaCl, 10 mM sodium-EDTA, 1% n-lauroylsarcosine) (Seutin et al. 1991). Samples were stored at room temperature for several months then placed at 4°C until needed for analysis. I carried out the DNA fingerprinting analysis in the laboratory of M. P. Sabour, at the Centre for Food and Animal Research, Central Experimental Farm, Agriculture Canada, Ottawa, Ontario.

DNA Analysis

In this study, I modified the following methods for DNA fingerprinting from those commonly used for other avian species (Burke and Bruford 1987, Birkhead et al. 1990, Gibbs et al. 1990, Seutin et al. 1991). I extracted the DNA from the marsh wren's nucleated red blood cells. With the Hae III restriction enzyme, I digested 20 micrograms (20 µg) of the DNA. I then ran 8 micrograms (8 µg) of the digested DNA on a 20 cm 1%

agarose gel at 4.5 V/cm for 20 hours in recirculated and cooled TAE (10 mM Tris, 100 mM NaCl, 100 mM EDTA, pH 8.0) buffer. Next I transferred the DNA to Hybond N+ nylon membranes (Amersham) via Southern transfer (Sambrook et al. 1989). Preparation of probes from plasmids followed procedures in Sambrook et al. (1989).

Three probes, Jeffrey's 33.15, Jeffrey's 33.6 (Jeffreys et al. 1985a), and Per (Shin et al. 1985) labeled with [α- ^{32}P] dCTP, via random priming, were tested to determine which provided the optimum hybridization patterns. Jeffrey's 33.15 produced a banding pattern most conducive to analysis. All results reported here are from Jeffreys 33.15 probe. Hybridization was carried out at 60°C (0.26 M Na Phosphate, 1 % BSA (Bovine Serum Albumin) (w/v), 7 % SDS (w/v), 1 mM Na_2 EDTA, pH 8.0) for three hours. Membranes were washed at low stringency (twice at room temperature in 2 X SSC/0.1% SDS (SSC: (20 X : 3 M NaCl, 3 M Na_3Citrate; SDS: Sodium Dodecyl Sulfate) for 15 minutes with a further 30 minute wash at 60°C in 2 X SSC/0.5% SDS). The membranes were exposed to X-ray film (Kodak AR) overnight at -80°C with intensifying screens.

Fingerprint Analysis

I scored bands on each gel between 24.7 and 3.0 kb consistently for all gels as bands below 3.0 kb resolved poorly. I considered two bands identical in two fingerprints on the same gel if the migration distance of the centre of the bands did not differ by more than 0.5 mm and if the bands did not differ more than two-fold in intensity (Westneat 1990). Two standards, one lane of a λ high molecular weight marker (8.3-48.5 kb) and two lanes of a 1 kb DNA ladder were run on either side of each gel. These internal markers were used to interpolate sizes of DNA bands which allowed comparisons of bands across gels (Birkhead et al. 1990). For each family, the putative father, putative mother and nestlings were run in consecutive lanes with the nestlings placed between the putative parents when both parents were available. This was done in order to avoid confusion when assigning bands from the nestlings to their putative parents. In some cases where the putative mother was not captured and only the putative father's DNA was available, I ran the nestlings' fingerprints between two fingerprints of the putative father.

The band sharing values between a nestling and each of its available putative parents was calculated for all nestlings in pairwise comparisons. The band sharing coefficient (BSC), was calculated using the equation, $s=2N_{ab}/(N_a+N_b)$, where N_{ab} is the number of shared bands between individuals a and b, and N_a and N_b are the number of bands scored for individuals a and b, respectively (Wetton et al. 1987).

Background band-sharing, an estimate of adult band-sharing within the population, was calculated from 19 apparently unrelated pairs of males run on adjacent lanes or within two or three lanes on the same gel.

Following the rules of Mendelian inheritance, it is expected that a nestling would inherit 50% of its genes from each of its parents (first-order relatives) (Jeffreys et al. 1985a, Burke and Bruford 1987, Birkhead et al. 1990). The proportion of bands shared between a parent and offspring would be 0.50. In unrelated individuals, the proportion of bands shared should be approximately equal to the background band sharing coefficient. From this, I would expect a bimodal distribution for the proportion of bands shared, where unrelated and first-order relatives distributions are distinct (Westneat 1990, Hunter et al. 1992).

As the result of random mutation, a novel band is expected to occur in 1 out of every 100-300 bands scored. Therefore, one or more novel bands in a nestling's fingerprint may indicate the possibility that one of the social parents may not be the nestling's genetic parent (Jeffreys et al. 1985a, Burke and Bruford 1987, Westneat 1990). Since the degree of relatedness in a population, as well as the mutation rate of the hypervariable region of the genome used in fingerprinting analysis (Jeffreys et al. 1985a), may greatly affect the number of novel bands which could be attributed to mutation alone, I calculated the mutation rate and the number of bands expected from mutation alone.

For determination of genetic parentage I followed the procedures in Westneat (1990). In families with two social parents (two-parent families), I calculated the number of bands which could not be assigned to either parent for each nestling's fingerprint. These unassigned (novel) bands may result from mutation, extra-pair fertilizations, intraspecific brood parasitism, or scoring errors (Hasselquist et al. 1995). In order to accurately determine genetic parentage, I calculated the number of bands in a nestling's fingerprint which could be attributed to mutation alone.

Mutation rate, μ, is the number of mutations per locus per generation and is calculated from the formula $\mu = m/F$, where m is the mean number of novel fragments and F equals the average number of fragments scored (for 2 parent nestlings). The mean number of novel fragments is calculated from the total number of single novel fragments (in nestlings with two parents)/number of nestlings with two social parents (Burke and Bruford 1987).

The Poisson equation, used to determine how many bands should be expected from mutation alone, calculates the probability that nestlings in the population will have 0, 1, 2 or more novel fragments. The equation states that if a nestling has 0, 1, 2 or more novel bands with a probability of less than 0.05, then the novel bands can be attributed to random mutation. The Poisson equation is calculated from $P=e^{-m}m^{b}/b!$, where e=natural log, m= the mean number of novel fragments, and b= expected number of novel fragments (Burke and Bruford 1987, Rabenold et al. 1990).

After determining the number of bands that should be expected from mutation alone for nestlings in two-parent families, I determined which two-parent nestlings were excluded nestlings. For the excluded nestlings, either one or both of their social parents was not their genetic parent. Band sharing values between included (two-parent) nestlings and each of their genetic parents were used to determine if either of the social parents of the excluded nestling were the genetic mother or father. If band sharing values, either nestling to social mother or nestling to social father, fell within the range of the included (two-parent) nestling's band sharing values I then determined which of the putative parents was the genetic parent of that excluded nestling. Following this analysis I determined for all of the two-parent nestlings which were included (social and genetic parents were the same individuals) or excluded (one of their social parents was not a genetic parent) nestlings for both the male to nestling and female to nestling comparisons. Mean band sharing values for all included two-parent nestlings for both nestling to genetic father and nestling to genetic mother as well as for all excluded two-parent nestlings were calculated. In order to determine if included and excluded nestlings were genetically unrelated groups two-tailed 95% confidence limits of the band sharing values between these two groups as well as between included nestlings and unrelated adults (background band sharing values) were calculated from the formula $t=(X_1-X_2)/(S_{x1}-S_{x2})$, where X_1 is the mean nestling to father band sharing coefficient for included two-parent nestlings, X_2 is the mean nestling to father band sharing coefficient for excluded two-parent nestlings or mean background band sharing coefficient, and S_x the sample variance of the mean is equal to the square root of the standard deviation (s.d.) of the mean divided by the mean. Degrees of freedom (d.f.) were calculated from the formula d.f.= $(n_{x1} + n_{x2} - 2)$, where n is sample size (see Table B3; Siegel 1956).

The range of BSC values for included nestlings and their genetic fathers in two parent families was used to determine which single parent nestlings were included and excluded nestlings. The lower value for the range of included two parent nestlings was used as the cut off for excluded nestlings. Therefore any one parent nestling with a BSC lower than this cut off value was considered an excluded nestling. Broods where neither parent could be caught were excluded from the analysis (5 broods, 20 nestlings).

In order to determine genetic paternity of the excluded nestlings (both two-parent and single-parent nestlings) I followed procedures by Westneat (1993). For each excluded nestling I first looked at the DNA fingerprints of males whose territory was the nearest neighbor of the cuckolded male and then I examined the DNA fingerprints of other males in the study area which were DNA tested. Paternity of the two-parent excluded nestlings was assigned when a male's fingerprint contained all or most (except one or two) of the novel paternal bands in a nestling's fingerprint and if the nestling and male pair had the highest band sharing values for the males tested. For nestlings in one-parent families paternity was assigned to males with which the nestlings had the highest band sharing values. On average for each nestling four males were tested as potential genetic fathers. I calculated a number of probabilities to confirm that I did not assign paternity incorrectly by chance alone. These included: the probability that a neighboring male would be identified as the genetic father by chance alone by the formula (1): $P=a^b$, where P=probability, a= mean band sharing value for unrelated adults in the population, and b=mean number of bands scored (two-parent nestlings); the probability that any two males would share > 80 % of their fragments by chance using the formula (2): $P=a^c$, where c= the mean number of paternal fragments x 80%; and the probability that any one of the males tested for paternity would be assigned paternity by chance alone from the probability calculated from formula (2) ÷25% (Westneat 1993).

Following paternity assignments of the extra-pair young I calculated the realized reproductive success of males which were DNA fingerprinted (see Chapter 2 for comparison of observed and realized reproductive success).

Results

Breeding Biology

Between 1992 and 1993, the two years included in the DNA fingerprinting study, the size of the breeding population decreased. In 1992 the breeding sex ratio was 1:1

(number of males defending territories to number of breeding females). In 1992 there were 54 males defending territories and 54 breeding females. In 1992 some territorial males (N=5) failed to acquire any females. In 1993 the breeding sex ratio was female biased (1:1.6). As well in 1993 the population size was much smaller than in 1992 with only 14 males defending territories and 23 females breeding in the study area. Additional details regarding the structure of this breeding population can be found elsewhere (see Chapter 2).

Determining Parentage

In this study I completed 13 autoradiographs (for an example see Appendix 1) from which I obtained a total of 141 DNA fingerprints. Combining the data for the two years of this portion of my research (1992 and 1993) I tested 74 % of the 10 day old nestlings in the population (110 nestlings from a total of 32 broods). Of these 110 nestlings 46 (42%) were in nests (13 broods) of polygynous males and 64 (58 %) were in nests (18 broods) of monogamous males. An average of 11.8 (± 4.5 s.d.) bands were scored per nestling fingerprint. The band-sharing of the adults in the population was 0.261 (± 0.116 s.d., N=19).

Of the 110 nestlings I tested I used 29 nestlings from 7 two-parent families to calculate the number of novel bands to be expected from mutation alone. The proportion of nestlings with different numbers of novel bands follows loosely a bimodal distribution (Figure 1) with the majority of nestlings having zero or one novel band (one mode) and with few nestlings having between two and eight novel bands (second mode). Mode is defined as a measurement of great concentration (Zar 1984). However, the two modes are nearly but not completely separate as the nestlings in the two novel bands group includes one individual (striped bar) which resulted from intraspecific brood parasitism. There are also two individuals (striped bars) with 5 novel bands each. These two nestlings were also the result of intraspecific brood parasitism. All other individuals (solid bars) in Figure 1 have novel bands resulting from either mutation or extra-pair fertilizations. I calculated the mutation rate for this population to be 0.01 which is consistent with reported avian mutation rates (0.011-0.004) (Jeffreys et al. 1985b, Burke and Bruford 1987, Westneat 1990). Mutation rate, μ, (0.14/11.8=0.01) was calculated from the mean number of novel bands, m, (4/29=0.14) divided by the mean number of bands scored, F (11.8). This mutation rate indicated that only 0 or 1 novel fragments could be expected from mutation alone in this population since the probability (calculated with the Poisson equation using the α=0.05 decision level) of a nestling having only 1 novel band was 0.012 while the probability of having 2 or more novel bands was less than 0.009. These results indicated that 2 or more novel bands occurring in a nestling's fingerprint occur due to reasons other than random mutation events alone.

As a result of this analysis I considered any nestling in two-parent families with 2 or more novel fragments an extra-pair young. In the cases in which there were two or more novel bands one of the social parents was not the nestling's genetic parent. The band sharing values determined for included nestlings of two-parent families (nestlings with 0 or 1 novel bands) were used to establish which parent was the genetic parent of the excluded two-parent nestlings (Wetton et al. 1987). The range of band sharing values for included nestlings (two-parent) between nestlings and genetic fathers was 0.333-0.616 and between nestlings and genetic mothers was 0.414-0.668. Thus any nestling with two or more novel bands and with a nestling to social father band sharing value of less than 0.333 or a nestling to social mother band sharing value of less than 0.414 was considered to not be the genetic offspring of that parent. Using this procedure I then defined each two parent nestling as an included or an excluded nestling for the male to nestling and female to nestling comparisons. In the case of a nestling not being the genetic offspring of a social mother I considered the excluded nestling to be the result of intraspecific brood parasitism. I concluded that nestlings which were not the genetic offspring of their social fathers were excluded offspring resulting from extra-pair fertilizations. I then calculated the mean band sharing values for all two-parent included and excluded nestlings and their two social parents (Table 1).

In comparing of the distribution of the nestling to father band sharing values for included (range: 0.363-0.639; solid bars) and excluded (range: 0.202-0.314; striped bars) nestlings for all nestlings in two-parent families I found that the two distributions did not overlap significantly (2-tailed 95% confidence limit, t=398.03, d.f.=27, P< 0.001; Figure 2). When comparing nestling to father band sharing values of included two-parent nestlings and the background band sharing values (range: 0.145-0.376) I found that the two distributions did not overlap significantly (2-tailed 95% confidence limit, t=171.57, d.f.=39, P< 0.001). Since the two (bimodal) distributions (Figure 2) were significantly different I concluded that: (1) excluded and included nestlings are two distinct groups in this population; (2) included and excluded nestlings are not genetically related; and (3) the social parents of included nestlings were the nestlings' genetic parents.

In order to determine paternity of nestlings in single-parent families I used the BSC of <0.363 as the value for excluding nestlings of single-parent families (N=81). The lower more conservative mean nestling to genetic father (two-parent) band sharing value was used as the decision level in one-parent families since the mean nestling and father value included the lower range for included nestlings for both their mothers and their fathers in two-parent families. Therefore any nestling from single-parent families with a band sharing value (male to nestling) of ≤ 0.363 was defined as an excluded nestling due to extra-pair fertilizations. The social father in these cases was not the genetic father of these nestlings.

Patterns of Extra-pair Fertilizations

In this study the frequency of extra-pair fertilizations was high in both years. In total 17 out of the 110 nestlings tested (15 %) were extra-pair young. In 1992 13% (10/76) of the nestlings were extra-pair young and in 1993 21% (7/34) of the nestlings tested were extra-pair young (Chi square; $\chi^2 = 0.51$, d.f. = 1, P = 0.48, Power = 0.16). The low power of this analysis may have resulted from the small number of young compared. Increased sample size is needed to clarify this result. These 17 extra-pair nestlings were in 12 nests of 9 males (36% of the 25 males tested) with some males having more than one extra-pair young in their nests. In 1992 18 males were tested of these 33% (6/18) were cuckolded. In 1993 of the 7 males tested 43% (3/7) were cuckolded. In 1992 38% (8/21) of the broods tested contained at least one extra-pair young and in 1993 36 % (4/11) of broods tested contained at least one extra-pair young (Table 2). For the broods containing extra-pair young I found that the number of extra-pair and non-extra-pair young for the two years of the study (Table 2) did not differ significantly (Fisher's Exact test; χ^2=1.19, d.f.=1, P=0.28, Power=0.28). The low power of this analysis presumably reflects the small sample size. However, in 1993 half of the young (N=7) in these EPY broods were EPY and half (N=7) were not (Table 2). Of the nestlings tested 53 % (9/17) of the nestlings which resulted from extra-pair fertilizations were in nests of primary polygynous females (first females to settle and mate with a male Welter 1935) with 24% (4/17) of the extra-pair nestlings in nests of secondary polygynous females and 24% (4/17) in nests of monogamous females.

Assigning Paternity

Combining the two years of data I assigned paternity to 16 out of the 17 extra-pair young. I found the probability, P, that a neighboring male of the cuckolded male would be assigned paternity by chance alone was 1.3 x10^{-7} (P=$0.261^{11.8}$). The probability, P, that any two males would share > 80 % of their paternal fragments by chance alone was 5.7 x 10^{-6} (P=$0.261^{8.99}$). And the probability that one of the four males tested as the possible genetic father would match as the genetic father by chance alone was 2.3 x10^{-5}. Although these probabilities do differ slightly I am confident that the true genetic sires of these excluded nestlings were determined. The only excluded nestling whose genetic father could not be determined was likely sired by a male within the population which was not sampled.

Of the extra-pair young which were assigned paternity polygynous males fathered 44% (7/16) and monogamous males fathered 56% (9/16) of the extra-pair young (χ^2=0.125, d.f.=1, P=0.724, Power=0.101). I found in 1992 that socially monogamous males fathered all of the extra-pair young (N=9) whereas in 1993 polygynous males fathered all (N=7) of the extra-pair young. In 1992 most of these extra-pair males (78%, 7/9) held territories which were not the nearest neighbor of the male who was cuckolded. Six out of seven (86%) of these extra-pair males in 1993 were the nearest neighbor of the cuckolded male (Fisher's Exact Test: P=0.021). As a result of this analysis I concluded that the number of extra-pair males which were nearest neighbors or not nearest neighbors did not differ significantly over the two years.

In order to determine if the cuckolding males (in 1992-monogamous males in 1993-polygynous males) traveled farther to the cuckolded nests in 1992 and 1993 I examined the proximity of the territories of these males to the cuckolded males' territories. I compared the distances from a cuckolding male's territory boundary to the nest containing the male's extra-pair young between the two years of the study. I found that in 1992 (monogamous) males traveled an average of 200.66 m (±118.24 s.d.) while in 1993 cuckolding (polygynous) males traveled an average of 91.25 m (±87.24 s.d.) to obtain extra-pair matings. However, this difference in distance was not significantly different (t-test, t=1.78. d.f.=11, P=0.103). Therefore, monogamous and polygynous males did not appear to travel greater distances to cuckold other males.

Costs and Benefits of Extra-pair Matings

For the males in the population who were DNA tested each male was assessed as to whether he benefited or suffered costs in terms of overall reproductive success (genetic offspring). Out of the 25 males tested 10 (40%) males did not have any detectable extra-pair fertilizations while 15 (60%) males either obtained extra-pair fertilizations or were cuckolded by other males. Of these 15 males (Table 3) 7 (47%) males had a higher realized than observed reproductive success 7 (47%) males had a lower realized than observed reproductive success and 1 (6%) male's reproductive success values did not change. However, the number of males in these three groups did not differ significantly (χ^2=3.333, d.f.=3, P=0.189, Power=0.339).

Overall polygynous males were cuckolded more often than were monogamous males since 13 out of the 17 extra-pair young (76%) were in nests of polygynous males while only 4 extra-pair young were in nests of monogamous males (χ^2=7.529, d.f.=1, P=0.006). When looking at each year separately this trend still continues. In 1992 6 out of the 10 (60%) extra-pair young were from polygynous nests. While in 1993 all (N=7) of the extra-pair young were from polygynous nests (Fisher's Exact Test: P=0.103, Power=0.468). Therefore on the strength of the trend seen here I concluded that polygynous males suffered a greater cost in both years of the study in terms of lost reproductive success due to extra-pair fertilizations.

In examining if mating status affected the likelihood of being cuckolded for both polygynous and monogamous males I examined the number of young lost by cuckoldry and the number of young gained by extra-pair matings. I found that polygynous males lost

13 young due to cuckolding but gained 9 young through extra-pair matings. This resulted in a net loss of four young for polygynous males. When examining monogamous males in the same way I found that monogamous males ended up with a net gain of 3 young (loss of 4 young through cuckoldry and a gain of 7 young through extra-pair matings). Therefore for this subset of the population polygynous males had a lower reproductive success than did monogamous males.

In order to determine if the status of males gaining extra-pair fertilizations could be explained by the status of males in the population I compared the number of cuckolding polygynous and monogamous males in 1992 and 1993 and the number of males of each status in the population for each year of the study. Of the males gaining extra-pair fertilizations in 1992 6 were monogamous and 0 were polygynous and in 1993 0 were monogamous and 3 were polygynous. In the study population in 1992 39 males were monogamous and 10 were polygynous while in 1993 6 males were monogamous and 8 were polygynous. Not all males in the population were DNA tested and some males fathered more than one extra-pair young.

In comparing the number of cuckolding males and the number of males in the population I found that the number of cuckolding males did differ for the two years of the study (Fisher's Exact Test: P=0.01). From the analysis I found in both 1992 and 1993 that the number of monogamous and polygynous males obtaining extra-pair fertilizations was related to the number of monogamous and polygynous males in the population (Fisher's Exact Test: 1992: P=0.58, Power=0.301; 1993: P=0.27, Power=0.526). On the basis of the high power of this analysis I am able to conclude that the number of monogamous and polygynous cuckolding males did not differ from the proportion of monogamous and polygynous males in the population.

Occurrence of Intraspecific Brood Parasitism

Combining data for 1992 and 1993 I found that 10 % (3/29) of nestlings in two out of seven broods tested (29%) from two-parent families one in each year of the study were excluded nestlings resulting from intraspecific brood parasitism. These excluded young were raised in nests of polygynous males in which a female evidently dumped an egg in the nest of another female mated to the same male. In all 3 cases the genetic father of the excluded nestling was the territorial male on whose territory the nestlings were raised. Therefore these were cases of quasi-brood parasitism (Birkhead et al. 1990). The genetic mother of these excluded nestlings could not be identified. In these cases the female which dumped the eggs was also mated to the territorial male where the egg was dumped (pers. obs.).

Discussion

Extra-pair fertilizations occurred in this population of marsh wrens at a high rate with 38 % of broods having at least one extra-pair young. These extra-pair young could have resulted from rapid-mate switching (Moller 1985, Birkhead et al. 1990) in which a female already inseminated by her social partner switches partners pairs with a second male and settles on the new male's territory thus cuckolding the second social mate. However, this is not likely since none of the territorial males in either year disappeared and was replaced during the breeding season. As well no female marsh wrens were observed abandoning the initial stages of nesting with their social partner (which included lining of the nest) and then initiating these same behaviours on a second territory. Although some female marsh wrens switch mates after successful fledging of their young or after a nest was depredated all females the days between resettlement and the days occupied in nesting activities were closely monitored throughout the breeding seasons. It is more likely that the source of extra-pair young in this population is extra-pair matings resulting in extra-pair fertilizations.

My results show that extra-pair fertilizations are an important part of an individual marsh wren's mixed reproductive system as well as being an important component of some individuals reproductive success (Gibbs et al. 1990). Since extra-pair fertilizations are carried out successfully by only a small proportion of males each year (two years combined, 9/24 males) and that number of individuals appears to be consistent over time (see Table 2 and Table 3) then it is probable that extra-pair fertilizations are part of the existing mating pattern of this marsh wren population. A mixed mating system in marsh wrens may allow males to increase their reproductive success since most marsh wrens breed for only one season (Welter 1935, Verner and Engelsen 1970, Leonard 1986). These males need to maximize their effort in one breeding season since it is likely that they will only get the one year to breed. Therefore a mixed system may be a way to get the most possible matings in a single breeding season.

High rates of extra-pair fertilizations in a population may result in realized reproductive success values which differ greatly from observed reproductive success values (see Chapter 2). Such findings may result in two sets of different conclusions regarding reproductive success and the reproductive strategies of marsh wrens. In this study equal numbers of males either raised or lowered their realized reproductive success through extra-pair fertilizations in comparison with their observed reproductive success. Some males both cuckolded other males and were cuckolded themselves (N=3). Other males were cuckolded but gained no reproductive success from extra-pair fertilizations (N=6) while some males cuckolded other males but were not cuckolded themselves (N=6). Although the number of males who were found to have higher or lower realized reproductive success did not differ the cost (losing reproductive success) and the benefit (gaining reproductive success) of extra-pair fertilizations was not shared equally by individual males in this population (some males paid the costs while other males gained benefits from extra-pair fertilizations).

The extent of extra-pair fertilizations in both years of this study involving both monogamous and polygynous individuals demonstrates that this behaviour is an important component of the reproductive system of marsh wrens in this population. Extra-pair matings may affect female choice of a social partner since she may be separately choosing her genetic (mating) partner and her social (nesting) partner (Westneat et al. 1990). These results bring into question previous work on this species (Welter 1935, Kale 1965, Verner 1965, Leonard 1986) which has not considered the possibility of extra-pair matings and their consequences for the marsh wren mating system. Extra-pair matings may affect previous conclusions found in both studies of marsh wrens and other species since many of these studies used the harem size (the number of females a male mates with) as a measure of the males mating success. However, in these avian studies it was assumed that females mate exclusively with their nesting partner (Weatherhead and Robertson 1977). This and other studies (Gibbs et al 1990) have demonstrated that the two choices do not always coincide.

The consistency in the proportion of young sired through extra-pair fertilizations in the two years of the study suggests that at least some females are separately choosing their social mate (who to nest with) and their genetic mate (who to mate with) for at least some of their young (Westneat et al. 1990). Choice of a breeding situation by female marsh wrens may thus involve two separate decisions about potential mates.

The finding that the proportion of extra-pair fertilizations in this population was similar over the two years (13% and 21% of young tested for 1992, and 1993, respectively) of the study suggests that the density of the population does not affect the degree of extra-pair fertilizations. However, the relationship between density of the population and the extent of extra-pair fertilizations needs to be further examined with additional years of data before it can be determined if a strong relationship exists. In this study the density of the population may have affected which males obtain extra-pair fertilizations and which males were cuckolded. Given the opportunity it is possible that any male in the population would attempt extra-pair fertilizations as a means of increasing his reproductive success. If this is the case then the mating status of males obtaining extra-pair fertilizations would on average reflect the dominant breeding strategy of the males in the population. As seen in my analysis the mating status of the cuckolding males was consistent with the dominant mating status of the population for both years of the study.

In 1992 the majority of these cuckolding males were non-neighbors of the cuckolded male. In 1993 nearly all cuckolding males were the nearest neighbors of the male they cuckolded. The density of the population in the two years and the areas of the marsh settled by monogamous and polygynous males may explain why in 1992 most of the cuckolding males were not the nearest neighbor of the cuckolded male and why in 1993 most of the cuckolding males were the nearest neighbor. In each year of the study polygynous males often defended territories in the far (shore) area of the marsh away from the upland edge of the marsh with monogamous males settling closer to the upland edge of the marsh (see Chapter 4). These settlement patterns resulted in monogamous and polygynous males defending territories which were generally spatially segregated from one another. In 1992 when the density of the breeding population was high and there were relatively few polygynous males in the population cuckolding (monogamous) males likely had to fly farther distances to territories of the polygynous males who may have been more vulnerable to being cuckolded. In contrast in 1993 when the density of the population was low and polygyny was dominant polygynous males likely found opportunities to obtain extra-pair fertilizations on territories of their nearest neighbors who were usually also polygynous males.

The majority of the cuckolded males in both years of the study were polygynously mated males even in 1992 when polygyny was rare. These polygynous males may have been more vulnerable to being cuckolded due to the trade-offs polygynous males may make between guarding their primary female seeking a second mate and pursuing extra-pair fertilizations (Hasselquist and Bensch 1991, Dunn and Robertson 1993, Westneat 1993).

In marsh wrens each male's courtship centre is generally spatially separated from other males' courtship centres on a male's territory (Verner 1965). A courtship centre is a spatially segregated area of the male's territory where a number of nests have been built close together. After building the nests which comprise the courtship centre the male will sing and display from within it attempting to attract a female (Welter 1935). Thus it would be difficult for a male marsh wren to guard one female while attempting to attract a second female at another location on the male's territory. As well synchronous settlement of females in this population (see Chapter 2 Results) would force males pursuing extra-pair fertilizations to occasionally leave their females unguarded during their fertilizable period. As indicated by my results lack of mate guarding may have led to the occurrence of extra-pair fertilizations in this population of marsh wrens since over half of the nestlings resulting from extra-pair fertilizations were in nests of primary females. These results are consistent with what would be expected if extra-pair fertilizations occurred due to the mate guarding hypothesis (Beecher and Beecher 1979, Birkhead 1979). According to the mate guarding hypothesis: (1) paternity of nestlings is related to the male's ability to guard his mates, (2) males may make a trade off between guarding their mate and attracting other mates or participating in extrapair matings; and (3) attracting a second mate or pursuing extrapair matings may result in higher rates of cuckoldry by the primary female (Beecher and Beecher 1979, Birkhead 1979).

A female's reproductive strategy may be more complex than has been previously considered. It has been demonstrated that females often solicit or at least participate in extra-pair fertilizations (Smith 1988, Birkhead et al. 1990, Moller 1990). Females may participate in extra-pair fertilizations in order to guard against a possibly infertile male (Trivers 1972, Gibson and Jewel 1982) to obtain genetic benefits for their young such as getting "good" genes or to increase their genetic diversity (Moller 1988, Smith 1988, Westneat et al. 1990). In this study the finding that the number of EPY and non-EPY in broods containing EPY was not significantly different indicates for broods containing EPY that only some of the young in a brood are the result of extra-pair matings. Therefore this result argues against either fertility insurance or good genes as the reasons why a female participates in extra-pair matings. Instead these results are consistent with the hypothesis that females are attempting to increase genetic variability of their offspring through extrapair matings. Further work in this area involving rigorous testing of the proposed hypotheses (see Smith and von Schantz 1993) may determine what evolutionary forces have led to this complex mixed reproductive strategy in female marsh wrens as well as in other species of birds.

Intraspecific Brood Parasitism

Intraspecific brood parasitism occurred in the study population (29 % of broods tested) at a higher rate than is usually found in most studies (Price et al. 1989, Hartley et al 1993). Since few females were DNA-tested (6 out of 77, 8%) due to difficulty of capturing them the number of cases of intraspecific brood parasitism may be over or under estimated by this study. In marsh wrens intraspecific brood parasitism as part of their mixed reproductive system may be a way for females to increase their reproductive success without having to provide parental care to the young.

DNA fingerprinting has in several cases (Birkhead et al. 1990, Morton et al. 1990) detected intraspecific brood parasitism in avian species where it had not been previously observed. In other studies observations of intraspecific brood parasitism have been reported (see Hartley et al. 1993, for review). Birkhead et al. (1990) discovered higher levels of intraspecific brood parasitism than previously recorded presumably as a result of closer observations of nest sites activities. I suggest that intraspecific brood parasitism in this population of marsh wrens may be occurring at much higher levels than detected by this analysis. It is likely that additional cases of egg dumping occurred since there was a high rate of predation of breeding nests with many nests being destroyed during egg laying (pers. obs.).

The degree of relatedness for social fathers and the excluded young resulting from intraspecific brood parasitism indicates that these excluded young are the result of quasi-brood parasitism (Birkhead et al. 1990). As suggested by Birkhead et al. (1990) this is a rare strategy in which females copulated with the territorial male then dumped one or more of her eggs in another female's nest who is mated with the same territorial male. Although a rare event quasi-brood parasitism would be expected to occur more often in polygynous breeding situations as was found in this study where more than one female is breeding simultaneously on a male's territory (Birkhead et al. 1990).

In addition one might speculate that in marsh wrens a high frequency of intraspecific egg destruction caused by adults of both sexes may create many situations when a laying female whose nest was destroyed by another conspecific must deposit an egg in another nest. Furthermore familiarity of her mate's territory and probable nest location of the other "co-wives" along with time limitation preventing any extended search for other laying possibilities may all lead to quasi-brood parasitism.

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Figure Legends

Figure 1: Bimodal distribution of novel bands for nestlings from two-parent families (N=29). Solid bars indicate novel bands due to extra-pair fertilizations (N=26). Striped bars indicate novel bands due to intraspecific brood parasitism (N=3).

Figure 2: Distribution of band sharing coefficients for included (range: 0.363-0.639; solid bars) and excluded (range: 0.202-0.314; striped bars) nestlings, for putative fathers and nestlings from two-parent families (N=29).

Figure 1:

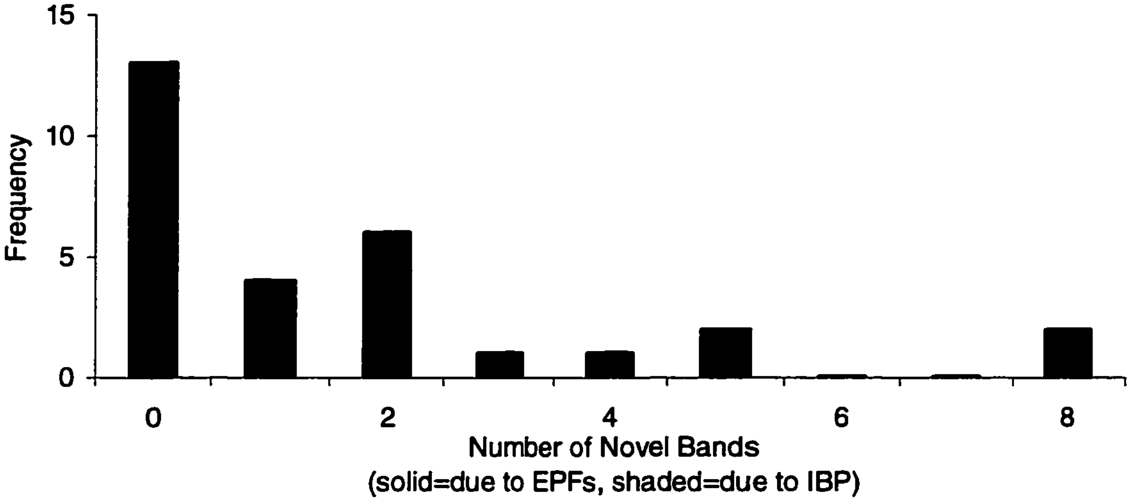
15
10
5
0
Frequency
0
2
4
6
8
Number of Novel Bands
(solid=due to EPFs, shaded=due to IBP)

Figure 2:

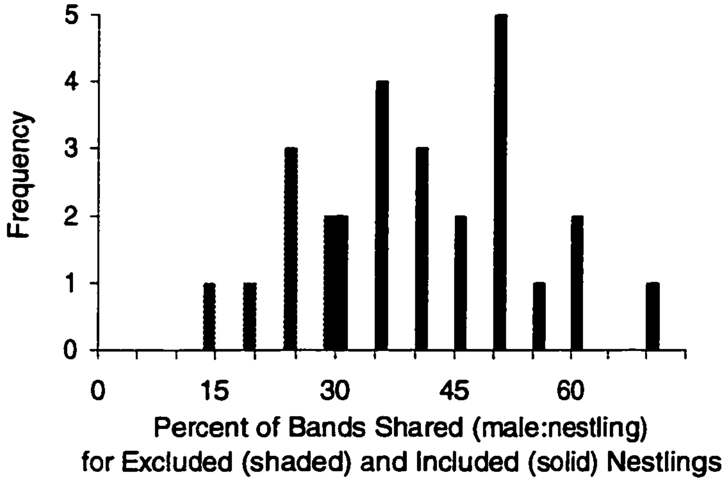
5
4
3
2
1
0
Frequency
0
15
30
45
60
Percent of Bands Shared (male:nestling)
for Excluded (shaded) and Included (solid) Nestlings

Table 1: Mean (± s.d.) proportion of bands shared (BSC) between included and excluded nestlings and their putative father and mother.

BSC	Excluded	(N)	Included	(N)
Nestling: Putative Mother	0.328 (±0.542)	3	0.558 (±0.128)	26
Nestling: Putative Father	0.258 (±0.557)	7	0.501 (±0.138)	22

Table 2: Brood size and number of extra-pair young (EPY) per brood for broods containing at least one extra-pair young for 1992 (Brood # 1-8) and 1993 (Brood # 9-12) combined.

Brood #	**Brood Size**	**# EPY**
1	5	2
2	3	2
3	5	1
4	4	1
5	5	1
6	6	1
7	2	1
8	5	1
9	4	3
10	4	2
11	2	1
12	4	1

Table 3: Cuckolding and cuckolded males' gains and losses of reproductive success through extra-pair young (EPY) for 1992 (males #1-11 and 1993 (males # 12-15) combined. Observed reproductive success is the total number of young fledged on a male's territory. Realized reproductive success is the total number of young sired determined through DNA Fingerprinting.

Male #	# EPY lost	# EPY gained	Observed R.S.	Realized R.S.
1	2		8	6
2	2		9	7
3	1	1	4	4
4	2		8	6
5	1		2	1
6	2		5	3
7		2	3	5
8		3	4	7
9		1	3	4
10		1	0	1
11		1	2	3
12	2	1	4	3
13	1	3	2	4
14	4		5	1
15		3	10	13

Chapter 2:

Breeding Ecology of Marsh Wrens: is polygyny beneficial for individuals of both sexes?

Abstract

Polygyny, a rare mating strategy, occurs in about 5 % of all bird species. The occurrence of polygyny in many avian species presumably depend on the balance between benefits and costs to females since females generally have a larger initial parental investment than males. Additionally the occurrence of polygyny may also depend on ecological factors which affect the benefits and costs to females. The goals of this study were to determine: (1) the ecological factors affecting the occurrence of polygyny in a study population; (2) the fitness consequences of mating polygynously for male and female marsh wrens (*Cistothorus palustris*); and (3) if males' observed and realized (measured with DNA fingerprinting) reproductive success values correspond. From these results I determined if mating polygynously is beneficial for both males and females in this population of marsh wrens. In the four years of the study the percent of polygynous males ranged from 19 % in 1992 to 66 % in 1979 and 49.1% in 1982 and 57 % in 1993. The low degree of polygyny in 1992 may have been due to an even sex ratio and a high population density which presumably limited males' ability to acquire additional mates. The high degree of polygyny in 1979, 1982, and 1993 may be attributed to a female skewed sex ratio (prevalence of females). In three years of the study (1979, 1992, 1993), polygyny was beneficial for males since polygynous males fledged more young than did monogamous males. In all four years polygynously and monogamously mated females did not differ significantly in the number of young fledged. However, the number of young fledged from nests of polygynous females was slightly higher in 1979 and 1992 than that from nests of monogamous females. Thus polygyny may have been beneficial for some females at least in 1979 and 1992. Comparison of observed and realized reproductive success values revealed that the two values did not differ significantly thus allowing the use of observed reproductive success values as an unbiased indicator of the realized reproductive success of males in this population.

Keywords: polygyny, DNA fingerprinting, marsh wrens, *Cistothorus palustris*

Résumé

La polygynie, une statégie peu fréquente de reproduction, est observée chez près de 5% des espèces d'oiseaux. La présence de cette stratégie est dépendante de l'équilibre entre les bénifices et les coûts pour les femelles qui sont polygynes puisque les femelles font un investissement initial plus important que les mâles au niveau de la reproduction. De plus, la polygynie peut dépendre de facteurs écologiques influençant les bénifices et les coûts pour les femelles. Les buts de cette étude étaient de: i) déterminer les facteurs écologiques influençant la présence de la polygynie dans une population étudiée; ii) étudier l'impact de l'accouplement polygynique sur l'aptitude darwinienne pour les mâles et les femelles troglodytes des marécages (*Cistothorus palustris*); et iii) déternminer si les valeurs "observées" et "réalisées" du succès de reproduction des mâles sont les mêmes; ceci étant mesuré par la technique de empreintes génétiques. Suite à l'obtention de ces données, j'ai pu déterminer si l'accouplement polygynique est adaptif pour les mâles et les femelles chez cette population de troglodytes des marécages. Lors des quatre années d'études, le pourcentage de mâles polygynes a varié de de 19 % (1992) à 66 % (1979) en passant par 49.1 % en 1982 et 57 % en 1993. Le taux peu élevé de polygynie en 1992 peut avoir été causé par un ratio mâle-femelle égal à un et une densité de population élevée. Le plus haut taux de polygynie, en 1979, 1982, et 1993 peut être attribué à un ratio mâle-femelle biaisé en faveur des femelles (1:1.6, mâles:femelles). Lors des années 1979, 1992 et 1993, la polygynie était adaptive pour les mâles, puisque les mâles polygynes ont produit plus d'oisillons que les mâles monogames. Lors des quatre années d'étude, les femelles monogames et polygynes ont produit un nombre similaire d'oisillons. En 1992, les femelles polygynes ont produit un peu plus d'oisillons que les femelles monogames. Par conséquent, la polygynie peut avoir été adaptive pour certaines femelles, du moins en 1979 et 1992 puisqu'elles ont produit plus d'oisillons Une comparaison des succès de reproduction observé et réalisé a revélé que ces deux valeurs ne différaient pas significativement, permettant donc l'utilisation des valeurs du succès reproducteur observé en tant qu'index du succès reproducteur réalisé des mâles de cette population.

Introduction

Polygyny is a rare mating strategy which occurs in about 5% of all bird species in which one male maintains pair bonds simultaneously with several females (Verner 1964, Verner and Willson 1966, Lack 1968). Ecological factors favoring polygyny may include the clumped distribution of resources which are important to females for breeding and which the male can defend such as nest sites or food (Emlen and Oring 1977). Polygyny may also be favored if the ratio in the breeding population (the breeding sex ratio) is skewed in favor of females (Skutch 1935). In this situation females may be forced to mate with an already mated male due to the shortage of unmated males (Emlen and Oring 1977).

The most common form of polygyny in birds is territorial polygyny where females mate and nest on a male's territory (Searcy and Yasukawa 1989). According to territorial polygyny theory polygyny should be favored when differences between traits of males and/or the males' territories are large enough that females who settle with an already mated male will have on average at least the same reproductive success as females who settle with an unmated male in a poor quality breeding situation (Verner 1964, Verner and Willson 1966, Orians 1969). This theory referred to as the polygyny threshold model has been supported mainly by studies of passerines nesting in marshes (Verner and Willson 1966, Orians 1969, Pleszczynska 1978, Garson et al. 1981) where food is abundant but heterogeneously distributed (Verner 1964, Verner and Willson 1966, Orians 1969). The clumped distribution of food (emergent insects) favours certain males controlling territories of high quality. These males should be able to attract multiple mates to their territories (Verner and Willson 1966, Emlen and Oring 1977). Alternatively males which become polygynous may be defending territories which are of high quality due to vegetation density, distance from an upland area, or territory size (Verner 1964, Pleszczynska 1978).

In order for polygyny to be advantageous and thus evolve over time, the reproductive success of the individuals mating polygynously must be at least as high as that of individuals mating monogamously. Polygyny is considered to be advantageous for males in that multiple mates create a potential for males to fledge more young than they would if they mated monogamously (Verner 1964, Orians 1969, Lightbody and Weatherhead 1987). In order for males to be able to breed polygynously females must be able to raise the young with little or no assistance from the male (Trivers 1972, Emlen and Oring 1977). In marsh-nesting species male emancipation is highly probable since emergent insects are abundant. Thus the occurrence of polygyny in a population would be dependent on the balance of the advantages and costs to females (Orians 1969) since females make the larger initial parental investment (Trivers 1972). According to parental investment theory at the start of breeding a female's investment is larger than the male's due to the energy required for the female to produce large gametes (Trivers 1972). Since females have initially invested more in each brood selection of high quality mates or territories by females would be favored in order to protect their investment (Verner and Willson 1966, Orians 1969). However, polygynously mated females may either suffer costs due to competition for male parental care and territory resources (Verner 1964, Verner and Willson 1966, Orians 1969) or may benefit by gaining access to better males (e.g., stronger, healthier, more aggressive, more genetically fit) or territories (Verner and Willson 1966, Orians 1969), or by cooperation with other females (e.g., in defense against predators; Altmann et al. 1977). As well polygynous females who settle asynchronously may reduce the costs of mating polygynously by not having to share male parental assistance in feeding the young (Leonard 1990).

One must also at least consider that polygyny, as a mating system, may in fact be a trait inherited from an ancestor and, therefore, may occur in a population not as the result of a set of current ecological conditions.This possibility, although thought provoking, was beyond the scope of this study.

Interpretation of ecological data involving the study of mating systems may be dramatically affected by comparison of males' observed and realized reproductive success (Gibbs et al. 1990). In several studies of birds observed and realized reproductive success values did not always correspond (Birkhead et al. 1990, Gibbs et al. 1990, Westneat et al. 1990). For this reason it is vitally important when using observed values of reproductive success that the reproductive success values be accurately determined (Burke et al. 1991, Weatherhead and Boag 1994).

As a mating system polygyny occurs slightly less frequently in the family Trogloditidae than does monogamy. Among North and South American wrens polygyny is known to occur at least in four species (house wren (*Troglodytes aedon*), marsh wren (*Cistothorus palustris*), sedge wren (*Cistothorus platensis*), and winter wren (*Troglodytes troglodytes*)), while monogamy is the dominant mating pattern in five species (Bewick's wren (*Thryomanes bewickii*), cactus wren (*Campylorhynchus brunneicapillus*), canyon wren (*Catherpes mexicanus*), Carolina wren (*Thryothorus ludovicianus*), and rock wren (*Salpinctes obsoletus*)) (Verner and Willson 1969).

The marsh wren is a highly territorial and polygynous species which breeds in fresh and saltwater marshes throughout North America (Welter 1935, Verner 1964). In this sexually monomorphic species both males and females forage primarily within the male's territory on a variety of marsh invertebrates (Bent 1948, Verner 1964, Verner and Willson 1966, Leonard 1986, Leonard and Picman 1988). The percent of polygyny in this species varies greatly between these study populations; from 2.4 % in Georgia salt marshes (Kale 1965), to 12.5% in Washington State (Verner 1965) and 44 % in Delta, Manitoba (Leonard 1986). The breeding biology of this species has been thoroughly investigated by Welter (1935), Verner (1965), Kale (1965), and Leonard (1986) using traditional observational techniques.

In this study I examined the breeding biology of the marsh wren in Delta, British Columbia, Canada. The breeding population of marsh wrens in Delta, B.C. consists mainly of migrants and a small number of year-round residents. Marsh wrens breeding in this area of British Columbia are known to migrate to and over winter in western Oregon and Washington (Larrison 1981). Previous work in Delta has found that this population naturally fluctuates in density from year to year (Picman, unpublished data) possibly as the result of losses due to emigration to other breeding areas, mortality during migration (Grant and Kirby-Smith 1992) and/or predation (Ricklefs 1969).

The goals of this study were: (1)to identify ecological factors which may influence the occurrence of polygyny in marsh wrens; (2) to establish the fitness consequences of mating polygynously for males and females; and (3) to determine if observed male reproductive success corresponds to realized male reproductive success. From these results I then determined if mating polygynously is beneficial for both male and female marsh wrens in terms of the number of young fledged.

Methods

Field work was conducted at the George C. Reifel Migratory Bird Sanctuary on Westham Island, in Delta, B.C., Canada between April and July of 1992 and 1993. Additionally I increased the sample size for this study by including two years of unpublished field data (1979 and 1982) from the Reifel Sanctuary that had been previously collected but not analyzed by Dr. J. Picman. The 1979 and 1982 data included two additional areas of the marsh not sampled in 1992 and 1993. Since the methodology for collecting the field data was consistent over the four years of the study I was able to make between-year comparisons. The main study site for all four years of the study consisted of a 600 x 200 m area of an extensive, homogeneous tidal marsh (see Appendix 2 a,b,c and d for maps of study area and male territories) located at the mouth of the Fraser River. Additionally in 1979 and 1982 another area of the marsh (400 x 300 m) adjacent to the main study area was sampled. I divided the study site into 20 x 20 m quadrats marked by 1.8 m high wooden stakes. The passerine breeding community of the marsh consists of red-winged blackbirds (*Agelaius phoeniceus*) and marsh wrens (Picman and Belles-Isles 1987).

In this study I compared males by their male physical and territory traits (see Chapter 4). Data collected for each male and territory variable examined in this study are summarized in Appendix 3 a, b, c, and d. The male traits I measured included: mating status (polygynous/monogamous), weight, wing length, condition index, and aggression. I also measured a number of territory traits. These included: territory size, number of (complete) nests built, vegetation density on territory, distance from the edge of the territory to the nearest redwing breeding nest, to the nearest marsh wren territory boundary, and to the upland edge of the marsh. The distances I measured for each male's territory, were considered important since intra-specific aggression among wrens and aggressive interactions between marsh wrens and redwing blackbirds have been frequently observed. These conspecific and heterospecific interactions have been found to affect marsh wren reproductive success (Picman 1988). In this study I considered it important to measure the distance from a male's territory to the upland edge since the upland edge of the marsh (a man-made dike) is the point of entry into the marsh for mammalian predators (pers. observation).

During the bi-weekly nest checks I collected data on the location and stage of nests, number of breeding females, number of eggs or nestlings present in nests, condition of the breeding nests (e.g., active, failed, depredated) and date the first egg was laid. Each breeding nest was categorized as either successful (nests where at least one young fledged), active (nest contained eggs or nestlings), failed (no nestlings fledged, eggs destroyed, or nestlings dead due to abandonment or high tides), or depredated (eggs found destroyed or nestlings found dead in or around nest). A nest was considered complete when the domed portion of the nest was built including an entrance hole lesss than 1 in. in diameter. I estimated female settlement date by the date when the first egg was laid (Kale 1965, Leonard and Picman 1988). In my analyses the actual date a female settled was later converted to a standardized date, with the first day of the field study being day zero. If more than one egg was found in the nest, I estimated the date the first egg was laid, assuming that one egg was laid per day (Kale 1965). I considered a nest successful if at least one nestling fledged. I measured female reproductive success, for each nesting attempt, by the number and weight of nestlings fledged from that active nest. I measured male observed reproductive success as the total number of young fledged on each male's territory and the weight of these nestlings.

I determined a males' mating status by the number of simultaneously breeding females on the males' territory. I used a male's weight and wing length as two measured of the male's physical quality. I then calculated a relative measure of each male's physical condition for each banded male (condition index = weight/wing length^3 ; Searcy 1979). After capturing each male, I measured wing length as the length of the flattened wing cord. In 1992, I measured aggression of territorial males towards conspecific intruders during an experiment involving 35 territorial males. In this experiment, I placed a tape recorder in the centre of a male's territory and played the song of a conspecific male from outside of the study area. I then recorded the territorial male's reactions along an index of aggression reactions (Searcy 1979). The index of reaction included four values: 0 indicated no reaction to the playback, 1 indicated the male singing on the territory, 2 indicated the male exhibiting low alarm calls, and 3 indicated the male exhibiting high alarm calls. For each trial, I played the playback song for a total of ten minutes. I tested each male only when one of the breeding nests on that male's territory contained nestlings. For each male, I repeated the experiment three times, always during the early morning. In order to obtain an index of each male's aggression, I averaged the three values for each male. For each male, I determined male territorial boundaries from observations of male-male, male-female interactions and male territorial activities (e.g., location of song perches, male flights). At the end of each breeding season, I calculated territory size using the minimum convex polygon method (Leonard and Picman 1988). For each territory I used a minimum of 20 points to calculated the size and dimensions of the territory. At the beginning of each breeding season, I measured vegetation density using a 1.8 m vertical stake with three 50 cm long horizontal bars spaced 50 cm apart. Along each 50 cm bar, 20 red dots were evenly spaced. I determined vegetation density by the number of complete dots visible from a distance of 10 m north of the stake when the stake was held perpendicular to the ground. The number of dots visible on the three bars was combined. The more dots which could be seen, the sparser the vegetation. Measurements of vegetation density were taken at each stake, along grid lines throughout the marsh. The value for each territory was determined by averaging vegetation density values at all stakes within a male's territory (Leonard and Picman 1988). I determined the location of each male's territory within the marsh, in relation to other marsh wren territories, the male's breeding nests, redwing breeding nests, and to the upland edge of the marsh, from the mapped territories at the end of each breeding season. In 1992, I attempted to measure food abundance using sticky plate traps (Leonard and Picman 1988), 20 x 20 cm pieces of clear plastic. I placed the plates on the grid stakes, at a height of 1 m. I sprayed each plate with a layer of insect adhesive, "Tangle foot". Sticky plates were placed on each 20 m stake (0-120m) of the 0, 100, 200, 300, 400, 500, and 600 east-west grid lines in the marsh. Twenty-four hours later, I collected, counted, measured, identified to order and categorized the emergent insects according to size into four size classes (small (1-3 mm), medium (3-5 mm), large (6 mm), extra-large (7-10 mm)). Each size class was given a value (1 to 4, respectively) in order to give relative values for the quantity of food in each class. Food abundance was calculated for each sticky plate by the number of insects of each size class multiplied by the value for that size class. Food abundance values were used to measure availability of food throughout the marsh. In 1992, the number of emergent insects at each stake location early in the season (mid-April) was measured. No measurements were taken in 1993 since in 1992 the insects trapped by the sticky plates were not the same as those consumed by marsh wrens. Therefore, I was unable to use the insect data to examine the distribution of marsh wren food resources in the marsh.

Detailed methodology of the blood sampling and DNA fingerprinting analysis can be found elsewhere (see Chapter 1). The DNA fingerprinting results were used to calculate males' realized reproductive success in 1992 and 1993, defined as the number of young sired by a male both on his territory and on other males' territories (Gibbs et al. 1990).

Throughout this study, statistical analyses involved parametric statistics where possible.These included Multiple Regression, ANOVA, and ANCOVA statistics. For each statistical test the assumptions of normality and homoscedasticity were tested. In cases where either one or both of these assumptions were violated by the data, I attempted to transform the data using the approapriate transformation, either log, arc sin, or square root transformations. If the transformation (s) did not correct the data so that the assumptions were not violated, I used non-parametric statistics (Kruskal-Wallis test, Mann-Whitney U-test, and Spearman Rank Correlation) were employed.

Results

Breeding Biology

The structure of this population of marsh wrens varied over the four years of the study. The density of the breeding population was high in 1979, 1982, and 1992, but low in 1993. In 1979, there were 57 male marsh wrens defending territories and 117 breeding female marsh wrens in the study area. In 1982, there were 57 male marsh wrens defending territories and 94 breeding females in the study area. In 1992 there were 54 males defending territories and 54 breeding females. In 1992, some territorial males (N=5) failed to attracted and mate with any females. In 1993 there were only 14 males defending territories and 23 breeding females.

In three out of the four years (1979, 1982, 1993) of the study, the breeding sex ratio was skewed in favor of females. In 1979, the average breeding sex ratio for the breeding season was 1:1.62 (Table 5, Chapter 4). In 1982, the average breeding sex ratio was 1:1.37 (Table 6, Chapter 4). In 1992 the average breeding sex ratio was 1:1 and in 1993, the average breeding sex ratio was 1:1.6 (Table 7, Chapter 4).

I found that the breeding sex ratios reflected the degree of polygyny in the four years of the study (males:Figure 1; females:Figure 2) with monogamy being the dominant breeding strategy in 1992 and polygyny being the dominant breeding strategy in 1979, 1982, and 1993 (Table 1).

In this study, a male was defined as polygynous when two or more females were observed breeding simultaneously on his territory. The difference in the number of individuals mating monogamously and polygynously between the four years was significant for both sexes (Table 1; males: χ^2=23.40, d.f.=3, P<0.001; females: χ^2=42.02, d.f.=3, P<0.001). Additionally 9% males in 1992 defended territories but did not acquire any mates. Of the individuals banded in 1992, including adults and nestlings, none returned to the study area in 1993.

In order to determine if females who became polygnous were first to settle, I examined if primary females settled earlier than monogamous females. If females who became polygynous, as the result of their partner acquiring a second mate, settled earlier than monogamous females then it would indicate that the polygynous males (who are settled with earlier) are chosen over the monogamous males. When examining this, I found that primary females did not settle significantly earlier than monogamous females in three of the four years of the study (see Appendix 4a and 4b for settlement dates).

I found that primary polygynous females did not settle significantly earlier than did monogamous females in 1979 (Mann-Whitney-U test: T=2552, P=0.72, Power=0.05), 1982 (Mann-Whitney-U test: T=1717. P=0.83, Power=0.754), or in 1992 (Kruskal Wallis: χ^2=0.006, d.f.=1, P=0.94) (Table 2). The consistency in the trend of the results over the three years supports the conclusion that primary females did not settle significantly earlier or later than monogamous females. However in the fourth year of the study, 1993, primary polygynous females did settle significantly earlier than did monogamous females (Table 2; Kruskal Wallis: $\chi^2=3.94$, d.f.=1, P=0.047).

In comparing traits of the territories or males of the earlier or later settling females, I found that the earlier settling females in 1992 did settle on territories closer to the upland edge than did later settling females (Stepwise Multiple Regression: N=93, distance to upland edge P=0.04, $R^2=0.05$; Figure 3). In comparing traits of the territories or males of females who settled earlier or later in the breeding season, I found that in 1993, earlier settling females settled on territories which had sparser vegetation (Stepwise Multiple Regression: N=45, vegetation density P=0.01, $R^2=0.13$; Figure 4).

For each male and habitat trait tested, mean values were calculated for the population for 1979, 1982 (Table 3), 1992 and 1993 (Table 4). When examining the four years of data together, some interesting trends are worth noting. As seen in these two tables, vegetation density was much higher (nearly two fold higher) in 1992 than in 1993 or 1979. This fluctuation in vegetation density may have been due to variations in the amount of logs and other debris which end up in the marsh, as the marsh is at the mouth of the Fraser River, used by the logging industry (pers. obs.). Over the four years of the study, it is interesting to note the change in the distance between marsh wren territories and redwing blackbird nests. Of the four years, this marsh wren to redwing distance was the shortest in the low marsh wren density year (1993). In the other three years this distance was fairly constant, as was the density of the breeding population.

In 1979 there was a high number of active nests (N=204) built during the breeding season. In 1982, 156 active nests were built during the breeding season. The total number of nests built by each male was not noted in 1979 and 1982.

Overall in 1992, male marsh wrens built 686 complete nests. Of these nests, only 14% were used for breeding (Table 5). Similarly, in 1993, only 26% of the 171 complete nests built were used for breeding (Table 5). Combining data for 1992 and 1993, I found that the number of nests used for breeding was significantly different from the number of complete nests built (χ^2=10.49, d.f.=1, P=0.001). Therefore there were a number of nests built by males each year which were not used for breeding.

In comparing the proportion of nests which were successful, failed, or depredated between the four years of the study (Table 6), I found that there were significant differences between the years (χ^2=56.48 d.f.=6, P<0.001). In 1979 59% of eggs laid resulted in fledged young. In 1982, only 25% of eggs laid resulted in fledged young (Table 7). In 1992, 27% resulted in fledged young. In 1993, only 18% of eggs laid resulted in fledged young.

In examining if size of their harem affects female reproductive success, I found there to be no significant relationship between harem size and reproductive success in any of the four years of this study. In 1979, monogamous (harems of 1) and polygynous (harems of 2, 3, and 4) female marsh wrens did not differ significantly in their reproductive success (number of young fledged per nest) (Table 8; Kruskal-Wallis, H=4.11, d.f.=3, P=0.25, Power=0.173). In 1982, monogamous and polygynous (harems of 2, 3, and 4) female marsh wrens did not differ significantly in their reproductive success (number of young fledged per nest) (Kruskal Wallis: H=1.206, d.f.=3, P=0.75, Power=0.05; Table 8). In an additional analyses, I combined data for females in harems of 3 or 4 females. I found that there was still no significant difference in reproductive success (Kruskal Wallis, H=4.11, d.f.=2, P=0.841, Power = 0.053).

In 1992, monogamous and polygynous (harems of two) female marsh wrens and did not differ significantly in the number of fledglings (Mann-Whitney U-test, T=1527, d.f.=1, P=0.33, Power=0.271; Table 9). In 1993, monogamous and polygynous (harems of 2, 3, and 4) females did not differ significantly in the mean number of nestlings fledged per nest (Kruskal-Wallis test, χ^2=4.82, d.f.=1, P=0.19, Power=0.053; Table 9). Unfortunately, the power of these analyses was poor. However, when looking at the four years of data together, there is a consistent trend in which female reproductive success did not differ significantly for females in harems of different size.

In three out of the four years of the study (1979, 1992, 1993) males with larger harems had significantly higher reproductive success than males with smaller harems. In 1979, male observed reproductive success did differ significantly for males with harems of different size (ANOVA; F=18.82, N=57, P< 0.001) with males in larger harems fledging more young (Figure 5). In 1982 male reproductive success did not differ significantly for males with harems of one to four females (Kruskal-Wallis; H=5.21, d.f.=3, P=0.16, Power=0.049) (Table 10). Male observed reproductive success, measured as the number of young fledged on a male's territory, differed significantly for males with harems of different sizes both in 1992 (Mann-Whitney U-test, T=370, d.f.=1, P<0.001) and 1993

(Spearman-Rank Correlation, $r_s=0.63$, $N=14$, $P<0.05$), indicating that males with larger harems fledged more young (Figure 6 and 7).

However, because of the low power of the analysis, the statistical results are inconclusive for 1982. The lack of a significant effect in this case may be the result of the three polygynous groups having such similar reproductive success values (see Table 10).

In 1992, I compared aggression of territorial males towards conspecific intruders in order to determine if more aggressive males fledged more young and or acquired more mates. There was no relationship between male aggression and male reproductive success (number of fledglings) (Kruskal-Wallis: $N=35$, $\chi^2=6.72$, d.f.=10, $P=0.75$, Power=0.054) or between male aggression and male status (Kruskal -Wallis: $N=35$, $\chi^2=0.60$, d.f.=1, $P=0.44$, Power=0.149). Mean aggression values for monogamous males (N=25, mean=2.441 (±0.83 s.d.) overlapped those of polygynous males (N=10, mean=2.634 (± 0.62 s.d.). The relatively low power of the two aggression analyses indicates that the outcome of these analyses are relatively unreliable, presumably due to small sample sizes.

Realized Reproductive Success

Following determination of paternity for the extra-pair young (see Chapter 1), I compared the observed and the realized reproductive success of the 15 males in 1992 and 1993 which had either higher or lowered realized reproductive success values in comparison to their observed reproductive success values (Table 3: Chapter 1). I related the two reproductive success measures using Pearson Correlation and found that the two measures of male reproductive success are strongly positively correlated ($r=0.75$, $N=15$, P=0.001) (Figure 8). Therefore, I conclude that the males' observed reproductive success is an unbiased estimator of the males' realized reproductive success (see Gibbs et al. 1990). However, it should be noted that the two reproductive success measures are not perfectly correlated. Therefore, realized reproductive success is not a perfect measure of individual males reproductive success but is a good indicator. Larger sample sizes which included each male in the study area may address this problem.

I compared traits of the males who had either higher (cuckolding males) or lower (cuckolded males) realized reproductive success values in comparison to their observed reproductive success values to determine if these two groups of males could be distinguished by their male physical or territory traits. Only those traits which were found to differ significantly between males are reported here. I found that males in these two groups did differ in two territory traits, in the distance from their territories to redwing breeding nests and in the size of their territories (Stepwise Multiple Regression, N=14, Model R^2=0.56, distance to redwing breeding nest, P=0.02, territory size, P=0.03). Territories of males who had a lower realized than observed reproductive success were larger in size (1065 ± 1004 s.d. sq m) and farther from redwing breeding nests (40.67 ± 26.62 s.d. m) than were territories of males with higher realized than observed reproductive success (territory size: 435 ± 278 s.d. sq m; distance to redwing breeding nest: 17.9 ± 21.76 s.d m). It should be noted in Multiple Regression analyses that a small sample size, as in this analysis, may result in less than conclusive results.

Discussion

The occurrence of polygyny in this population of marsh wrens, in all four years of the study, appears to be closely related to two key factors, the sex ratio and the size of the breeding population.

In 1992, with an even sex ratio, few females settled with already mated males. However, polygyny did occur in 19% of males, despite the fact that there were bachelor males (5/54) defending territories. The size of the breeding population (54 territorial males) in 1992, likely led to smaller territories per male. As a result of the more crowded conditions (limited size of territories) in 1992, males may not have been able, in many cases, to attract more than one female per territory. As a result, in 1992, polygyny was less frequent, and those males which did mate polygynously only acquired a maximum of two females.

In examining 1992 and 1993 together, it is interesting to note that males in this population had on average less than 2 breeding attempts per breeding season. This value is indicative of the high rate of monogamy in 1992 and the low density of the breeding population in 1993 as well as the relatively long cycle of breeding for marsh wrens. For marsh wrens in Delta, their breeding cycle may be as long as 60 days from initiation of a nest through initiation of a second nest, if the first nest was successful (pers obs, Picman unpubl. data).

As the breeding sex ratio increased in favor of females in 1993, polygyny became more prevalent possibly as the result of females being forced to mate with already mated males. In 1993, when breeding density was low and the sex ratio favored polygyny (skewed in favor of females), a number of territories were sufficient in size to support multiple mates. As a result, in 1993 some polygynous males attracted harems of three and even four females. The low breeding density in 1993 may have been due to natural fluctuations in population size (Picman, unpublished data) perhaps caused by heavy over-winter losses during 1992-1993 when unusually heavy snow falls occurred in southern British Columbia and western Oregon and Washington (Grant and Kirby-Smith 1992).

According to observed reproductive success measures, males mating polygynously fledged more young than did males mating monogamously, in three out of four years of the study. As seen in Figures 5, 6, and 7 in 1979, 1992 and 1993, as harem size increased so did the number of fledglings per male. However, when examining male reproductive success using realized reproductive success measures for a sub-group of males DNA tested in 1992 and 1993, I found that polygynous males sired fewer fledglings than did monogamous males (see Chapter 1). Therefore, it appears, at least for a sub-group of males, that mating polygynously is not necessarily beneficial to males in this population of marsh wrens. The findings of this study suggest that polygyny was costly at least for some males which suffered fitness costs due to lost paternity.

When I compared traits of males or the males' territories for males which had realized reproductive success values higher or lower than their observed reproductive success values, I found that there was a significant difference in the territory traits between these two groups of males. These results established that males with higher realized than observed reproductive success (most often monogamous males) defended smaller territories which were located closer to redwing breeding nests than were the territories of males with lower realized than observed reproductive success (most often the polygynous males). Interspecific competition between redwings and marsh wrens may have limited the ability of some males, perhaps the cuckolding (mainly monogamous) males, to attract a second female (Picman 1988). The levels of extra-pair fertilizations may have been higher for monogamous males as a result of their territories being located closer to redwing active nests. This closer proximity to redwings may have limited the male marsh wren in the number of mates they could attract as a result of heterospecific aggression (Picman 1988). An interesting follow up to this study would be to examine if either a males' realized or observed reproductive success was correlated with the distance to redwing breeding nests and/or the size of the males' territory.

When examining female reproductive success, I found that polygynous females fledged at least an equal number of young (per nesting attempt) as monogamous females in each year of the study. However, in 1979, 1992, and 1993 the trend in the data (mean number of young fledged) suggests that polygynous females fledged slightly more young than monogamous females. Unfortunately, small sample sizes, resulting in the low power of this analysis prevent me from reaching any conclusions on the effect of mating status on female reproductive success. As this analysis included all of the breeding nests in the study population, it is not possible to have a larger sample size. However, I found that the data was consistent for the four years of the study, in that reproductive success for females was not affected by harem size for any of the breeding seasons studied.

Although a fair number of extra-pair fertilizations occurred in this marsh wren population (15 % of nestlings tested, see Chapter 1), I demonstrated that the observed and the realized reproductive success values, for the subset of the marsh wren population tested, were statistically correlated. On the strength of the correlation, I concluded that the observed reproductive success values obtained for marsh wrens in this study can be used as an reasonable index of fitness in additional comparisons (Table 3, Chapter 1).

According to the observational data for the four years of the study, polygyny was beneficial for males in this population in terms of their reproductive success since polygynous males fledged more young than did monogamous males. However, the results in Chapter 1 regarding males' realized reproductive success, suggests that mating polygynously may not be beneficial to male marsh wrens. Polygyny does not appear to be costly to females in this study area since female marsh wrens, in three years of this study, fledged at least as many young as did monogamously mated females.

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Figure Headings

Figure 1: Breeding sex ratio and the percent of polygynous males for 1979, 1982, 1992, and 1993. Trend line and R^2 value included.

Figure 2: Breeding sex ratio and the percent of polygynous females for 1979, 1982, 1992, and 1993. Trend line and R^2 value included.

Figure 3: Date of female settlement per active nest vs distance of males' territory from the upland edge of the marsh (m.), 1992. N=93. R^2 of less than 0.05 indicates no relationship between the independent and dependent variables.

Figure 4: Date of female settlement per active nest vs vegetation density on males' territory in 1993, N=45.

Figure 5: Male reproductive success (mean (± s.d.) number of fledglings) for males with harems of one (N=19), two (N=21), three (N=14), or four (N=3) females, in 1979.

Figure 6: Male reproductive success (mean (± s.d.) number of fledglings) for males with harems of 1 (N=39) and two (N=10), in 1992. Bachelor males (N=5) were not included in this analysis.

Figure 7: Male reproductive success (mean (± s.d.) number of fledglings) for males with harems of one (N=6), two (N=5), or three or more (N=3) females, in 1993.

Figure 8: Pearson Correlation of observed (number of young fledged from male's nests) and realized (number of young sired by males as determined through DNA Fingerprinting) reproductive success of individual male marsh wrens, r=0.75, N=15.

Figure 1:

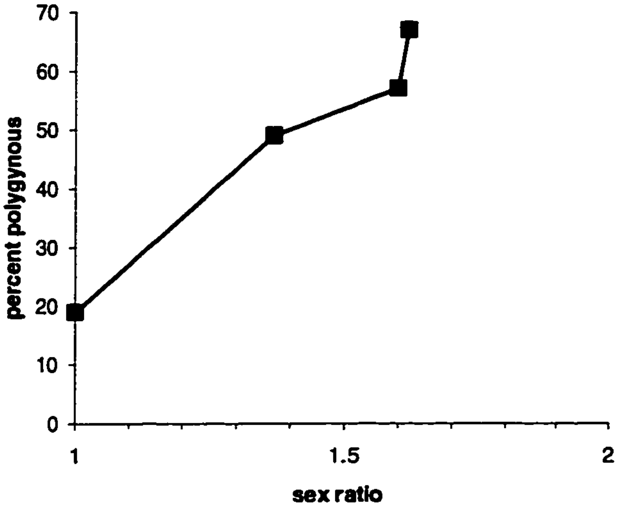
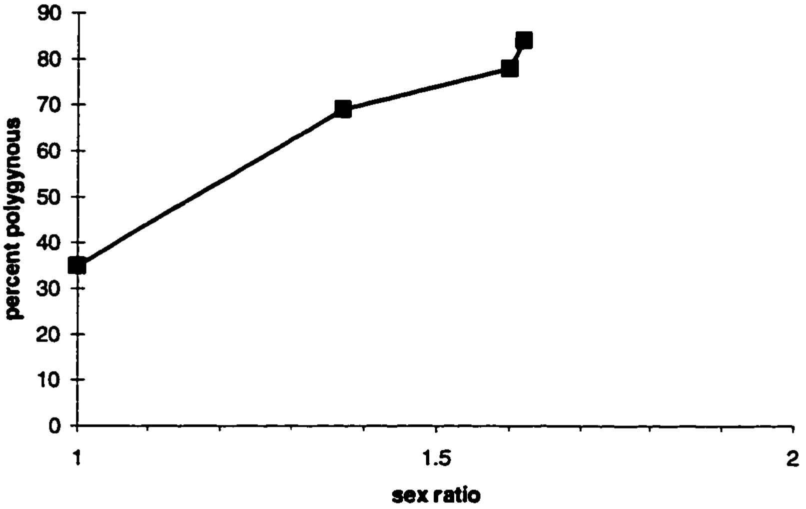


Figure 2:



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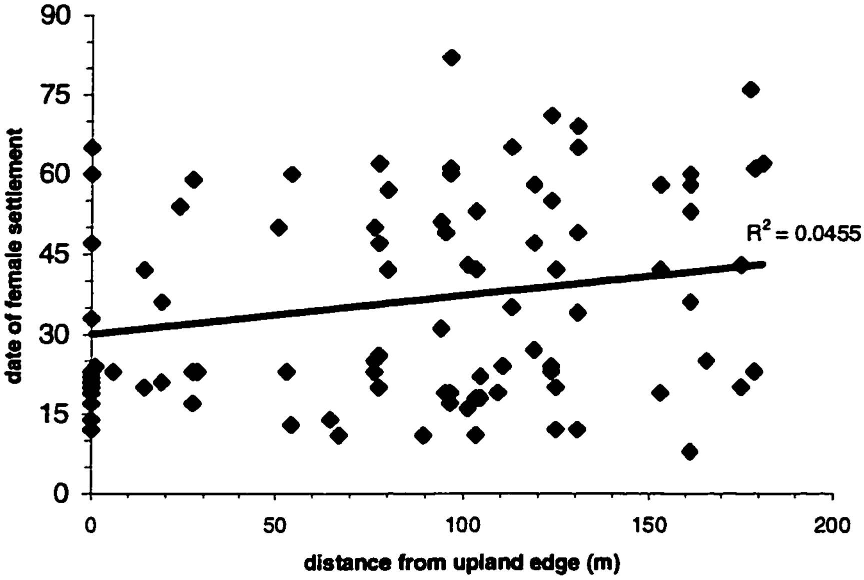


90
75
60
45
30
15
0
date of female settlement
0
50
100
150
200
distance from upland edge (m)
R² = 0.0455

Figure 4:

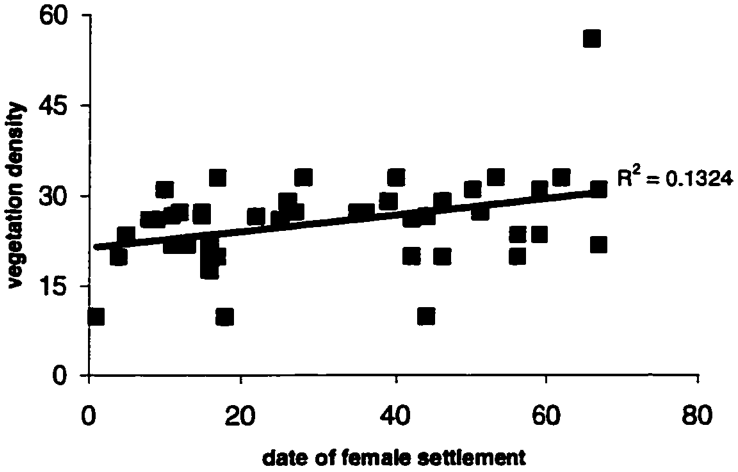
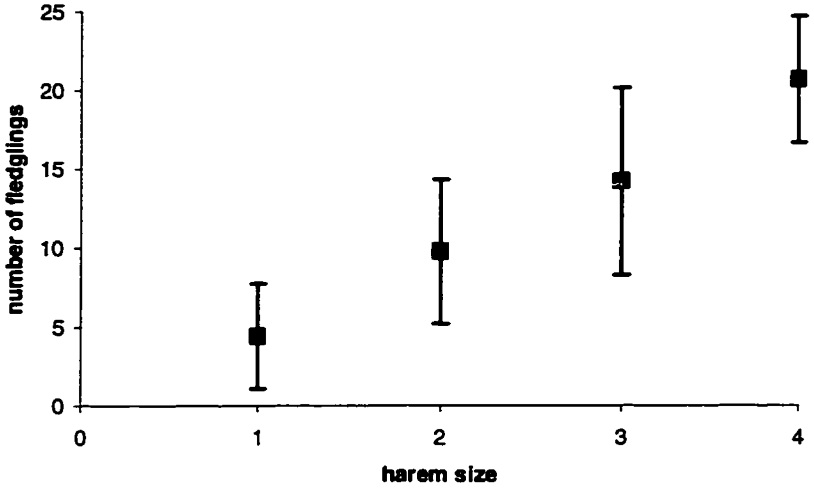

60
45
30
15
0
vegetation density
0
20
40
60
80
date of female settlement
$R^2 = 0.1324$

Figure 5:



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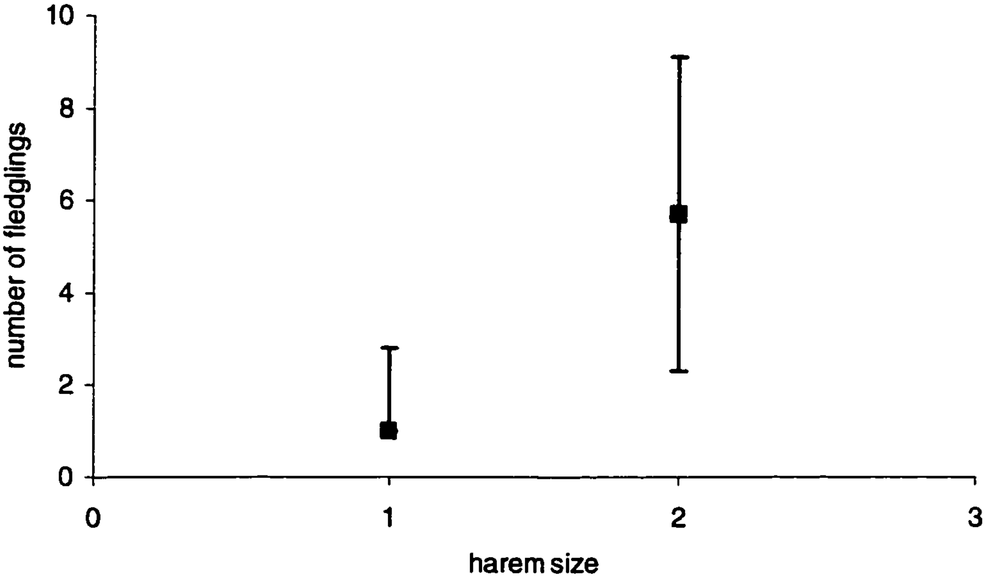

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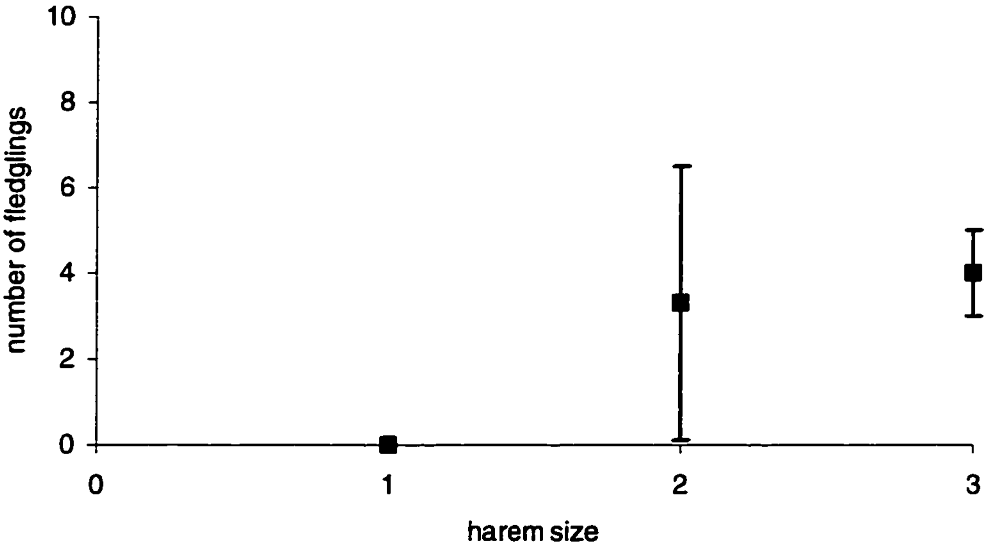

Figure 8:

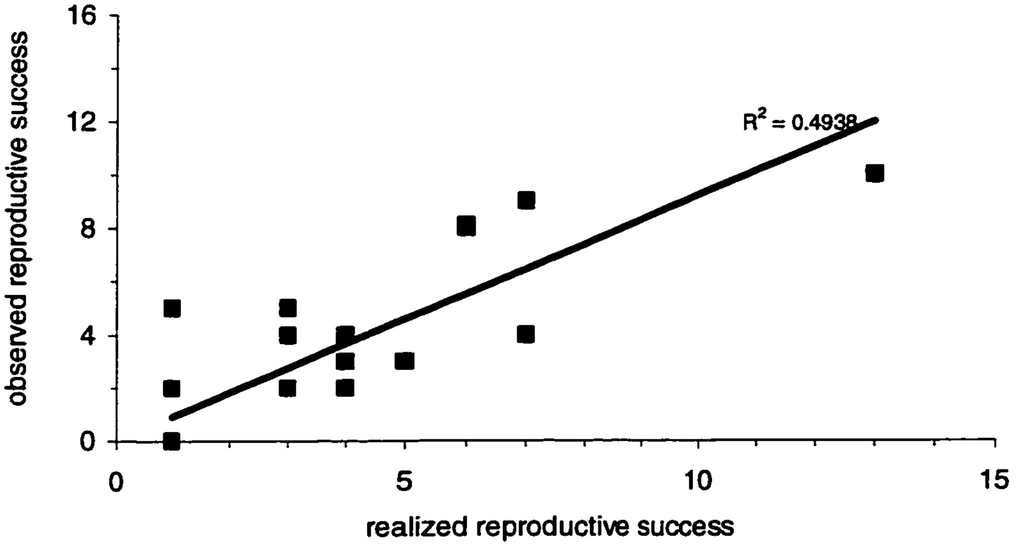
16
12
8
4
0
0
5
10
15
observed reproductive success
realized reproductive success
$R^2 = 0.4938$

Table 1: Degree of Polygyny in Marsh Wrens for Males Defending Territories and Breeding Females in 1992 and 1993.

	1979	1982	1992	1993
Males	38/57 (67%)	28/57 (49%)	10/54 (19%)	8/14 (57%)
Females	98/117 (84%)	65/94 (69%)	19/54 (35%)	18/23 (78%)

Table 2: Settlement dates (mean number of days ± s.d.) of primary polygynous and monogamous females for 1979, 1982, 1992, and 1993. Sample size (N).

year	**primary polygynous**		**monogamous**	
		N		N
1979	28.4 (20.05)		32.88 (26.1)	19
1982	38.28 (17.01)	36	39.73 (20.63)	60
1992	35.8 (19.67)	20	34.7 (19.24)	62
1993	20.31 (18.21)	13	92.3 (177.28)	10

Table 3: Mean Values (± s.d.) for the Male and Habitat Variables Tested in 1979 and 1982. * indicates data unavailable.

	1979	1982
Male Variables		
male weight (g)	12.3 (± 0.5)	*
male wing length (cm)	52.4 (± 1.4)	53.1 (± 0.6)
Habitat Variables		
territory size (sq.m.)	1307.8 (± 1627.2)	1409.8 (± 776.1)
nests (complete)	*	*
vegetation density	32.1 (± 7.3)	*
distance to upland edge (m)	84.8 (± 63.1)	80.8 (± 66.7)
distance to marsh wren territory (m)	24.6 (± 11.4)	18.9 (± 19.1)
distance to redwing active nest (m)	25.0 (± 15.1)	26.9 (± 19.4)

Table 4: Mean Values (± s.d.) for the Male and Habitat Variables Tested in 1992 and 1993.

	1992	1993
Male Variables		
male weight (g)	12.5 (± 0.98)	12.71 (± 0.57)
male wing length (cm)	53.07 (± 1.98)	52.36 (± 0.95)
Habitat Variables		
territory size (sq.m.)	407 (± 327)	1065 (± 681)
nests (complete)	12.52 (± 5.59)	12.21 (± 4.81)
vegetation density	42.82 (± 8.06)	24.3 (± 6.17)
distance to upland edge (m)	82.22 (± 55.98)	77.02 (± 54.21)
distance to marsh wren territory (m)	12.18 (± 8.17)	22.61 (± 13.75)
distance to redwing active nest (m)	33.38 (± 23.46)	15.38 (± 14.69)

Table 5: Number of complete and breeding nests built by male marsh wrens in 1979, 1982, 1992 and 1993. In parenthesis: percent of total nests built. * indicates data unavailable.

	1979	**1982**	**1992**	**1993**
# Complete Nests	*	*	686	171
#Breeding Nests	204	156	93 (14%)	45 (26%)

Table 6: Status of breeding nests in 1979, 1982, 1992 and 1993. Nests were categorized as either successful (at least one young fledged), active (still active at the end of the breeding season), failed, or depredated. Number (%).

* indicated no active nests recorded.

	successful	**active**	**failed**	**depredated**
1979	134 (66%)	*	7 (3%)	63 (31%)
1982	49 (31%)	*	9 (6%)	98 (63%)
1992	27 (29%)	5 (5%)	6 (6%)	55 (59%)
1993	12 (27%)	7 (16%)	2 (4%)	24 (53%)

Table 7: Number of eggs and percent of eggs resulting in fledged young in 1979, 1982, 1992, and 1993.

	number of eggs	**percent of young fledged (N)**
1979	940	59 % (550)
1982	602	25 % (151)
1992	391	27 % (106)
1993	209	18 % (38)

Table 8: Reproductive success (mean ± s.d. number of young fledged) for monogamous and polygynous females in 1979 and 1982. N stands for sample size.

mean ± s.d. number of fledglings

harem size	1979	N	1982	N
1	2.24 ± 2.3	54	1.05 (±1.75)	62
2	2.64 (± 2.3)	84	0.99 (±1.62)	69
3	3.08 (± 2.23)	50	0.71 (±1.19)	21
4	3.38 (± 1.71)	16	0.0	4

Table 9: Reproductive success (mean ± s.d. of young fledged) for monogamous and polygynous females in 1992 and 1993. In 1992, asterisks (*) indicate an absence of individuals in that group.

mean ± s.d. number of fledglings

harem size	1992	N	1993	N
1	0.9 (±1.8)	63	0.0	10
2	1.5 (±2.0)	30	1.2 (±1.9)	21
3	*	0	0.9 (±1.6)	8
4	*	0	0.8 (±1.3)	6

Table 10: Male reproductive success (mean ± s.d. of young fledged over the breeding season) for males with harems of 1, 2, 3, or 4 females in 1982, N=57.

harem size	**mean # of fledglings ±s.d.**	**N**
1	1.97 ± 2.56	29
2	3.43 ±2.96	21
3	3.40 ± 2.61	5
4	2.50 ± 0.71	2

Chapter 3:

Importance of Predation in a Marsh Wren Population in Delta, British Columbia

Abstract

Predation of breeding nests may be a strong evolutionary force affecting avian reproductive strategies through female choice of a breeding situation and reproductive success of individuals. The goals of this study were to determine the extent of predation on breeding nests and to relate this to female choice, and male and female reproductive success. In three (1982, 1992,1993) out of four years of this study, over 50 % of breeding nests were depredated. In the fourth year, 1979, only 31% of breeding nests were depredated. In 1979 and 1982, nests of polygynous and monogamous males were depredated nearly equally. However, in both 1992 and 1993, nests of polygynous males were depredated less often than nests of monogamous males. In addition, only in 1992, males with depredated or successful nests on their territories differed in their weight (body mass) and in the distance of their territories to the upland edge of the marsh. Males with depredated nests had a higher mean weight than males with successful nests while males with successful nests had territories located farther from the upland edge than males with depredated nests. Predation by avian predators accounted for nearly 75 % or more of the predation of breeding nests in both 1992 and 1993. The high rate of predation in this study area in all four years of the study indicates that predation of breeding nests greatly affects reproductive success of marsh wrens and may therefore affect female choice of a breeding situation.

Keywords: nest predation, mating status, marsh wrens, *Cistothorus palustris*

Résumé

La prédation des nichées peut être une force évolutive puissante qui peut influencer les stratégies reproductrices des oiseaux au niveau du choix des femelles pour un contexte reproducteur particulier et au niveau du succès de la reproduction. Les buts de cette étude étaient d'établir l'importance du phénomène de la prédation des nichées et de relier ce phénomène au choix des femelles et au succès reproducteur des mâles et femelles. Lors des années 1982, 1992 et 1993, plus de 50% des nichées ont été victimes de prédation. En 1992 et 1993, les nichées des mâles polygynes ont été moins fréquemment victimes de prédation que les nichées des mâles monogames. En 1979, 31% des nichées ont éte victimes de la prédation. En 1979 et 1982, les nichées des mâles polygnes et des mâles monogames ont eté similairement affectées par la prédation. De plus, seulement en 1992, les mâles associés avec des nichées victimes de prédation et les mâles ayant réussi leurs nichées avaient une masse corporelle significativement différente et des territoires situés à des distances significativement différentes du bord terrestre du marécage. Les mâles associés avec des nichées victimes de prédation avaient un poids moyen plus élevé que les mâles avec des nichées réussies. Ces derniers avaient des territoires localisés plus loin du bord terrestre du marécage que les premiers. Les oiseaux sont responsables de près de 75% de la prédation des nichées en 1992 et 1993.

Introduction

Factors affecting nesting success of birds may include predation, starvation, abandonment, infertile eggs, and adverse weather (Ricklefs 1969). Of these factors, predation has been found to be an important selective force affecting the ability of marsh-nesting passerines such as marsh wrens, *Cistothorus palustris*, (Kale 1965), yellow-headed blackbirds, *Xanthocephalus xanthocephalus* (Willson 1966) and red-winged blackbirds, *Agelaius phoeniceus* (Robertson 1972) to reproduce and survive. Among passerines, marsh-nesters have been found to suffer the highest rates of nesting mortality due to predation (Ricklefs 1969), as has been demonstrated in several studies of red-winged blackbirds (Robertson 1972, Holm 1973, Weatherhead and Robertson 1977, Searcy 1979, Orians 1980). In one red-winged blackbird study conducted in Delta, B.C., Picman et al. (1988b) found that predation was the primary cause of nesting mortality, accounting for between 37 % and 52 % of nest failures over the seven years of the study. As a result of the high rates of predation in marsh-nesting passerines, predation may be an important driving force influencing the reproductive strategies of these species (Kruuk 1964, Lack 1968, Ricklefs 1969). Predation may potentially affect the mating pattern by affecting the quality of a males territory to potential mates. If a male's territory has suffered a great deal of predation, it is likely that this male may have difficulty in acquiring additional mates throughout the season.

The extent to which predation may affect avian reproductive systems may depend on factors such as intensity of nest defense, predator type and density, ease of predator detection of prey, and/or temporal or spatial predictability of predation events (Picman

1988a). The type of predator, be it mammalian, avian, and or reptilian, is most often inferred from the condition of the depredated nest and its contents noted at the time of discovery (Sealy 1994). In some cases, conclusive determination of predator identity has been obtained using cameras to observe nest site activities (Barkley 1972, Hussell 1974, Picman 1987, Major 1991).

Marsh wrens are sexually monomorphic passerines (Welter 1935, Verner 1965). High rates of intraspecific nest destruction by male and female marsh wrens have been demonstrated by Picman (1977). Nest destruction by females is thought to result in reduced competition for male parental assistance and/or territory resources within harems (Picman 1977). In previous studies of marsh wrens, predation rates of breeding nests have varied greatly from 18.5 % (Verner 1965) in Washington State, to 40.2% (Leonard and Picman 1987) in Delta, Manitoba, to highs of between 58.4% and 93.2% (over four years) in Georgia (Kale 1965).

Although predation has been found to occur at varying levels in studies of marsh-nesting passerines, including marsh wrens, the role of predation affecting a female's choice of territory or mate or an individual's reproductive success, needs further examination.

The goals of this study were: (1) to determine the role of predation in determining nesting success in a population of marsh wrens in Delta, British Columbia, Canada; (2) to determine the type of nest predators; (3) to examine differences in nest predation patterns between nests of monogamous and polygynous males; and (4) to relate these findings to factors affecting female choice, and male and female reproductive success.

Methods

This study was conducted at the George C. Reifel Migratory Bird Sanctuary, in Delta, British Columbia, Canada, between April and July of 1979, 1982, 1992 and 1993. The study site has been described in detail elsewhere (see Chapter 2). Data on male mating status (number of simultaneously breeding females), location and stage of nests (egg laying, incubation, nestling, fledgling) , condition of breeding nests (active, failed, depredated, successful), and type of predator (avian or mammalian) for depredated nests were collected during bi-weekly nest checks.

Breeding nests were defined as active nests if the nests contained eggs or nestlings. Nests were defined as failed if the eggs in the nest were cold (abandonment), or stuck to the lining (weather, flooding) of the nest, or when dead nestlings were found in the nest apparently unharmed (starvation). If a nest was found empty prior to the fledging period (day 12-14 post hatching) it was considered depredated. However, if a nest was found empty after this period (day 16-20 post hatching), with no evidence of predation at or around the nest, then nestlings were considered to have fledged and the nest to be successful (Leonard and Picman 1987).

I determined the type of predator for each predation event in 1992 and 1993 according to the appearance of the depredated nest following Leonard and Picman (1987). Data on the type of predator was not collected in 1979 and 1982. If the nest was still intact with only the contents (eggs or nestlings) missing or if broken pieces of the eggs were found in the nest, I considered the nest to be depredated by an avian predator. If I found nestlings in or around the nest with small holes in their heads I considered them also to be depredated by avian predators, most likely marsh wrens (Picman 1977). Nests which I found to be torn from the cattail stalks, ripped open from the top or at the entrance hole with the contents missing or with pieces of nestlings in or around the nest, I considered to be depredated by a mammalian predator. Possible predators, previously observed in this study area include marsh wrens, crows (*Corvus brachyrhynchos*), marsh hawks (*Circus cyaneus*), and raccoons (*Procyon lotor*) (Picman et al. 1988a).

Throughout this study, statistical analyses involved parametric statistics where possible. Male and territory traits (independent variables) were compared for nests being depredated or successful (dependent variable) with Multiple Regression Analyses. In these analyses comparing a dependent variable (e.g., a nest being depredated or not) was to determine if these nests differed in the traits of the male or territory where that nest was located. From the results, I hoped to relate why a nest was depredated or not to a measurable male or territory trait. In cases where the data was found not to be normally distributed, non-parametric tests (Logistic Regression) were employed.

Results

Of the breeding nests, 31 % (63/204) were depredated in 1979 and 63% (98/156) were depredated in 1982, while 59 % (55/93) of breeding nests were depredated in 1992 and 53% (24/45) of breeding nests were depredated in 1993.

In three (1982, 1992, 1993) out of four years of the study, I found that over 50% of the active nests were depredated while less than 35 % of the active nests were successful. In order to determine if this number of nests depredated was significantly higher than the number of nests which were successful over the four years of the study, I compared the number of breeding nests which were depredated or not depredated for the four years of the study together. I found that there were significantly more nests depredated than not depredated (χ^2=42.79, d.f.=3, P<0.001; Table 6, Ch2).

I found that the number of depredated and not depredated nests for monogamous and polygynous males was not significantly different in three (1979, 1992, 1993) out of the four years of the study (see Table 1 for χ^2, P values, and results of power analyses). When examining the data for 1979, 1992, and 1993, I concluded that there was no significant difference in the number of nests depredated for monogamous and polygynous males. I based this conclusion on two points: (1) the strength of power analyses in 1992 and 1993; and (2) on the basis of the trend in the data for these three years. This trend suggests that monogamous and polygynous nests did not differ in their likelihood of being depredated. However, when I examined the four years together, I found that there was a significant effect of mating status (Table 1). This result is not unexpected since the percent of nests depredated on polygynous males' territories was lower than that of monogamous males in 3 out of 4 years of the study (Table 1). However, in two of the those years the sample sizes were too small for these trends to be statistically significant.

In order to determine if males with depredated or successful nests on their territories differed in their male or territory traits (see Chapter 2 for list of traits), I compared the males' physical and the males' territory traits for males with all (male physical and territory, see Chapter 2) traits measured and for males where only data for territory traits was available, for each year separately. As described below, in three (1979, 1982, 1993) out of the four years of this study, I found there to be no significant relationship between a nest being depredated and any male physical or territory trait.

In 1979, I found that no male or territory variables were significantly associated with a nest being depredated (Multiple Regression; F=1.302, N=204, P=0.26, Power = 0.556). The high power of this analysis strongly supports the finding that in 1979 there is no relationship between male and territory traits and a nest being depredated. In light of the earlier result that monogamous and polygynous males did not differ in the percent of nests depredated, this finding is not surprising. The lack of a relationship in these two analyses may have resulted from the fact that predation was relatively low in 1979.

In 1982, I again found that there was no relationship between male or territory traits and a nest being depredated (Multiple Regression, F=0.37, N=141, P=0.83, Power = 0.229). A lack of a relationship between a nest being depredated and the male or territory traits may be the result of there being no feature of the male or the male's territory which make a nest more susceptible to predation.

In 1993, no significant differences were found for male or territory traits either for nests of males with all traits (N=26, Logistic Regression, P >0.05) or for nests of males with only territory traits measured (N=45, Logistic Regression, P >0.05). This lack of any trend (in 1979, 1982, and 1993) suggests that in spite of the low statistical power of some of these analyses, that there is some confidence in the conclusion of no relationship.

In 1992, I found for nests of males with all traits (N=44), that male weight was significantly associated with a nest being depredated (Logistic Regression, Concordance =

57%, P=0.03), with a higher mean weight for males with depredated breeding nests (12.89 ± 1.31 g (s.d.)) than for males with successful nests (12.11 ± 0.55 g (s.d.)). The comparison of territory traits for all males (N=87) with depredated and successful nests in 1992, indicated that the mean distance to the upland edge was significantly shorter for territories with depredated nests than for territories with successful nests (Logistic Regression, Concordance = 60%, P=0.05). Distance to upland edge for territories with depredated nests was shorter at 72.6 meters (± 54.33 s.d., N=32) than for territories with successful nests at 97.98 meters (± 59.78 s.d., N=55).

To determine if heavier males built more nests or defended territories closer to the upland edge of the marsh, for the 1992 data, I examined, in two analyses, male weight, the number of nests built per male, and the distance to the upland edge. I found no significant relationship between male weight and the number of nests a male built (Table 3) or between male weight and the distance of the male's territory from the upland edge of the marsh (Table 4; Simple Linear Regressions: number of nests, F=0.32, d.f.=19, P=0.58, R^2=0.017, Power=0.05; distance to upland edge, F=0.053, d.f.=19, P=0.82, R^2=0.003, Power=0.057). Despite the lack of statistical support, it is interesting to note two trends in the data. First regarding male weight and the number of nests built (see Table 3), I observed that heavier males built fewer nests. Second (see Table 4), I observed that lighter males were defending territories located closer to the upland edge of the marsh. However, as seen in Table 4, two categories with the heaviest males (N=3) defended territories which were at the upland edge of the marsh. A lack of statistical support for these two trends may be the result of the variability in the data as well as low sample sizes.

To determine if more nests were built on territories located farther from the upland edge, I examined the number of nests built per territory and the distance to the upland edge. I found no significant relationship between these two variables (Simple Linear Regression, F=0.30, d.f.=46, P=0.59, Power=0.05). In three previous analyses examining possible factors affecting the number of depredated nests on a male's territory, I was unable to conclude that there was no effect of either male size on the number of nests built, nor male size and proximity of the male's territory to the upland edge of the marsh, nor the number of breeding nests and the location of the territory with respect to the upland edge of the marsh, possibly due to the low power of these analyses resulting from low sample sizes. Therefore, I am unable to conclude that these factors did not affect a nest being depredated during these two breeding seasons.

In 1992 and 1993, I found that avian predators were responsible for the majority of depredated nests in this population. In 1992, 75 % (41/55) of nests were depredated by avian predators, and in 1993, 83 % (20/24) of nests were depredated by avian predators. The percent of nests depredated by avian predators was not significantly different for nests of monogamous or polygynous males (χ^2=1.78, d.f.=3, 0.75 >P>0.50 ; Table 2), although the power of this analysis was low (Power = 0.088), presumably due to a small sample size. The data, however, suggest that predation by avian predators was very important and relatively unaffected by mating status of the territorial male.

Discussion

In this study population, over 50% of breeding nests were depredated in three out of four years of this study. The high level of predation, in this population of marsh wrens, presumably presents a strong selective force affecting individual reproductive strategies (Ricklefs 1969). Similar rates of predation in 1982, 1992 and 1993 indicate that density of the breeding population did not affect the degree of predation in this population.

In 1992 and 1993, the high rate of predation by avian predators may have been due to intense inter- and intra-specific competition for breeding sites and access to territory resources (e.g., emergent insects) (Picman 1988b). Since marsh wrens are known to be highly competitive both with conspecifics and with redwings, increased competition would likely result in higher levels of predation of marsh wren nests by other marsh wrens or by redwings. Appearance of depredated nests, with nests and contents being relatively undisturbed, indicates that marsh wrens were the main avian predator. This is not surprising since intraspecific competition among female marsh wrens has been shown to be high in the Delta, B.C. population (Picman 1977). However, from these results, I cannot conclude that the type of predator, avian or mammalian, had any effect on the reproductive system or reproductive success of individuals in this population of marsh wrens in 1992 and 1993.

As a marsh-nesting passerine, it is not unexpected that marsh wrens would suffer high rates of predation from both avian and mammalian predators (Ricklefs 1969). The topography of the marsh may have also played a role in the high rate of predation, as there was easy access to the marsh via the upland dike by mammalian predators between the two high tides each night.

In 1992, I found that males defending territories with depredated versus successful nests differed significantly in their body mass and the distance to the upland edge. Why less heavy males had fewer depredated nests is unclear. In this population, the majority of polygynous males defended territories at the sea shore edge of the marsh farthest from the upland edge of the marsh (see Chapter 2). Therefore, it is not surprising that in 1992, territories farther from the upland edge suffered less predation. However, in 1979, 1982, and 1993, no male or territory traits were found to differ significantly for depredated and successful nests. Therefore, it is difficult to conclude from these data that rates of predation affected female choice of a breeding situation in these three years of the study. It is also possible that predation of a nest was not affected by any male or territory traits.

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Table 1: Percent of depredated breeding nests of polygynous and monogamous males in 1979, 1982, 1992 and 1993. Number of depredated nests/number of all nests (in parenthesis). Chi-square (χ^2) analysis of number of depredated and successful nests, P values, degrees of freedom (d.f.) = 1 for individual years and d.f.=3 for four years combined, for all analysis. * = Fisher Exact Test.

	polygynous	**monogamous**	χ^2	**P**	**power**
1979	31 % (53/171)	30 % (10/33)	0.016	0.90	0.048
1982	56 % (62/111)	80 % (36/45)	6.99	0.008	
1992	45 % (13/29)	66% (42/64)	2.76	0.10	0.46
1993	49 % (19/39)	83% (5/6)	*	0.19	0.34
total	42 % (147/350)	63 % (93/148)	42.36	< 0.001	

Table 2: Percent of nests depredated by avian predators for polygynous and monogamous males. Number of depredated nests by avian predators /number of all nests (in parenthesis).

Breeding Nests Depredated By Avian Predators

	polygynous	monogamous
1992	77% (10/13)	74% (31/42)
1993	79% (15/19)	100% (5/5)

Table 3: Number (mean ± s.d.) of complete breeding nests built by males vs male weight (g) for 1992.

Male Weight (g)	N	**Number of Nests (Mean (± s.d))**
11.5	4	15.25 (±5.68)
12.0	7	15.57 (±2.94)
12.5	4	13.5 (±3.51)
13	3	12.33 (±10.07)
14	2	10.5 (±4.95)
15.5	1	11.0

Table 4: Distance (mean ± s.d.) from male marsh wren's territory (m) to the upland edge of the marsh vs male weight (g) for 1992.

Male Weight (g)	**N**	**Distance to Upland Edge (mean ± s.d.)**
11.5	4	50.88 (±45.03)
12.0	7	77.82 (±53.96)
12.5	4	106.47 (±82.70)
13	3	118.83 (±91.23)
14	2	0
15.5	1	0

Chapter 4:

Polygyny in Marsh Wrens: Tests of Alternative Evolutionary Models

Abstract

Mating systems, including monogamy, polygyny and polyandry, have been widely studied in a number of avian species. The evolution of polygyny, in particular, has often been attributed to the benefits outweighing the costs for females (who are mating polygynously). In this study, I examined the factors which may have led to the occurrence of polygyny in a population of marsh wrens (*Cistothorus palustris*), a regularly polygynous marsh-nesting passerine, by testing eight of the currently held polygyny models. Models were classified into a hierarchy based on their four key assumptions and four key predictions. In 1979, 1982, and 1992, the occurrence of polygyny in this population could be best explained by the skewed sex ratio and the polygyny threshold models. In 1993, the occurrence of polygyny could be best explained by the random settlement model. Since three out of four years of the study supported female choice/cost/ compensation models, I conclude that the occurrence of polygyny in this marsh wren population is usually associated with a skewed sex ratio in the breeding population and female choice of a breeding territory.

Keywords: polygyny models, mating system, evolution, marsh wren, *Cistothorus palustris*.

Résumé

Les modèles d'accouplement d'oiseaux, incluant la monogamie, la polygynie et polyandrie, ont été étudiés abondamment. L'évolution de la polygynie a souvent été attribuée au fait que les bénifices surpassent les coûts pour les femelles s'accouplant de façon polygynique. Dans ce chapitre, les facteurs pouvant avoir mené à l'apparition de la polygynie dans une population de troglodytes des marécages (*Cistothorus palustris*) sont examinés en vérifiant la pertinence de huit modèles connus de polygynie. Les modèles ont été classifiés selon une hiérarchie basée sur quatre suppositions-clés et quatre prédictions-clés. En 1979, 1982, et 1992, la polygynie s'explique plus facilement par le modèle du "seuil de polygynie". En 1993, les modèles du ratio sexuel biaisé et de la colonisation au hasard semblent mieux expliquer la polygynie. Puisque trois des quatre années de données suggèrent des modèles impliquant un choix de la femelle associé avec une évaluation de coût-compensation, je conclus que la présence de polygynisme dans cette population de troglodyte des marais semble être associée avec le choix du territoire de reproduction par la femelle et un ratio sexuel biaisé dans la population reproductrice.

Introduction

Polygyny is a rare mating strategy among avian species in which one male maintains pair bonds simultaneously with several females (Verner 1964, Verner and Willson 1966, Lack 1968). Polygyny may occur in a population, as a result of females choosing to mate with already mated males, in order to increase their reproductive success through access to better resources such as male parental care, male quality, or territory quality (Verner 1964, Orians 1969, Altmann et al. 1977). However, in order for male or territory traits to affect female choice of a breeding situation they must satisfy three conditions: the traits must affect female reproductive success, be assessable prior to mating, and vary sufficiently between males and territories (Searcy 1979, 1982). Females may use a number of factors to choose a mate. These may include male physical qualities (genetic or behavioural) or territory qualities (Searcy and Yasukawa 1983). A number of studies have determined that female passerines tend to use territory traits, such as food availability, vegetation type and density, quality of the nest site, or safety from predation, rather than male traits in choosing a mate (Verner 1964, Kale 1965, Orians 1969, Holm 1973, Pleszczynska 1978, Searcy 1979). However, some studies have suggested that male traits, such as good genes, reproductive experience, body size, or male parental care, are important for female choice (Weatherhead and Robertson 1979, Yasukawa 1981, Eckert and Weatherhead 1987). At the time of settlement, females may use indirect indicators of future behaviour or future male physical or territory qualities. These may include nuptial feeding, courtship intensity, number of nests built or intensity of territorial defense (Searcy 1979, Searcy and Yasukawa 1981, Wittenberger 1981, Leonard and Picman 1987, 1988).

It has also been suggested that polygyny may occur in the absence of female choice (Searcy and Yasukawa 1989). Following the assumption that all females breed, it is feasible that females may be forced to mate with already mated males due to limited breeding opportunities resulting from few nest sites, a short breeding season or life span, or a female skewed sex ratio where females are forced to mate with an already mated male or not mate at all (Verner 1964).

Ecological factors, such as the temporal and spatial patterns of distribution of resources (e.g., mates, food, and nest sites), may affect the degree of polygyny in a population (Emlen and Oring 1977). When such resources are both economically defendable and unevenly distributed, over space or time, then the potential for polygyny to occur is increased since some individuals will be able to obtain more resources and defend them better than others (Emlen and Oring 1977). Therefore, habitat type may greatly influence the type of mating system observed, as seen in the prevalence of polygyny in marsh-nesting species whose food is abundant but heterogeneously distributed (Verner 1964, Verner and Willson 1966, Greenlaw 1989).

Polygyny Models

Several researchers have proposed possible explanations for the occurrence of polygyny in avian species, in the form of theoretical models (for review, see Searcy and Yasukawa 1989). These models state assumptions, defined here as conditions within the breeding population which facilitate and are necessary for the occurrence of polygyny, and predictions, defined here as situations which should occur, based on the rules of the proposed polygyny theory (Verner 1964, Altmann et al. 1977, Weatherhead and Robertson 1979, Alatalo et al. 1981, Lightbody and Weatherhead 1988, Leonard 1990). These models include: unbalanced (skewed) sex ratio hypothesis (see Skutch 1935); polygyny threshold model, PTM (Verner 1964, Orians 1969); cooperative female choice model (Altmann et al. 1977); sexy son hypothesis (Weatherhead and Robertson 1979); and female deception (polyterritoriality) model (Alatalo et al. 1981); neutral mate choice model (Lightbody and Weatherhead 1988); random settlement model (Lightbody and Weatherhead 1988); and asynchronous-settlement model (Leonard 1990).

I. Skewed Sex Ratio Hypothesis

The skewed sex ratio hypothesis was first introduced by Skutch (1935) and has been elaborated by Mayr (1939), Verner (1964), and Wittenberger (1976). This hypothesis assumes: (1) no reproductively capable unmated males are available at a time when some females settle with already mated males; and (2) a female biased sex ratio leads to polygyny. Females, according to this hypothesis, are forced to pay the cost of polygyny or forgo reproduction because of the unavailability of unmated males.

II. Balanced Sex Ratio Hypothesis

Two key assumptions of the balanced sex ratio hypothesis include: (1) unmated males are available when females mate with already mated males; and (2) an even (1:1) sex ratio exists in the population. All of the eight models tested in this study, discussed below, are based on the assumption of a balanced sex ratio in the breeding population.

1) Polygyny Threshold Model

According to the polygyny threshold model (Verner 1964, Orians 1969), polygyny may occur in a population when females mating with an already mated male in a good quality breeding situation have at least the same fitness gains (reproductive success) as females mated with a monogamous male in a poor quality breeding situation (Verner 1964, Orians 1969). The assumptions of the polygyny threshold model are: (1) females make a choice of mate based on traits of available males and/or their territories; (2) females who mate polygynously incur costs due to sharing resources (e.g., food, male parental care); (3) females are compensated for mating polygynously by acquiring a higher quality mate and/or territory; and (4) females must be aware of the presence of other females at time of settlement (Verner 1964, Orians 1969, Altmann et al. 1977). The polygyny threshold model predicts: (1) male or territory traits of polygynous males correlate positively with harem size, in that females mating polygynously have a higher quality breeding situation than do monogamous females; and (2) secondary and monogamous females settling at the same time have equal fitness gains.

2) Sexy Son Hypothesis

The sexy son hypothesis (Weatherhead and Robertson 1979) is an extension of the polygyny threshold model. The sexy son hypothesis is a female choice model based on the quality of the male's territory and the quality of the male. The threshold that must be met for polygyny to be adaptive to females according to this model is not differences in breeding situation quality (as in the polygyny threshold model; Verner 1964, Orians 1969), but rather it is differences in female's long term fitness gains realised through her sons. According to the sexy son hypothesis females may initially have a lower reproductive success by choosing the highest quality male which may defend a low quality territory, in order to obtain the good ("sexy") genes for her sons. Sexiness of the male is assumed to be inherited by his sons. As a result, the female is compensated for mating polygynously by long term fitness gains through her "sexy" sons. The assumptions of this model include: (1) females assess quality of the male independently of the male's territory quality; (2) females use both male quality and male's territory quality when choosing a mate; (3) high quality males may not possess high quality territories; (4) females mating with males of high quality possessing low quality territories may initially have a lower reproductive fitness than females mating with males possessing high quality territories; and (5) male fledglings of these females inherit some of their father's attractiveness and as a result attract more females and produce more offspring, then females are compensated for the initial lower reproductive success by having higher long-term fitness realised through their sons (Weatherhead and Robertson 1979). The sexy son hypothesis predicts: (1) harem size does not necessarily correlate with the current male or territory traits, but may correlate with reproductive success of the female's sons; and (2) reproductive success, in the current breeding season, of polygynous females may be less than that of monogamous females, since they are not compensated for the costs of mating polygynously.

3) Cooperative Female Choice Model

The cooperative female choice model (Altmann et al. 1977) is based on female choice and states that a female's fitness may be improved by the addition of co-wives to her harem as a result of co-operative interactions within the group of females (e.g., due to detection of predators and group defence) (Lazarus 1972, Altmann 1974). This model assumes: (1) if a male's harem has not reached its maximum number, where female fitness is also maximised (point of diminished returns), the addition of another female will improve the fitness of all the females in the harem; and (2) females are compensated for mating polygynously by gains, such as co-operative nest defence (Altmann et al. 1977). This model predicts: (1) within limits, female reproductive success will increase as harem size increases; and (2) female settlement should be spatially clumped. One limitation of this prediction is that it does not distinguish between breeding situations where female reproductive success is affected by territory or male quality rather than female-female cooperative interactions.

4) Female Deception Model

The female deception (polyterritoriality) model (Alatalo et al. 1981) explains the evolution of polygyny where a male defending two or more spatially separated territories is attempting to attract a female to each of his territories. According to this model, females are unable to establish at the time of settlement the males' mating status. The assumptions of this model are: (1) males are able to conceal their mating status by being polyterritorial; (2) females mating polygynously suffer costs (e.g., reduced male parental care); (3) secondary females are not compensated for mating polygynously; (4) secondary females have a high search cost (in searching for mates) and a restricted search pattern (von Haartman 1969, Alatalo et al. 1981). The female deception model predicts: (1) male or territory traits correlate positively with harem size since female choice is largely based on quality of the nest site; and (2) secondary females have lower reproductive success (number of fledglings) than monogamous and primary polygynous females settling at the same time. This second prediction is based on observations made on the pied flycatcher, *Ficedula hypoleuca* (Alatalo et al. 1982) that monogamous and primary polygynous females are assisted by the male in feeding their young more often than are secondary females nesting at the same time.

5) Neutral Mate Choice Model

Lightbody and Weatherhead (1988) first introduced the neutral mate choice hypothesis as a model for the evolution of polygyny. This model proposes that female choice of a breeding situation is neutral, in that her random choice of where and with whom to mate with does not affect her reproductive success. This model assumes: (1) females sharing territories are neither co-operative nor competitive; (2) variation in differences in male or territory quality does not explain variation in female fitness or harem size; (3) male and territory qualities are unpredictable at time of settlement; (4) female choice is random, but optimal in that the breeding situation of the female will not affect her reproductive success; and (5) expected reproductive success for females sharing a territory is equal (Lightbody and Weatherhead 1988). The neutral mate choice model predicts: (1) harem size is not correlated with reproductive success, for females settling at the same time; and (2) if females settle randomly with respect to male and territory traits, then harem size should correlate positively with territory size.

6) Random Settlement Model

The random settlement model (Lightbody and Weatherhead 1988) assumes females do not choose breeding situations based on male or territory traits. In this model, female choice is random and not optimal in that female reproductive success may be affected by her breeding situation (Lightbody and Weatherhead 1988). This model assumes: (1) female settlement is random; (2) females can assess male and territory traits at the time of settlement but that settlement is random with respect to these traits; and (3) variation in male and/or territory traits may affect female reproductive success. The random settlement model predicts: (1) the distribution of matings throughout the breeding area will be random; and (2) female reproductive success will correlate positively with male and/or territory traits.

7) Asynchronous Settlement Model

The asynchronous settlement model (Leonard 1990) proposes that females on the same territory settle asynchronously in order to reduce the costs of mating polygynously. According to this model, the threshold that must be reached for polygyny to occur is the degree of asynchrony in female settlement which would compensate females for the costs of mating polygynously. This temporal threshold must be large enough so that polygynously mating females do not have reduced reproductive fitness as a result of decreased male parental care due to overlapping nesting stages of other females on the same territory. This model assumes: (1) females choose to mate with already mated males; (2) females settle asynchronously to compensate for the costs of mating polygynously, by reducing competition for male parental care; and (3) females should be able to detect the presence of another female in the male's territory and determine that female's stage of nesting (Leonard 1990). The asynchronous settlement model predicts: (1) the days between female settlement correlate positively with female reproductive success, in that the more asynchronous the settlement between females on a territory, the greater their reproductive success; and (2) secondary and monogamous females settling at the same time should have equal reproductive fitness, since secondary polygynous females are compensated by higher levels of male parental care.

Tests of the assumptions and predictions of the polygyny models have been carried out for a few species (e.g., red-winged blackbird, *Agelaius phoeniceus*, Weatherhead and Robertson 1977; marsh wrens *Cistothorus palustris*, Leonard 1990; pied flycatcher, Alatalo and Lundberg 1990; house wren *Troglodytes aedon*, Johnson et al 1993). However, these tests have usually involved testing only one or two models at a time (Altmann et al. 1977, Garson et al. 1981, Lightbody and Weatherhead 1987, Leonard 1990, Slagsvold and Lifjeld 1994).

Searcy and Yasukawa (1989) proposed a hierarchy of the polygyny models based on their assumptions, as a way in which all of the models could be tested simultaneously. By testing between the alternative hypotheses, it may be possible to determine which hypothesis (-es) best explains the occurrence of polygyny in a given species (Searcy and Yasukawa 1989). Testing of the theoretical models should involve testing of both the assumptions and predictions of the models (Davies 1989). Testing the assumptions of any model must first be carried out prior to testing any predictions, because if the assumptions are not validated, then the model must be rejected (Wittenberger 1976). Following this step, for models where the assumptions were validated, the predictions of the models can be tested.

In order to determine why polygyny has occurred in this population of marsh wrens, I tested eight of the currently held polygyny models using a modified approach of Searcy and Yasukawa (1989). In order to determine which model or models best describes the occurrence of polygyny in marsh wrens, I sequentially eliminated models as possible explanations by testing their key assumptions. I then distinguished between the remaining models using the predictions of those models (see Table 2). Using this approach I was able to distinguish between the models without having to test all of the assumptions and predictions of each model.

Hierarchical organization of polygyny models

In this study, I categorized the models in a hierarchy according to their key assumptions (breeding sex ratio, choice, cost, and compensation) (see Table 1). The models I tested differed in at least some of their key assumptions (see Table 2), enabling me to establish their plausibility as potential explanations for the occurrence of polygyny in marsh wrens. The models were divided by their assumptions into first, skewed/balanced sex ratio, second, choice/no choice, third, cost/no cost, fourth, and compensation/no compensation models (Table 1). A female biased skewed sex ratio may lead to the occurrence of polygyny in a population assuming that all females in a population breed. However, there are several examples of populations where polygyny occurs despite the fact that the adult sex ratio in the breeding population is even or despite the presence of unmated males (Willson and Pianka 1963, Verner 1964, Orians 1969, Wittenberger 1976, Altmann et al. 1977). Choice models assume that females choose their breeding partner on the basis of the traits of his and/or his territory. Thus if female choice is occurring, females should settle non-randomly with respect to male or territory traits, and harem size should correlate positively with female reproductive success and/or male or territory traits. Cost models assume that there is a cost to mating polygynously, in that females in larger harems suffer fitness losses due to mating polygynously. No-cost models assume that females to not suffer costs due to mating polygynously. Compensation models, contrary to no-compensation models, assume that any losses suffered due to breeding polygynously are compensated by access to high quality breeding situations (e.g., better resources, increased parental care, or genetic quality of the male; Verner 1964).

In order to further distinguish between the models, I selected the predictions which allowed me to distinguish between models which are grouped together (i.e., cost/no compensation models, such as sexy son and female deception models) (see Table 2). The first prediction examines a relationship between male physical quality and/or male's territory quality and female reproductive success. The random settlement model predicts a positive correlation whereas the neutral mate choice model predicts no correlation. The second prediction examines how mating status (harem size) affects female reproductive success, allowing me to distinguished between the cooperative model and the four competitive models (polygyny threshold, sexy son, deception, asynchronous settlement models). The cooperative female choice model predicts that as harem size increases within certain limits, female reproductive success should increase. According to the cooperative female choice model a female's reproductive success should increase until the point of diminished returns, at which point (a certain number of co-wives) further increases in harem size may result in decreased reproductive success for the females due to increasing intensity of competition among them for limited resources. The competitive models (polygyny threshold model and female deception model, sexy son hypothesis) predict that female reproductive success will decrease with addition of females to any given territory. The third prediction relates male and territory traits to harem size. The polygyny threshold and female deception models predict a positive correlation. The sexy son hypothesis predicts that a male trait (the sexiness of the male) should correlate with harem size in a positive manner. More specifically that the sexier the male, the higher the reproductive success of the females' male offspring in the future (Weatherhead and Robertson 1979). However, it is beyond the scope of this study to assess the reproductive success of the males offspring in the next breeding season. To provide at least a partial test of this third prediction for the sexy son hypothesis, I examined whether any male trait which I measured correlated with harem size. Finally, the asynchronous settlement model does not predict any relationship between male and/or territory traits and harem size. The fourth prediction relates female reproductive success to the number of days between settlement of primary, secondary, etc. females. This prediction applies specifically to the asynchronous settlement model which predicts a positive correlation. The polygyny threshold model has been developed for simultaneous polygyny and for this reason does not make any prediction on the role of breeding asynchrony in a given harem.

In this study, I examined factors leading to the occurrence of polygyny in a population of marsh wrens in Delta, British Columbia, Canada. To date few polygynous passerine species have been studied using Searcy and Yasukawa's (1989) approach for testing polygyny models (see Johnson et al. 1993). Verner (1964) proposed that in a population of marsh wrens in Washington State, polygyny occurred as the result of variation in the quality of male territories (the amount of emergent vegetation as an indicator of the abundance of food on males' territories). Verner (1964) concluded that the variation was large enough that females mating with already mated males defending high quality territories had higher reproductive success than females mating with males defending low quality territories. These findings led to the development of the polygyny threshold model (Verner 1964). Leonard (1986) examined the evolution of polygyny in a population of marsh wrens in Delta, Manitoba. Leonard (1986) concluded that polygyny occurred in that population not as the result of high levels of heterogeneity among breeding situations (as proposed by the polygyny threshold model), but rather as the result of a high degree of asynchronous settlement among females. The asynchronous settlement model was then developed to explain the evolution of polygyny in the Delta, Manitoba marsh wren population (Leonard 1990).

The goals of this study were: (1) to determine the factors which have led to the occurrence of polygyny in this population and (2) to determine which model (s) offered the most plausible explanation for the occurrence of polygyny in this population of marsh wrens. This second goal was achieved by testing the key assumptions and predictions of the currently held polygyny models.

Methods

This study was conducted at the George C. Reifel Migratory Bird Sanctuary in Delta, B.C., between April and July of 1979, 1982, 1992 and 1993. Details of the study site and data collection can be found elsewhere (see Chapter 2).

Adults, captured using mist nets, and nestlings, taken from nests prior to fledging, were weighed, their wing length measured, and a blood sample taken for later DNA fingerprinting analysis. Detailed description of these procedures can be found elsewhere (see Chapters 1 and 2). Data involving the number of nests, mates, fledglings, male and territory traits, and breeding sex ratio were collected during bi-weekly nest checks of each males' territory (see Chapter 2). Male traits examined included wing length, weight, and aggression. Territory traits examined included number of nests built, territory size, vegetation density, distance from the upland edge of the marsh, distance to redwing active nests, and marsh wren territory boundaries (see Chapter 2).

In order to test each assumption, the following analyses were carried out. To test if the sex ratio was skewed in favor of females, thereby leading to the occurrence of polygyny, I calculated the number of males defending territories and the number of breeding females with active breeding nests for each week of the breeding season. The breeding sex ratio (BSR) was calculated for each week as the number of females divided by the number of males. A breeding sex ratio greater than one indicated a skewed sex ratio in favor of females. I then determined if the weekly breeding sex ratios correlated with the number of polygynous matings in the population measured by the number of breeding pairs which were polygynously mated each week. The breeding sex ratio was calculated for each week of the breeding season as new females may have been settling or resettling after a nest failure (pers. obs.).

For all analyses involving females, I used each nesting attempt as an individual data point (see Chapter 2 methods for further details). Female choice was tested in three ways in order to determine if there were any correlates of female choice in this population and if the choices made by breeding females were adaptive (Searcy 1982). In order to establish if females choose the breeding situation, I proceeded as follow, I first determined if there was a correlation between harem size and any of the male and/or territory traits which I measured (male and territory traits measured are described in Chapter 2). Following that, I tested if male and/or territory traits which correlated positively with harem size also correlated with female reproductive success (number of fledglings). A positive correlation would indicate that a given preference is adaptive; see Searcy 1982). As a third test of female choice, results of the DNA fingerprinting (see Chapter 1) analysis were used to determine if females were generally choosing their social mate as their genetic mate. This third analyses allowed me to examine if females were choosing their social partner as their mating partner.

The test of the random settlement model in 1992 and 1993 involved a comparison of the observed settlement pattern of females in the breeding population to a simulated random settlement pattern of females (calculated using the Poisson distribution). The results of this test and of the correlation analysis (harem size versus male/territory traits) were used to determine whether choice occurred or if females settled at random. Throughout each breeding season, during the bi-weekly nest checks, I determined the number of females breeding on each male's territory and the date each female settled on a territory (estimated from the date the first egg was laid). I calculated the observed settlement pattern by noting how many females settled (initiated new nesting attempts) during each week of the breeding season. I then counted the number of male territories, for each week of the study, which had harems of 0, 1, 2, 3, or 4 females breeding on the male's territory. To establish the random settlement pattern, I calculated the expected number of territories with 0,1,2,3, and 4 females for each week in both years of the study. To achieve this, I used the formula $P(X) = e^{-\mu}\mu^{x}/x!$, where $P(X)$ = the probability of 0, 1, 2, 3, and 4 females breeding per territory; X= the expected number of females per territory; e = natural log; μ = weekly breeding sex ratio. I then compared the observed and expected number of territories with harems of 0, 1, 2, 3, and 4 or more females using Chi-square analysis for each week of the study.

In order to determine if females mating polygynously suffered costs, in terms of reproductive success, I compared the reproductive success of secondary polygynous and monogamous females. I controlled settlement date using ANCOVA to eliminate any affect of settlement date on reproductive success for this analysis in 1992 and 1993. Polygynous females suffered costs in terms of reproductive fitness if secondary polygynous females had a lower reproductive success (number of young fledged) compared to monogamous females. I also examined cost in terms of male and territory traits, since mating polygynously is considered costly to females if they mate with poor quality males or with males defending poor quality territories. Quality refers to features of the male or territory which affect female reproductive success (Searcy and Yasukawa 1989). I assumed that there was at least partial compensation of the costs of breeding polygynously if polygynous females fledged equal numbers of young as monogamous females. Females may also be compensated by mating with higher quality males or with males defending higher quality territories.

Following the tests of the key assumptions, I tested four key predictions of the eight models. To test these predictions I used Logistic Regression, Mann-Whitney U test, Kruskal-Wallis test, and ANOVA. The four key assumptions and key predictions which I tested are listed in Table 2. For each model tested, I indicated (see Table 2) that the data were consistent (Y = yes) or were inconsistent (N = no) with an assumption or a prediction of a given model. Using these two symbols (Y,N), the data are summarized in Table 2 allowed me to distinguish between the alternative models.

Results

Polygyny Models

Results of tests of the four key assumptions and predictions and their consequences for each of the polygyny models are summarized in Table 3.

Assumptions

1. Sex Ratio

I found that the sex ratio was skewed in favor of females in three out of four years (1:1.62 in 1979, 1:1.37 in 1982, and 1:1.6 in 1993) and even in one year (1:1 in 1992). In comparing the number of cases of polygyny and the weekly breeding sex ratio, I found in three of the four years (1979, 1992, 1993) that the number of cases of polygyny did vary with the BSR in the study population (both variables measured weakly) (Table 4 and Table 6) (Simple Linear Regression; 1979: $y=0.94 + 1.16x$, $F=88.55$, $N=12$, $P<0.001$, $R^2=0.90$; 1992: $y = -22.46 + 23.27x$, $R^2=0.76$, $F=29.11$. d.f.=9, $P<0.001$; 1993: $y = -16.28 + 17.36x$, $R^2=0.63$, $F=15.27$, d.f.=9, $P=0.004$). This effect was most pronounced in 1993 when the sex ratio was highly female biased (1:1.6). In 1993 when comparing the weekly sex ratio to a sex ratio of 1:1, I found that the 1993 weekly sex ratio did differ significantly from 1:1 (Mann Whitney U test: $N=11$, $T=181$, $P<0.0001$). This data indicates that the breeding population was usually skewed in favor of females, and that the degree of polygyny increased as the BSR of the population increased, at least in the three years (1979, 1992, and 1993).

However, in 1982, the number of cases of polygyny did not vary significantly with the BSR of the population.(Table 5) (Simple Linear Regression, $y=1.22 + 0.35x$, $F=1.93$, $N=12$, $P=0.20$, $R^2=0.16$, Power = 0.25). Unfortunately, the power of the 1982 analysis is low. Therefore, the 1982 analysis is rather inconclusive.

2. Female Choice: Correlates

When testing for correlates of female choice, in 1979 and 1982 , (as explained below) I found a significant relationship between harem size (harems of 1-4) and two male territory traits (territory size and distance between marsh wren territories; see Chapter 2 methods) in both 1979 and 1982. In 1979 females from smaller harems nested on territories which were nearer to other conspecific territories than were territories of females from large harems. In 1982, the opposite relationship was found. Furthermore, in 1979 and 1982, larger territories attracted larger harems than smaller territories (1979: Multiple Regression: F=12.89, N=57, $P<0.001$, $R^2= 0.56$; territory size $P<0.001$, distance between marsh wren territories $P<0.001$; regression equation: $y = 2.3 + .00034 *$ territory size - .03 * distance between marsh wren territories) (1982:Multiple Regression:F=6.08, N=57, P,0.001, $R^2=0.319$; territory size (P=0.013) and distance between marsh wren territories (P=0.04); $y = 1.59 + .0003 *$ territory size $+ .0001 *$ distance between marsh wren territories).

In three years of this study (1979, 1982, and 1992), the relationship found in this analysis between harem size and territory size does not likely indicate female choice. Rather I suspect that larger territories were a consequence of larger harems since territory size increased as a male acquired new mates and since territory size was measured at the end of the breeding season. These results indicate that female choice of mate may have been occurring in both 1979 and 1982 on the bases of the distance between conspecific territories. However, it should be noted that the effect appears to work in opposite directions in 1979 and 1982.

Testing for correlates of female choice, in 1992, I found that harem size was significantly associated with two territory traits, territory size and distance to the upland edge of the marsh (Logistic Regression: N=93; Concordance = 79.7%, territory size: P=0.001; distance to upland edge: P=0.003). According to these results, in 1992, polygynous females nested on territories which were on average larger (713 m^2 ± 456 s.d.) and farther from the upland edge (96.63 m ± 61.77 s.d.) than monogamous females (territory size: 406 m^2 ± 264 s.d.; distance from upland edge: 78.54 m ± 53.54 s.d.). In 1993, no significant relationship was found between harem size and male or territory variables (Logistic Regression, N=44 (harem size for each breeding nest).

From these data, female choice appears to be occurring as the result of the spacing of territories either from distance between territories or distance to the upland edge. Although territory size was a significant correlate of harem size in three of the four years, I can not conclude that females were choosing since male territories increased in size as they acquired more mates and since territory size was measured at the end of the breeding season.

In order to establish to what extent a female's choice of her breeding situation affects her immediate fitness (i.e., number of fledglings), I examined whether a female's reproductive success (number of fledglings) varied with their male's traits or with the male's territory traits. In both 1979 and 1982, female reproductive success was not significantly associated with different male or territory traits (1979: Multiple Regression; F=0.54, N=204, P=0.75, Power=0.38; 1982: Multiple Regression; F=1.31, N=156, P=0.27, Power=0.63). These results, suggest that neither a female's choice of a male nor his territory traits affected her reproductive success. For the 1979 analysis, the lack of power limits the strength of the conclusion. However, relatively low power of the 1979 analysis suggests that the result has to be interpreted with caution. The relatively high power of the regression analysis of 1982 data, however, suggests that the conclusion for this year is more reliable.

In 1992 and 1993, female reproductive success (number of fledglings) differed significantly for females with different male or territory traits (Logistic Regression: 1992: Concordance = 71.5%, N=93, distance to upland edge P=0.01, territory size P=0.009, vegetation density P=0.02; 1993: Concordance = 66.4%, N=44, territory size P=0.002). In 1992, females with higher reproductive success nested on territories which were farther from the upland edge of the marsh which were larger in size and had vegetation of lower density (Figure 1). During the study I noticed that vegetation was less dense in territories which were in the sea shore areas of the marsh, farthest from the upland edge, where destruction of vegetation was most extensive due to the tides and floating debris. In 1993, reproductive success of females increased with increasing territory size (Figure 2).

From these results, it appears that although females are choosing to mate with their social partner, that they are not suffering in terms of reproductive success as a result of choosing to mate polygynously and thereby competing with other females for territory resources and male parental care.

Female Choice: Random Settlement Model

In 1992, females settled synchronously, while in 1993 settlement of females on males territories was more asynchronous (see Chapter 2 Results for further details). When comparing observed and hypothetical random settlement of females, I found that in 1992, in 9 out of the 11 weeks, the observed and random settlement patterns differed significantly (N=11, P < 0.01) (see Table 7 for χ^2 and P values and Table 8 for observed and hypothetical settlement data) . However, in 1993, the observed and random settlement patterns did not differ significantly in any of the 10 weeks of the breeding season (N=10, P>0.05; see Table 9 for χ^2, P values, and power calculations and Table 10 for observed and hypothetical settlement data). Therefore, the distribution of harems of different sizes in this population of marsh wrens was not random in 1992, but appeared random in 1993. Determining if observed settlement of females was random for each week of the breeding season allowed me to examine if the pattern of settlement changed over the season. It should be noted that some of the Chi-square results in Tables 7 and 9 may have been significant by chance due to the large number of Chi-square calculations in this analysis. Unfortunately, for 1979 and 1982, the random settlement model was not tested due to lack of data.

3. Cost

When examining the cost of mating polygynously I found that in all four years of the study reproductive success of females did not differ for monogamously and polygynously mated females.

To determine if polygynous females suffered costs, in terms of reduced reproductive success, I compared reproductive success of monogamous and polygynous females. Since monogamous and polygynous females settled synchronously in both 1979 and 1982 (see Chapter 2), I compared their reproductive success directly (i.e., without controlling settlement date). In 1979, I found that these two groups of females did not differ significantly in the number of young fledged, with monogamous females fledging

2.24 ± 2.3 s.d. (N=54) young and polygynous females fledging, on average, 2.87 ± 2.22 (N=150) young (Mann Whitney U: T=4941, N=204, P=0.11, Power=0.80). In 1982, monogamously and polygynously mated females also did not differ in their reproductive success (Mann Whitney U : T=4973, N=156, P=0.70, Power=0.18) with monogamous females fledging, on average, 1.05 ± 1.75 (N=62) young and polygynous females fledging, on average, 0.88 ± 1.51 (N=94) young. Therefore, in 1979 and in 1982, females mating polygynously did not appear to suffer lower reproductive success than monogamous females. The high power of the 1979 analysis indicates that this is likely a valid conclusion. In 1982, however, the power of the analysis was rather low and consequently the reliability of this analysis is low. However, as the direction of the means was opposite in 1982 and 1979, it is much more likely that I can accept the null hypothesis for this analysis that polygynous females did not suffer costs in terms of reproductive success.

In examining costs to females of mating polygynously, I found that in 1992 and 1993 combined, that secondary polygynous (N=5) and monogamous (N=13) females which initiated nesting at the same time did not differ significantly in the number of young fledged (ANCOVA, N=18, P=0.89, R^2=.20) or in weight of their fledglings (Appendix 5) (ANCOVA, N=18, P=0.43, R^2=.21). This result suggests that polygynous females did not suffer costs. Therefore, despite the low power of the 1982 analysis, the trends in this data appear to strongly support the conclusion that female reproductive success is not affected by mating status in any of the years of this study.

4. Compensation

In order to determine if females mating polygynously were compensated for the costs of mating polygynously, I examined whether monogamous and polygynous females differed in the traits of their males or their male's territories (their breeding situation). I found in three of the four years (1979, 1982, 1992) of the study that females were compensated in terms of the traits of their social partners' territories. If polygynous females are found to have a higher quality breeding situation (e.g., more fit males, higher quality territory) then this would indicate that they have been compensated for costs of polygyny in some way.

In 1979, monogamous and polygynous (harem size of 2 or more) females did differ in their male's territory traits (Multiple Regression: $F=13.36$, $P<0.001$, $R^2=0.26$). Nests of polygynous females, in 1979, were located closer to each other on adjacent territories ($P<0.001$), nested on territories which were farther from the upland edge of the marsh ($P<0.001$) and were larger in size ($P<0.001$) than monogamous females as shown by the following equation with female status as the dependent (y) variable. (Regression equation: $y = 1.8 + 6.25 \times 10^{-5}$ *vegetation density - 6.152×10^{-4} * distance to redwing active nest - 0.012 *distance between marsh wren territories + 1.954×10^{-3} * distance to the upland edge +9.304×10^{-5} *territory size). Therefore in 1979 females did appear to be compensated in terms of male territorial traits for mating polygynously.

In 1982 monogamous and polygynous females differed significantly in one male territory trait, territory size ($P<0.001$) (Multiple Regression: $F=5.87$, $P<0.0021$, $R^2=0.14$, $N=156$). In 1982 I found no significant relationship between female status and distance to redwing active nest ($P=0.94$), distance between marsh wren territories ($P=0.15$), or distance to the upland edge ($P=0.66$) (Regression equation: $y = 1.29 - 1.63 \times 10^{-4}$ * distance to redwing active nest - 3.95×10^{-3} *distance between marsh wren territories + 2.99×10^{-4} * distance to the upland edge + 2.22×10^{-4} *territory size).

In 1992 I found that polygynous females were compensated at least partially by two territory traits, territory size and distance to upland edge since they selected a higher quality breeding situation (larger territories farther from the upland edge) than did monogamously mated females (Figure 1, see Female-Choice Correlates above for statistical results). In 1993, however, polygynous females did not seem to be compensated by nesting with higher quality males or by nesting on higher quality territories. In 1993, however, females who mated with males who defended larger territories did fledge more young (Figure 2, see Female Choice Correlates above).

In summary (see Table 3), testing the key assumptions I found that the breeding sex ratio was balanced in 1992 but skewed in 1979, 1982, and 1993. I found that the breeding sex ratio did not affect the degree of polygyny in the population in 1992, but did affect the degree of polygyny in 1979, 1992, 1993. In 1979, 1982, and 1992, I found that female marsh wrens were choosing their breeding situation, based on two territory traits, territory size (1979, 1982, 1992), distance to upland edge (1992), and distance between marsh wren territories (1979, 1982). However, in 1993, when settlement was probably random, I found that females were not choosing their breeding situation. In all four years, I found that females mating polygynously did not appear to suffer any net costs, in terms of reproductive success, since polygynous females fledged at least as many young as did monogamous females. However, females may have suffered costs (in terms of competition between females) for which they were compensated, by high quality breeding situations. In 1979, 1982, and 1992 females mating polygynously were at least partially compensated in two ways, in terms of equal reproductive success and in terms of their breeding situation, by mating with males defending higher quality territories. However, in 1993, polygynous females were not compensated in terms of their breeding situation but were at least partially compensated for the costs of mating polygynously in terms of their reproductive success.

Predictions

Testing the models' predictions (see Table 2), enabled me to distinguish between the remaining models (see Table 3 for summary of results). I report here whether the results of the various tests either supported or did not support the predictions of the hypotheses discussed earlier in this chapter. The results of the tests of the predictions in turn either support or contradict the corresponding hypothesis(es). I will discuss the consequences of the tests of the predictions on whether the hypothesis(es) are supported by each years data below.

In testing the key predictions of the polygyny models I found that in both 1979 and 1982, the first prediction (female reproductive success is positively correlated with male/territory traits) was not supported by the results since female reproductive success was not affected by male or territory traits (see section: Female Choice, above). In testing for correlates of female choice (see above), I found in 1992 and 1993 that reproductive success of females was affected by the territory traits of their mate (prediction one: female reproductive success correlating with male/territory traits).

With respect to the second prediction (harem size correlates positively with reproductive success) I found that in both 1979 and 1982 females in harems of different size, did not differ in the number of nestlings fledged. These results, therefore, did not support the second prediction (see Chapter 2 results). Testing the second prediction (effect of harem size on reproductive success), I found that harem size had no significant effect on female reproductive success since females in harems of different size did not differ in the number of nestlings fledged (for details, see Chapter 2).

The third prediction (harem size correlates positively with one or more male traits) was supported in both 1979 and 1982 (see Female Choice above). As found above (female choice: correlates), males' territory traits correlated with harem size in 1992 but not in 1993 (third prediction: a relationship between male and/or territory traits and harem size).

In testing the fourth prediction, I examined if reproductive success (number of young fledged per nest) of secondary and tertiary females correlated positively with the degree of synchrony in female's settlement. In this study, the degree of synchrony was defined as the number of days between the settlement of the primary and secondary females on a male's territory. In 1979 and 1982, I found that female reproductive success was not significantly associated with the degree of synchrony of a females settlement (1979: Spearman-Rank Correlation, r_s=-0.151, N=97, P=0.14, Power=0.31; Table 11) (1982: Spearman-Rank Correlation, r_s=-0.149, N=59, P=0.26, Power=0.20; Table 11). Testing the fourth prediction, for 1992 and 1993, I found that female reproductive success was not significantly associated with the degree of synchrony of female settlement in either 1992 or 1993. (1992: Spearman-Rank Correlation, r_s=-0.204, N=17, P=0.43, Power= 0.12; 1993: Spearman-Rank Correlation, r_s=-0.106, N=22, P=0.63, Power=0.07). From these results, I concluded that female reproductive success was not significantly associated with the degree of synchrony in the settlement of females in any of the four years of this study. As a result of the relatively low power of the analyses for all four years of results, these results must be interpreted with caution.

Discussion

DNA fingerprinting analysis (see Chapter 1) indicated that females, in 1992 and 1993, were not always choosing their social mate as their genetic mate, since 15 % of nestlings tested resulted from extrapair matings of the females with non-socially mated males. This DNA evidence shows that female marsh wrens in this study population are separately choosing their social and genetic partners (see Chapter 2 for further discussion). As well, this result shows that females are choosing their breeding location based on territory traits and not male traits.

Factors Favoring Polygyny

In three of the four years of the study (1979, 1982, 1993), the skewed sex ratio was the most important factor influencing the occurrence of polygyny in this population. As seen below, additionally female choice (1979, 1982, 1992) and random settlement of females (1993) were also important factors influencing the occurrence of polygyny.

Overall in this population, the skewed sex ratio is the main factor causing polygyny to occur, with female choice or random settlement then determining the distribution of the polygynous females in the population.

In both 1979 and 1982, the study population was skewed in favor of females. Additionally, in both years, females preferentially settled with males which defended higher quality territories (territories located farther from other conspecific territories) indicating female choice of a breeding situation. Females settling with already mated (polygynous) males, did not suffer net costs in terms of lower reproductive success, than monogamous females. Since it is expected that polygynous females do suffer some costs, it is quite feasible that polygynously mating females were compensated for costs they faced, in terms of having a higher quality breeding situation than did monogamous females.

The two most important factors affecting the occurrence of polygyny in 1992 were female choice and cost/compensation. In 1992, the results demonstrated that female choice of certain territory traits (territory size and distance to upland edge) occurred in this population and that the choice was beneficial since both harem size and female reproductive success correlated positively with these two traits. In 1992, the results indicated that female choice of a breeding situation was based on territory rather than male quality, since reproductive success of monogamous and polygynous females was not related to their mating status (see Johnson et al. 1993).

However, in 1993, no male or male's territory traits correlated with female choice, since no significant relationship was detected between male or territory traits and harem size. Interestingly, female reproductive success did correlate with territory size in 1993. When comparing observed and hypothetical random settlement patterns, I found that female settlement was random in 1993. Therefore, I conclude that female choice was likely not occurring in this population of marsh wrens in 1993 when females apparently settled at random.

Polygyny Models

In this study, I used a hierarchical organization of the polygyny models to test which model(s) provided the best explanation for the occurrence of polygyny for each year of this study. This strategy allowed me to discriminate among the alternative explanations, as discussed below, in an organized and logical manner.

In three out the four years (1979, 1982, 1992), with females choosing their breeding situation, based on male's territory traits, and a skewed sex ratio in favor of females (1979, 1982), the polygyny threshold (all three years) and skewed sex ratio (two years) models seem to best explain the occurrence of polygyny. In 1993, with females not choosing their breeding situation, a skewed sex ratio favoring females, and random settlement of females, the random settlement and skewed sex ratio models seem to best explain polygyny in 1993. The 1993 results, when considered in contrast with the three previous years, suggest that the type of polygyny is affected by the varying conditions in different years. Therefore, overall when looking at the four years together, the results show that polygyny in this population can best be explained by a combination of two models, the skewed sex ratio and polygyny threshold models. I have explained these conclusions in more detail in the follow two sections of this chapter.

Assumptions

In testing the first assumption (breeding sex ratio correlating with percent of polygyny), the results in 1979, 1982, and 1993) supported the skewed sex ratio model, but did not support the balanced sex ratio model, with a female biased sex ratio correlating positively with the percent of polygynous matings. In 1992, with a balanced sex ratio, the results supported the balanced sex ratio model and did not support the skewed sex ratio model (see Table 3).

In testing the second assumption (female choice), with polygynous females mating with males defending high quality territories (in 1979, 1982, and 1992), the results supported the choice models (cooperative female choice, polygyny threshold, sexy son, deception, asynchronous settlement), but did not support the no choice models (random and neutral mate choice). In 1993, with females settling randomly, the no choice models were supported and the choice models were not supported.

In testing the third assumption (cost), the results in all four years of the study supported the cost models (polygyny threshold, sexy son, deception, asynchronous settlement) but did not support the no cost model (cooperative female choice) since polygynous females did not suffer a net cost in terms of the number of young fledged.

Tests of the fourth (compensation), in 1979, 1982, and 1992, supported the compensation models (polygyny threshold and asynchronous settlement), but did not support the no-compensation models (sexy son and deception models) in 1992 but not in 1993, since polygynous females mated with males defending higher quality territories in 1992. However, the results of this fourth assumption, did not support he compensation models since polygynous females did not mate with males defending higher quality territories in 1993.

In summary, tests of the polygyny models' key assumptions suggest that in 1979 and 1982 that the skewed sex ratio, polygyny threshold, and asynchronous settlement models were plausible explanations for polygyny in these two years of the study, For 1992, testing the key assumptions supported the polygyny threshold and asynchronous settlement models as plausible explanations for polygyny in 1992. For 1993, testing the key assumptions resulted in the skewed sex ratio and the no choice (random settlement and neutral mate choice) models as plausible explanation for polygyny in 1993.

Predictions

As a result of the tests of the key assumptions a number of models which were not supported by the data were eliminated as plausible explanations for polygyny in different years of the study. Therefore, only two key predictions were needed to further distinguish between the remaining plausible models (see Table 3). For 1979, 1982, and 1992, I found that tests of the fourth prediction (degree of synchrony correlated with female reproductive success) supported the polygyny threshold model but did not support the asynchronous settlement model. This is because female reproductive success, all three years, was found to not correlate positively with the degree of synchrony in the settlement of females. In 1993, tests of the first prediction (female reproductive success correlating with male or territory traits) enabled me to distinguish between the random settlement and neutral mate choice models. I found that in 1993, with female reproductive success being correlated with size of her male's territory, that the results supported the random settlement model, but did not support the neutral mate choice model.

In summary, the results for the four years of this study clearly show that the skewed sex ratio model (1979, 1982, 1993) and the polygyny threshold model (1979, 1982, 1992) best explain the occurrence of polygyny in this population.

Using a hierarchical system for testing between the models (see Searcy and Yasukawa 1989), I was able to distinguish between the 8 models without having to test all of their assumptions and predictions. As I have shown in this study, this approach to examining polygyny models was both feasible and practical since I was able to examine all of the polygyny model simultaneously within one study (Searcy and Yasukawa 1989).

However, the final step in studying the occurrence of polygyny in marsh wrens would require experimental manipulation of traits which affect female choice to demonstrate cause-effect relationships.

An inherent problem of testing polygyny models is that, in general, each model has been developed specifically for one population of one species (Verner 1964: marsh wrens, Alatalo et al. 1981: pied flycatcher). As well, it is possible that polygyny may have multiple causation at any one time in the population. As a result, it is not surprising that researchers have had difficulty applying these somewhat species or population specific models in subsequent studies to their study populations and have instead developed their own models (Weatherhead and Robertson 1979, Leonard 1990). Therefore, more studies should involve testing of all possible factors which may have led to the occurrence of polygyny or monogamy in their species without a bias to only one model. And to secondly examine the various factors influencing the occurrence of polygyny between populations of a single species. However, it should be noted that when testing the polygyny models it may be difficult to distinguish between them since some of the models (e.g., sexy son hypothesis, Weatherhead and Robertson 1979; asynchronous settlement model, Leonard 1990), present an extension of another model (polygyny threshold model in this case), and therefore, are not mutually exclusive in many of their assumptions and predictions.

The body of research in this area of behavioral ecology (see Searcy and Yasukawa 1989 for review), has clearly demonstrated that no single model can explain the evolution of polygyny in all avian species or the occurrence of polygyny in individuals within the same population (Alatalo and Lundberg 1990, Johnson et al. 1993). This may be occurring since species and individuals may be affected by different environmental factors. Geographical variation in territory quality, parental care, and other environmental factors among populations of the same species may result in different factors leading to the occurrence of polygyny within that species (Searcy and Yasukawa 1989). Therefore, different theoretical models may be applicable to different populations of the same species, as has been demonstrated in marsh wrens by this and other studies (polygyny threshold model, Verner 1964; asynchronous-settlement model, Leonard 1990).

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Figure Legends

Figure 1 a, b, c: Female marsh wren reproductive success (mean ± s.d.)(number of fledglings) for each nesting attempt vs male and territory traits in 1992.

Figure a: distance to upland edge of marsh (m) from border of male's territory;

Figure b: territory size (sq m) of male's territory where nest was located;

Figure c: vegetation density of male's territory where nest was located. Higher values for vegetation density indicate a lower degree of emergent vegetation).

N=93.

Figure 2: Female marsh wrens reproductive success (mean ± s.d.) (number of fledglings) for each nesting attempt vs male's territory size (sq m) where active nest was located for 1993. N=45.

Figure 1a:

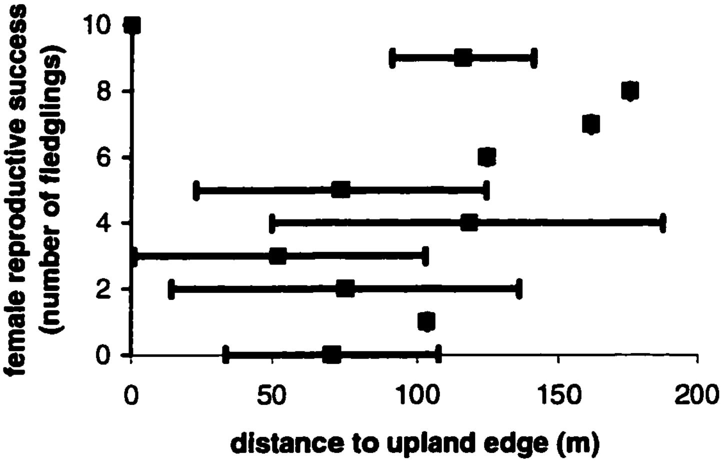


Figure 1b:

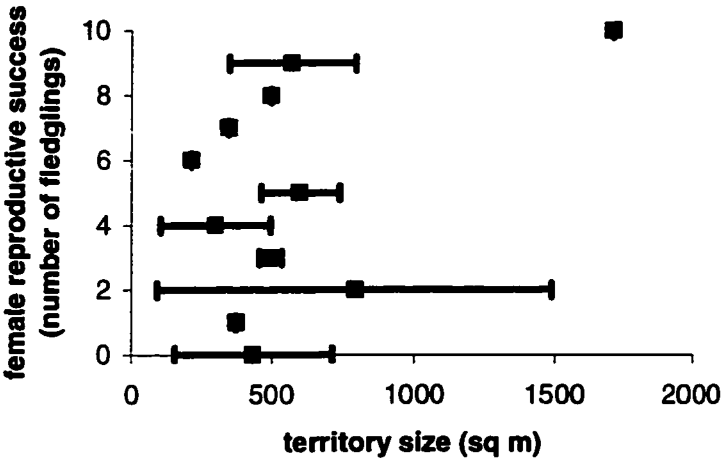


Figure 1c:

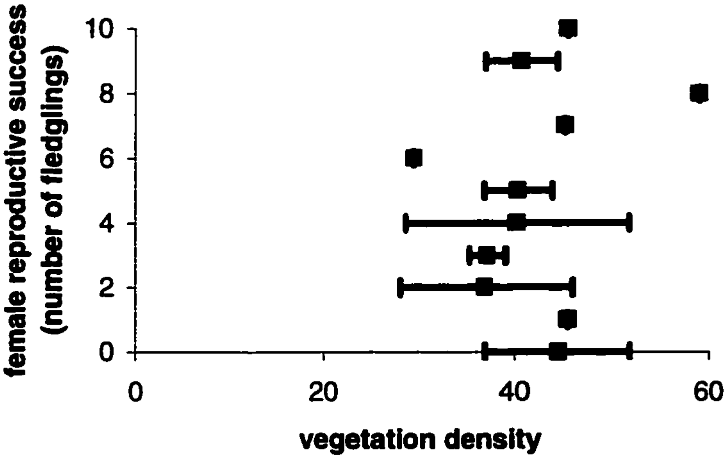


Figure 2:

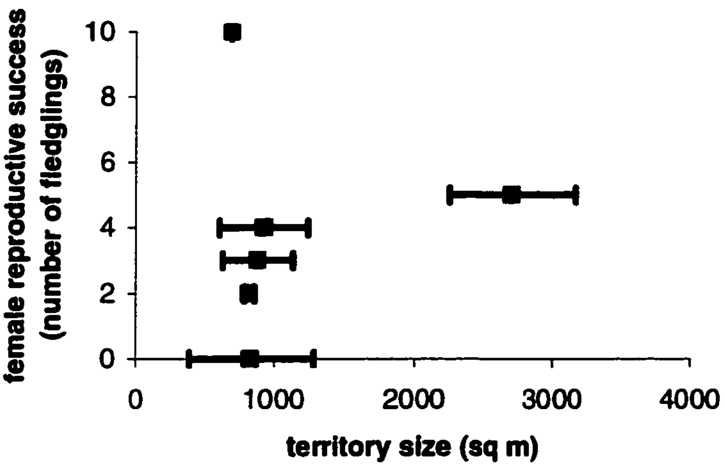

female reproductive success
(number of fledglings)
10
8
6
4
2
0
0
1000
2000
3000
4000
territory size (sq m)

Table 1: Hierarchy of Polygyny Models

MODELS

I. Skewed Sex Ratio

II. Balanced Sex Ratio

- A. Non-Choice Models
    - 1. neutral mate choice model
    - 2. random settlement model
- B. Choice Models
    - 1. No Cost Models
        - a. cooperative female choice model
    - 2. Cost Models
        - a. No Compensation Models
            - 1. sexy son model
            - 2. deception (polyterritoriality) model
        - b. Compensation Models
            - 1. polygyny threshold model
            - 2. asynchronous-settlement model

Table 2: Key Assumptions and Predictions of Eight Polygyny Models.

Models: Skewed Sex Ratio (SKEW), Neutral Mate Choice (NEUT), Random Settlement (RAND), Cooperative Mate Choice (COOP), Polygyny Threshold Model (PTM), Sexy Son (SEXY), Deception (DECP), Asynchronous Settlement (ASM).

Symbols: R.S.= reproductive success, Y= key assumption or key prediction corresponds with assumptions or predictions of the model, N= key assumption or key prediction does not correspond to assumptions or predictions of the model, - = assumption or prediction is not included in assumptions or predictions of the model. * indicates for the sexy son model the third prediction was not tested.

	MODELS							
	SKEW	NEUT	RAND	COOP	PTM	SEXY	DECP	AS
ASSUMPTIONS								
-female biased sex ratio	Y	N	N	N	N	N	N	N
-females choose	-	N	N	Y	Y	Y	Y	Y
-net cost to polygyny	-	-	-	N	N	Y	Y	Y
-compensation for costs	-	-	-	-	Y	N	N	Y
PREDICTIONS								
-female R.S. correlated male/territory traits	-	N	Y	-	-	-	-	-
-variation in harem size explains variation in female R.S.	-	-	-	Y	N	N	N	N
-male traits correlated with harem size	-	-	-	-	Y	*	Y	-
-degree of synchrony correlated with female R.S.	-	-	-	-	N	-	-	Y

Table 3: Results of the tests of the four keys assumptions and predictions for 1979, 1982, 1992, and 1993. Results for each year are indicated by a Y for results which agree with the assumption or prediction and a N for results which do not agree with the assumption.

	1979	*1982*	*1992*	*1993*
assumptions				
-female biased sex ratio	Y	Y	N	Y
-females choose	Y	Y	Y	N
-net cost to polygyny (reproductive success)	N	N	N	N
-compensation for costs (polygynous females higher quality breeding situations)	Y	Y	Y	N
predictions				
-female R.S. correlated with male/territory traits	N	N	Y	Y
-variation in harem size correlated with variation in female R.S.	N	N	N	N
-male traits correlated with harem size	Y	Y	Y	N
-degree of synchrony correlated positively with female R.S.	Y	Y	N	N

Table 4: Breeding sex ratio (BSR) (female:male) and number of cases (%)of polygynous matings for each week of the breeding season in 1979.

week #	BSR (1:)	#polygynous matings
1	1.0	0/11 (0 %)
2	1.08	2/26 (7.7 %)
3	1.45	33/64 (51.6 %)
4	1.57	59/85 (69.4 %)
5	1.85	76/96 (79.2 %)
6	1.98	80/99 (80.8 %)
7	2.11	72/83 (82.8%)
8	1.82	68/91 (74.7%)
9	1.45	38/71 (53.5%)
10	1.77	60/83 (72.3 %)
11	1.80	52/74 (70.3%)
12	1.59	41/62 (66.1%)

Table 5: Breeding sex ratio (BSR) (female:male) and number of cases of polygynous matings for each week of the breeding season in 1982.

week #	**BSR (1:)**	**#polygynous matings**
1	1.0	0/1 (0 %)
2	1.73	2/19 (10.5 %)
3	1.13	8/35 (22.9 %)
4	1.21	19/56 (33.9 %)
5	1.35	32/69 (46.4 %)
6	1.39	35/68 (51.5 %)
7	1.43	43/76 (56.6 %)
8	1.40	46/63 (73.0 %)
9	1.51	39/68 (57.4 %)
10	1.50	40/60 (66.7 %)
11	1.49	32/52 (61.5 %)
12	1.26	14/34 (43.8 %)

Table 6: Breeding sex ratios (female:male) and the percent of breeding pairs mated polygynously in 1992 and 1993.

week		breeding sex ratio	percent polygynous
1992	1	1	0
	2	1.1	0
	3	1.1	9.8
	4	1.1	9.5
	5	1.1	13.5
	6	1.1	8.6
	7	1.1	10
	8	1.2	15.6
	9	1.1	14.8
	10	1.1	14.3
	11	1	7.1
1993	1	1	0
	2	1.125	22.2
	3	1.417	75
	4	1.615	71.4
	5	1.45	77.3
	6	1.5	57.9
	7	1.83	71.4
	8	1.91	63.2
	9	1.55	47.1
	10	1.5	22.2
	11	1.25	22.2

Table 7: Comparison of Observed and Hypothetical Random Settlement Patterns in 1992 by χ^2 analysis.

week	χ^2	**P**
2	52.1	< 0.005
3	30.02	<0.005
4	7.11	<0.01
5	7.31	<0.01
6	23.53	<0.005
7	18.10	<0.005
8	0.57	>0.25
9	2.27	>0.10
10	6.06	<0.025
11	8.5	<0.005
12	6.07	<0.025

Table 8: Observed and hypothetical random settlement patterns for each week of the 1992 breeding season, each week for 0 to 4 females per male territory. Data omitted for cases where there were no females observed on a male territory.

week	# females/territory	observed	hypothetical
2	0	48	17.7
3	0	39	17.7
	1	9	17.7
4	0	22	15.1
	1	26	17.6
5	0	9	15.2
	1	35	17.6
	2	4	10.1
6	0	8	16.0
	1	35	17.6
	2	5	9.7
7	0	10	15.6
	1	33	17.5
	2	5	9.8
8	0	18	15.8
	1	26	17.6
	2	4	9.7
9	0	20	14.3
	1	24	17.3
	2	4	10.5
10	0	22	15.4
	1	21	17.5
	2	5	10.0
11	0	25	16.3
	1	18	17.6
	2	5	9.5
12	0	27	17.7
	1	18	17.7
	2	3	8.8

Table 9: Comparison of Observed and Hypothetical Random Settlement Patterns in 1993 by χ^2 analysis.

week	χ^2	**P**	**power**
2	1.98	>0.10	0.094
3	2.02	>0.10	0.334
4	3.12	>0.05	0.062
5	0.15	>0.50	0.058
6	1.82	>0.10	0.08
7	0.07	>0.75	0.051
8	0.88	>0.25	0.065
9	0.03	>0.75	0.062
10	2.33	>0.10	0.074
11	0.28	>0.50	0.085

Table 10: Observed and hypothetical random settlement patterns for each week of the breeding season for 1993.

week	# females/territory	observed	hypothetical
2	0	11	4.5
	1	3	5.1
3	0	6	3.4
	1	1	4.8
	2	1	3.4
4	0	3	2.8
	1	4	4.5
	2	7	3.6
5	0	2	3.3
	1	6	4.8
	2	4	3.5
	3	2	1.7
6	0	1	3.1
	1	5	4.7
	2	6	3.5
	3	2	1.8
7	0	2	2.2
	1	5	4.1
	2	4	3.8
	3	2	2.3
	4	1	1.1
8	0	3	2.1
	1	5	4.0
	2	4	3.8
	3	1	2.4
	4	1	1.1
9	0	2	3.0
	1	6	4.6
	2	4	3.6
	3	1	1.8
	4	1	0.7
10	0	2	4.2
	1	5	5.1
	2	5	3.0
	3	2	1.2
11	0	4	4.0
	1	9	5.0
	2	1	3.1

Table 11: Reproductive success (number of nestlings) and the degree of synchrony (number of days between settlement) between primary and secondary females in 1979, 1982, 1992, and 1993.

1979		1982		1992		1993	
#fledge	#days	#fledge	#days	#fledge	#dav	#fledge	#days
0	3	0	0	4	15	0	5
4	2	0	0	2	6	0	30
4	8	0	18	0	42	0	52
4	17	0	18	0	19	0	13
0	28	2	7	3	23	0	11
5	12	0	5	0	5	0	22
5	12	0	20	0	4	0	23
5	1	4	25	0	23	2	40
0	28	0	23	0	21	0	8
0	15	4	20	3	6	2	7
0	13	0	3	0	15	0	33
0	3	0	11	0	22	2	4
0	28	0	11	0	20	2	3
0	13	0	14	0	16	0	16
2	23	2	0	0	28	0	1
5	9	0	18	0	5	0	15
4	6	4	1	5	7	0	21
5	22	0	6			0	25
1	2	0	29			6	22
0	5	0	27			0	1
0	12	0	21			0	17
4	27	0	17			0	7
4	13	3	31				
6	2	0	18				
5	0	5	15				
5	1	4	10				
4	7	0	29				
0	3	0	24				
5	11	2	8				
2	12	0	20				
0	13	0	20				
3	27	0	15				
1	10	0	19				
5	28	4	8				
6	25	0	13				
5	3	0	14				
3	1	0	3				
4	3	0	4				
5	3	2	5				
3	16	0	23				
4	3	3	7				
3	12	1	5				
6	5	0	26				
4	5	0	9				
0	16	0	13				
5	6	0	6				
5	2	0	25				

0	4	0	7				
0	13	0	0				
6	24	3	6				
5	10	1	21				
0	21	0	16				
5	32	0	16				
3	16	2	15				
4	1	0	9				
4	17	0	23				
3	24	0	29				
5	17	0	31				
5	5	0	20				
0	21						
0	33						
5	9						
5	12						
5	4						
2	1						
0	2						
4	9						
1	15						
4	30						
5	22						
6	23						
0	17						
0	17						
3	30						
5	16						
5	29						
5	15						
0	34						
0	24						
0	21						
4	8						
3	24						
5	12						
6	3						
2	15						
4	26						
4	11						
1	29						
0	28						
5	4						
5	22						
5	24						
0	1						
0	18						
4	2						
0	8						
5	15						

General Conclusions

In examining the occurrence and evolution of polygyny in marsh wrens, I was able to fulfill the goals of my study. These included: (1) determining realized reproductive success of males by establishing paternity of nestlings; (2) determining if polygyny was beneficial for individuals of both sexes; (3) identifying factors affecting mate and territory choices; and (4) determining factors which have led to the occurrence of polygyny in marsh wrens. How these goals were met is explained below.

From the DNA analysis (Chapter 1) I found that the observed reproductive success of males (i.e., the number of young fledged on a males' territory) is a relatively unbiased indicator of males' realized reproductive success (Chapter 2). As a result of this finding, I conclude that the ecological results of my study reflect the breeding biology in this population of marsh wrens in a reliable way.

Results of DNA fingerprinting analysis indicated that marsh wrens of both sexes actively participate in mixed reproductive systems such as extrapair copulations resulting in extrapair fertilizations and intraspecific brood parasitism. The consistency in the rates of these strategies over the two years of the study suggest that marsh wrens in the Delta, B.C. population regularly utilize mixed reproductive systems in order to increase their reproductive success. This study is the first report of a mixed reproductive system in this species (Chapter 1).

In this population, I found that polygyny was generally beneficial for males since polygynous males fledged significantly more young in three out of four years of the study than did monogamous males. In all four years, female status did not appear to affect female reproductive success since the number of young fledged in nests of monogamous and polygynous females was not significantly different. Although not a significant results, polygyny may have been beneficial for some females in 1979, 1992, and 1993 since the mean number of young fledged by polygynous females was slightly higher than the number of young fledged by monogamous females in these three years (see Chapter 2).

In this study, 66 % of males in 1979, 49.1 % of males in 1982, 19 % of males in 1992 and in 57% of males in 1993 were polygynous. The degree of polygyny in this population of marsh wrens appears to be closely associated with the breeding sex ratio of the population. An even sex ratio and a high population density likely resulted in high rates of monogamy in 1992, while a female biased sex ratio resulted in high rates of polygyny in 1979, 1982, and 1993 (see Chapter 2).

One key factor which greatly affected the reproductive success of individuals in this study population was the high rate of and spatial variation in nest predation. With over 50% of breeding nests depredated in three of the four years, it is likely that predation played an important role in female choice of a breeding situation. Interestingly, in two of the years (1979 and 1982) of the study nests on polygynous males' territories were not depredated significantly more or less than were nests on monogamous males' territories (Chapter 3). However, in 1992 and 1993 polygynous nests were depredated significantly less than were nests of monogamous males. Territories of polygynous males differed from territories of monogamous males in three (1979, 1982, 1992) of the four years of the study. In 1979 and 1982 territories of polygynous males were located further from conspecific territories than were territories of monogamous males. And in 1992, territories of polygynous males were located farther from the upland edge than were territories of monogamous males. However, in 1993, I found no such relationship (Chapter 4).

A second important factor affecting the occurrence of polygyny in this population was the presence or absence of female choice of a breeding situation. In 1979, 1982, and 1992, when female choice was occurring, females were basing their choice on territory rather than on male traits (territory size and distance of territory to other conspecifics' territories in 1979 and 1982, and the distance to the upland edge of the marsh in 1992) (Chapter 4). DNA fingerprinting results (Chapter 1) further supported the finding that not all females were choosing the same individual as their social (who to nest with) partner and their genetic (who to mate with) partner for at least some of their young (1992 and 1993 data). I also found that female settlement in 1992 was non-random, thereby supporting the conclusion that females were actively choosing. In 1993, however, I found no correlates of female choice in this population. When comparing observed and hypothetical random settlement patterns, I found that female settlement was random in 1993. Based on this evidence, I concluded that female choice was likely not occurring in this population of marsh wrens in 1993.

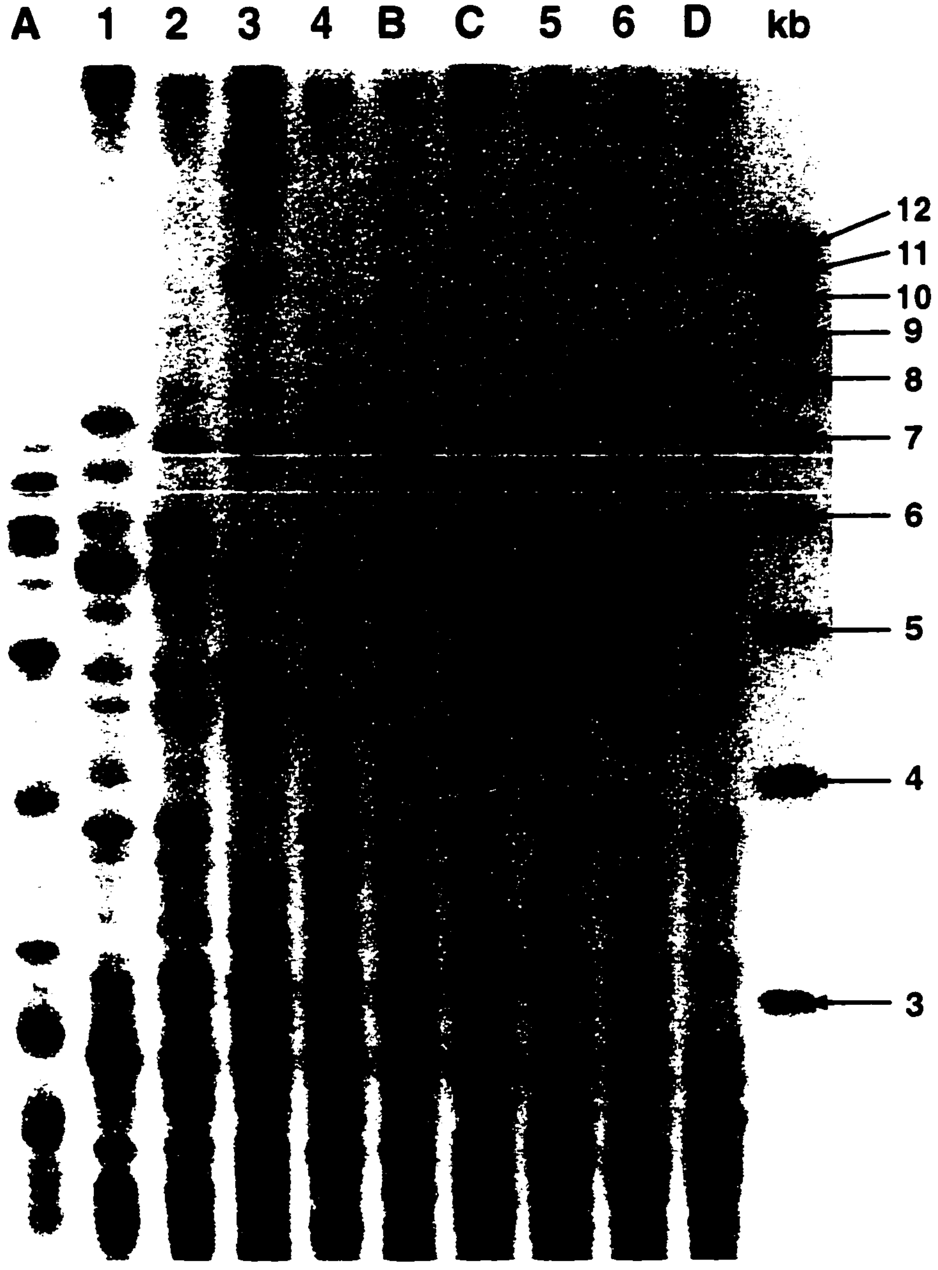
In this study I was able to establish which of the eight polygyny models best explained the occurrence of polygyny in this population of marsh wrens. This study was the first simultaneous test of all polygyny models. For each year of the study, except 1992, a combination of two models explained the occurrence of polygyny in this population. Of the polygyny models, the skewed sex ratio model explained why polygyny occurred in this population in 1979, 1982, and 1993. Additionally, for three of the four years (1979, 1982, 1992), the polygyny threshold model provided a plausible explanation for polygyny in this population. In 1993, along with the skewed sex ratio model, the random settlement model best explained the occurrence of polygyny in this marsh wren population.

It should be noted that in this study the low sample sizes, particularly in 1993, resulted in a number of analyses being unsupported, with P values greater than 0.05. However, the corresponding power values for some of these analysis were quite low, making them rather inconclusive. However, when the four years of the data were examined together, the trends in the data for these non-significant results, along with higher power values in the other years analyses have allowed me in most situations to accept the null hypotheses.

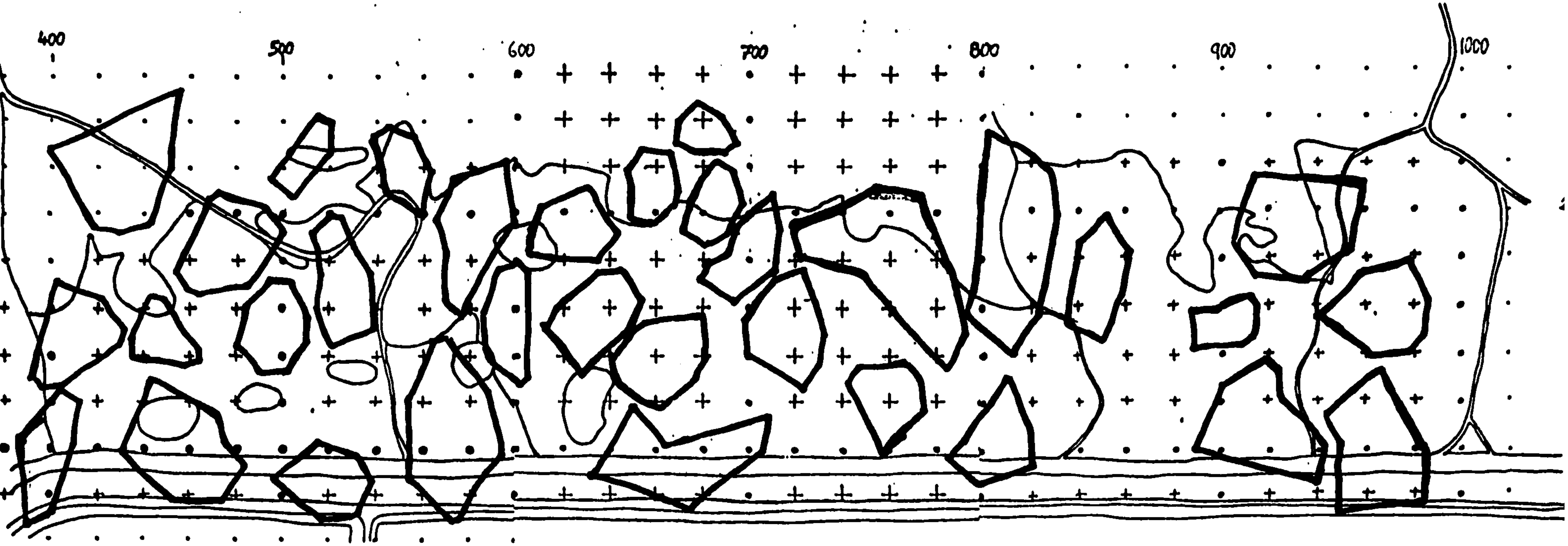
Appendix 1: Sample autoradiograph of two marsh wren families. The first family includes the putative father (A), putative mother (B), and four nestlings (1-4). The second family includes the putative father (C), putative mother (D), and two nestlings (5,6). The standard marker is from 12 to 3 kb. The size of the fragments are, in kb: 12.216, 11.198, 10.180, 9.162, 8.144, 7.126, 6.106, 5.090, 4.072, 3.054.

Appendix 2a (1979) and 2b (1982): Map of study area and male territories for 1979 and 1982.

Appendix 1

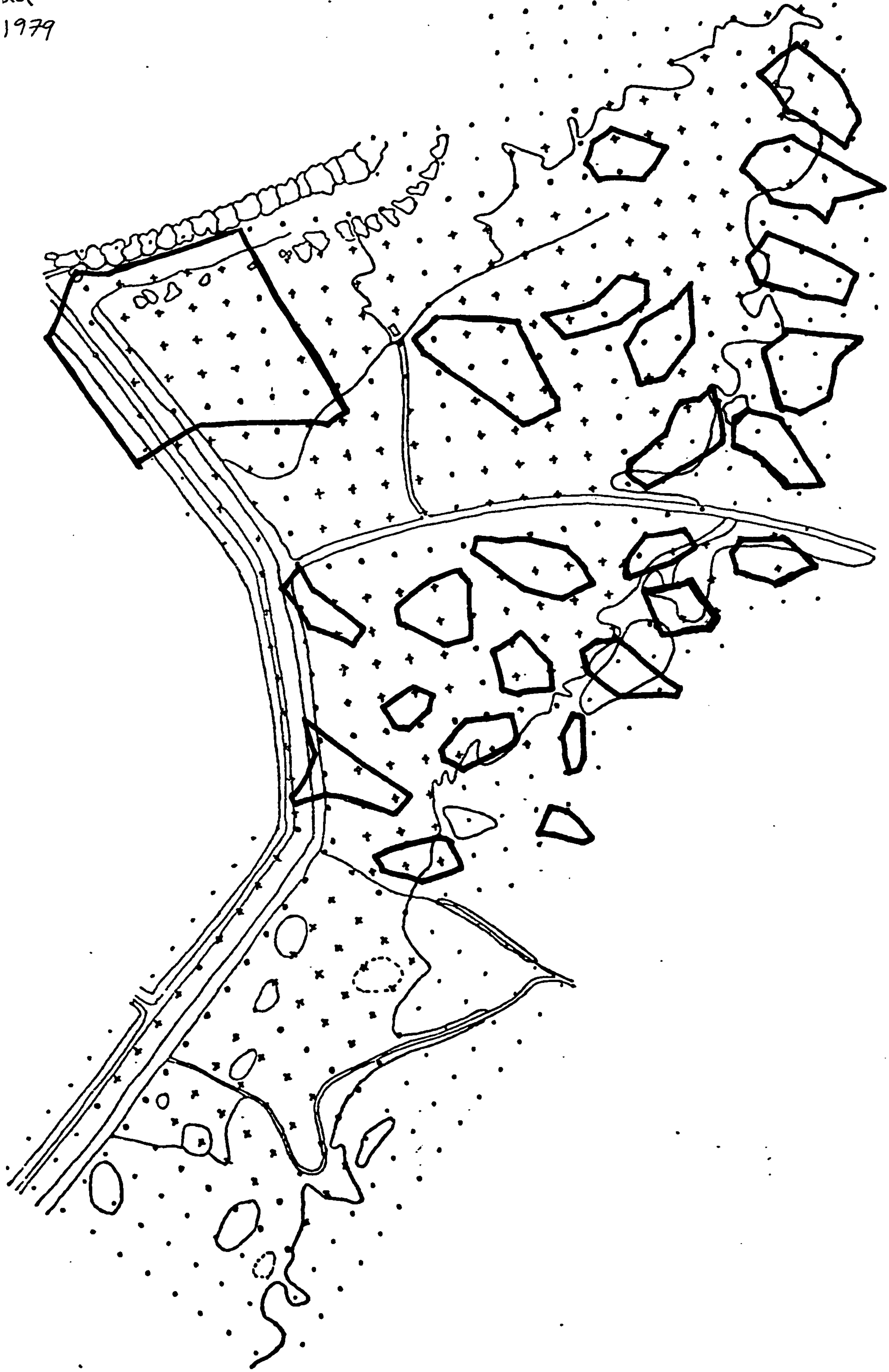


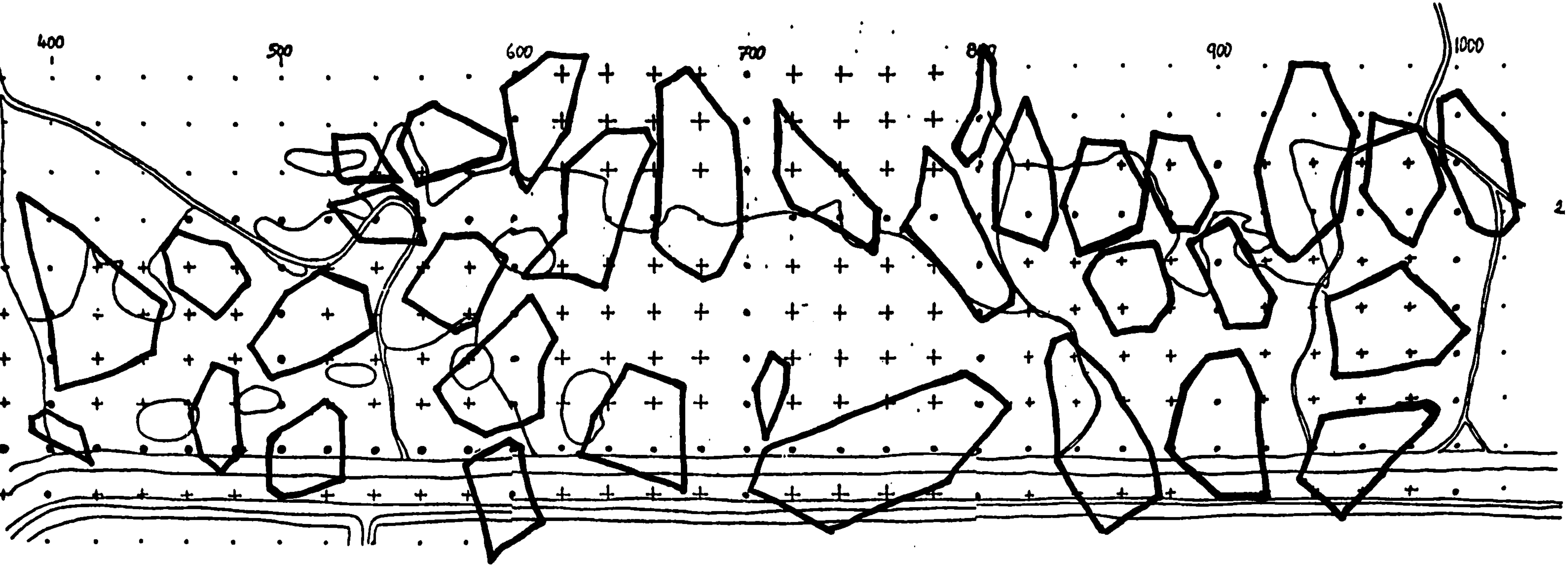
Appendix 2a (1979) and 2b (1982): Map of study area and male territories for 1979 and 1982.



779

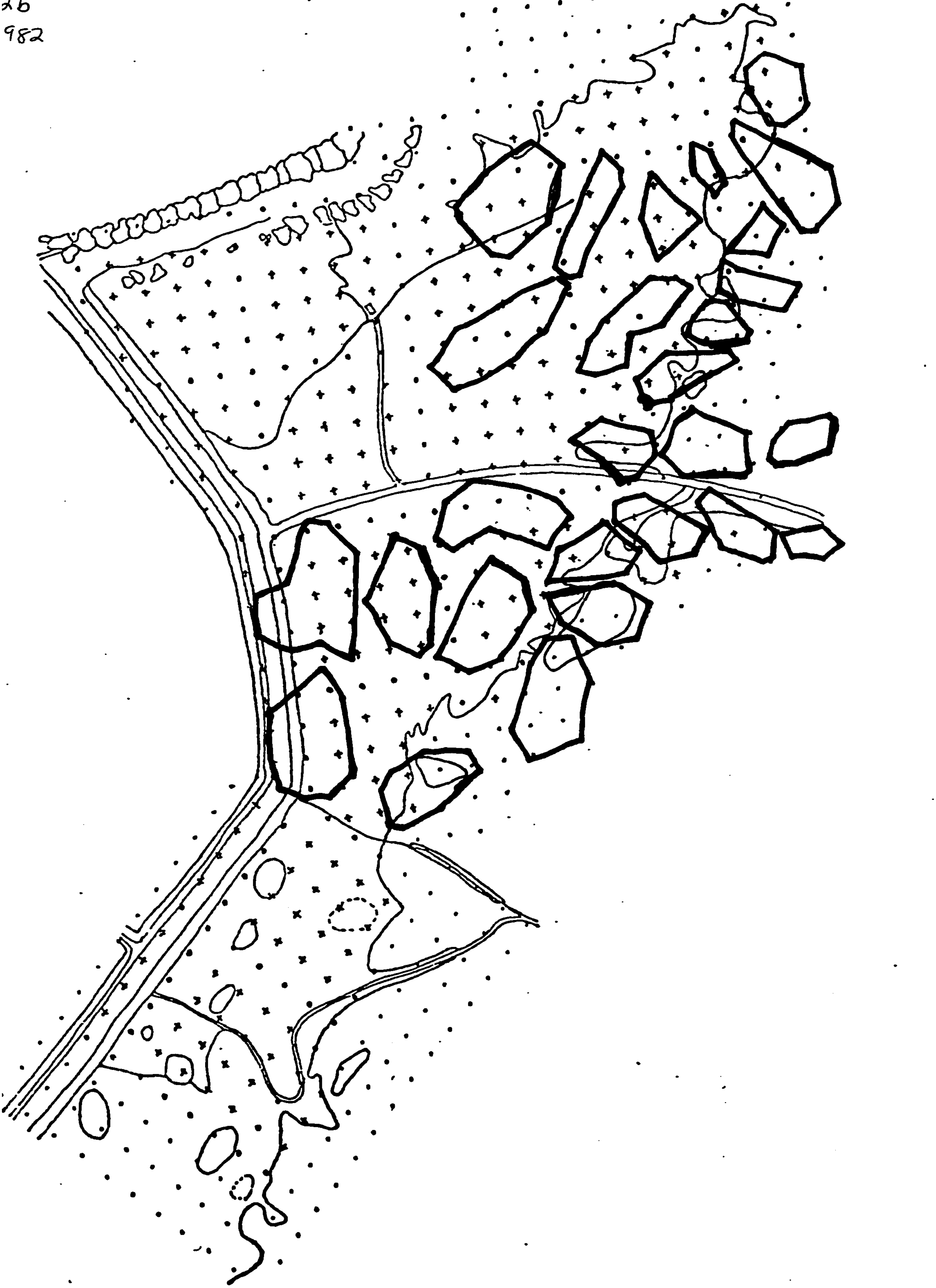
2a
1979



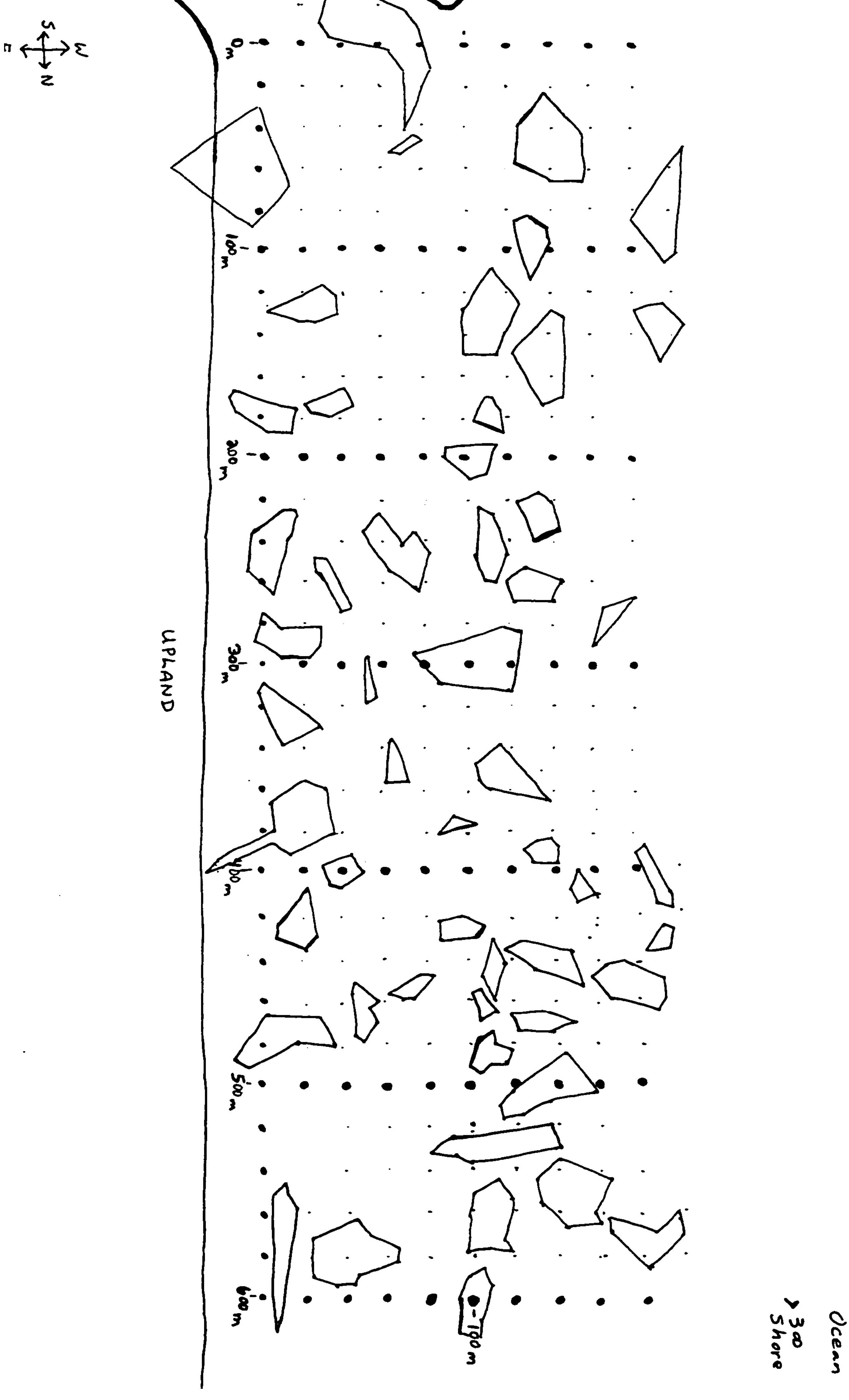

400
500
600
700
800
900
1000
2

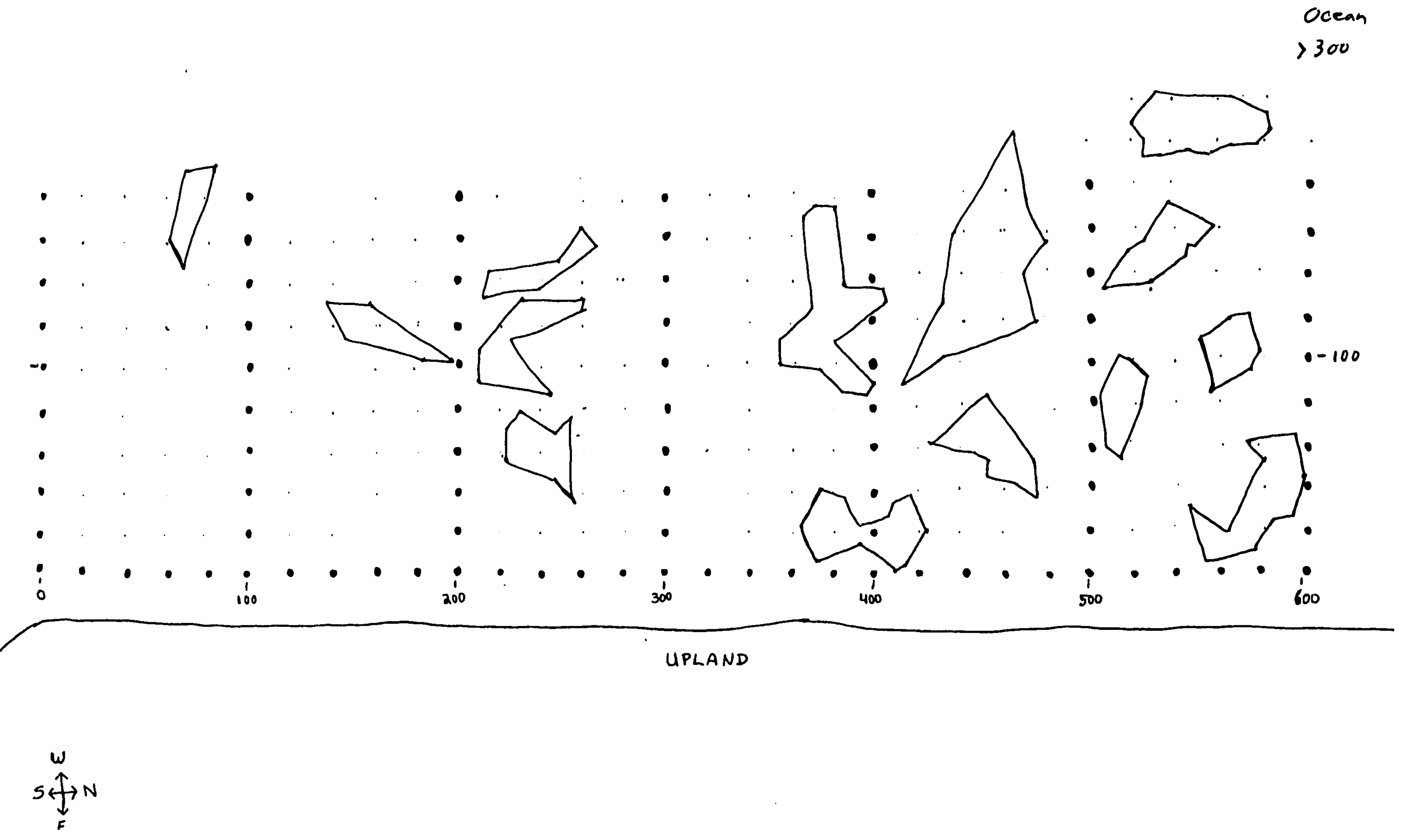
26

982



Appendix 2c (1992) and 2d (1993): Map of study area and male territories for 1992 and 1993.


S
W
N
E
0m
100m
200m
300m
400m
500m
600m
UPLAND
100m
Ocean
>30
Shore


Ocean
>300
-100
0
100
200
300
400
500
600
UPLAND
W
S
N
F

Appendix 3a (1979) and 3b (1982): Summary of data collected for each male.

male # is the individual number assigned to each male

status is the mating status of the male, 1=monogamy, 2=polygyny

#femal is the harem size of that male

status is the highest status of those females (1=monogamy, 2=polygyny (harem of 2), 3=polygyny (harem of 3), 4=polygyny (harem of 4))

fledge is the number of fledglings sired (observed reproductive success)

weight is the weight of the male in grams

winglg is the wing length of the male in centimeters

terr is the size of the male's territory in square meters

veg is the density of the emergent vegetation

dsedg is the minimum distance from the upland edge of the marsh to the boundary of a male marsh wren's territory

dsmw is the minimum distance between two adjacent marsh wren territories

dsrw is the minimum distance between a male marsh wren's territory boundary and an active redwing nest

Appendix 3a

male#	status	#femal	status	#fledge	weight	winglg	terr	veg	dsedg
1	2	5	3	17			1.23e+004	29.8	1.4
2	2	3	3	15			1475	36.6	100.2
3	2	2	2	15	12.5	53	1311	36.75	100.8
4	2	3	3	6	11.75	52.5	3279	28	58
5	2	3	3	6	12.5	52.5	820	35.86	159.1
6	2	2	2	6	12.5	52	1803	34.2	176.8
7	2	2	2	9	13.5	53	656	28.67	140.3
8	2	2	2	2	11.5	53	1311	36.33	232.7
9	2	3	3	8	12.25	50	984	31.8	102.8
10	2	3	3	13			1311	37.67	157.3
11	2	3	3	24	12.25	52	984	32.5	106.2
12	1	1	1	4			656	35	246
13	2	2	2	12			1311	25.6	14
14	2	2	2	3	12.5	53	820	27	84.33
15	2	3	3	20	12.75	51.5	820	42	172.2
16	2	2	2	14	12.25	52.5	328	35.75	154.5
17	2	4	4	23			1148	30	94.67
18	2	2	2	18	12.5	53	656	40.75	216.3
19	2	2	2	8	11.75	51	1148	42	126
20	1	1	1	10	12.75	57	164	36.5	63
21	2	3	3	9	13.5	52	442	26.33	16
22	1	1	1	5			164	40.5	140
23	2	3	3	17			328	32.14	232.7
24	2	3	3	19	12.25	52	656	30.6	55.8
25	1	1	1	3	11.75	52	1475	41.67	60.67
26	1	1	1	8			1475	25	1
27	2	2	2	12			2131	35.75	81.25
28	2	3	3	16	12.75	53	2622	27.2	91.2
29	2	2	2	15	11.75	53	984	24.5	16.67
30	1	1	1	9	12	57	328	38.5	53
31	2	2	2	5	12.5	52.5	1639	29.67	4.33
32	1	1	1	3	12.75	51	820	42	43.5
33	2	2	2	15	12.75	51.5	1475	23.4	100.4
34	1	1	1	9	11.75	50.5	1311	25	45.5
35	2	2	2	9	12.25	52	328	32.33	81.33
36	2	2	2	15			1148	31	88.5
37	2	2	2	10			984	25.25	66
38	2	2	2	11			820	39	10
39	3	3	3	21	13	52	2787	33.57	78.14
40	1	1	1	0	12.5	52.5	2295	28	1
41	1	1	1	0	12	52.5	1148	38	34.5
42	1	1	1	0			164	48	127
43	3	3	3	8			1475	29	63
44	1	1	1	5			656	34	12.5
45	1	1	1	7			984	32.5	95.5
46	4	4	4	16			1475	31.75	73
47	1	1	1	5			164	30	49
48	1	1	1	5	11.75	53	328	36	1
49	1	1	1	0	11.75	52	328	14	123
50	2	2	2	8	12.75	52	1148	31.6	84.6
51	2	2	2	9	11.25	52	1803	23	1.75
52	2	4	4	23			1475	30.5	88
53	2	2	2	4	12.25	51	1803	24.2	105
54	2	2	2	5	11.5	52	1148	49	62
55	1	1	1	0			492	27	120
56	1	1	1	5			656	8	22
57	1	1	1	6			1803	31.5	1

Appendix 3a

dsrw
26.6
14.5
12.1
19.3
12.1
15.7
45.8
41
15.7
24.1
6.3
65.8
13.9
25.3
16.5
25.3
30.4
13.9
25.3
32.9
11.4
72.4
12.7
20.3
12.1
15.7
32.5
30.1
14.5
26.5
21.7
9.6
45.8
22.9
31.3
44.6
8.4
19.3
22.9
36.1
27.4
80.7
20.5
27.7
33.7
9.5
21.4
22.6
31
9.5
31
10.7
19.1
21.4
35.7
8.3
22.6

Appendix 3b

male#	status	#fledge	winglg	terr	dsrw	dsmw	dsedg
1	1	0		656	36	90	2
2	1	0	53	820	27	90	43
3	3	0	53	2131	24	3	163
4	2	4	53	1967	6	20	59
5	1	3		820	23	7	107
6	3	6	53.5	2295	48	8	1
7	1	0	53	1311	34	61	223
8	2	4	53	1475	32	4	63
9	1	0	54	2131	73	31	137
10	1	0		328	25	8	145
11	1	0		1148	18	10	163
12	1	0		1475	34	23	96
13	1	0		328	62	45	22
14	2	0		1639	23	23	137
15	2	3		1148	36	5	243
16	1	0	52	1311	22	4	154
17	1	0	53.5	164	93	23	301
18	1	5	53	2951	33	6	102
19	2	2	53	1148	5	13	118
20	2	4	53	1311	3	7	52
21	4	3	53	2622	7	18	53
22	3	6	53.5	2295	29	16	101
23	1	0		2951	44	6	1
24	1	8		984	48	7	199
25	2	4		2787	24	22	4
26	1	0	54	1311	26	33	80
27	2	9	54	656	47	12	122
28	1	4	52.5	820	35	32	8
29	2	5	53	984	46	15	85
30	1	0	53	656	37	6	103
31	3	2	53	2787	17	1	39
32	2	12	53	820	39	1	119
33	1	0	53.5	1148	37	32	1
34	1	5	52	1475	13	19	45
35	1	0		328	63	38	3
36	2	2		328	9	1	108
37	1	4	53	164	17	45	12
38	2	1	52.5	1475	4	1	73
39	2	4	53.5	2787	21	27	1
40	1	5	53	2295	34	28	7
41	2	2		1967	5	1	102
42	1	5		492	64	24	1
43	1	3		1311	22	31	129
44	2	1	54.5	2295	18	6	63
45	2	3		1475	20	17	56
46	1	8	52.5	984	41	15	102
47	1	3		984	12	22	1
48	3	3	54.5	2161	4	13	63
49	2	1	54	1311	16	7	59
50	2	1	52	1148	21	10	99
51	2	7	53	2951	6	1	1
52	2	3	53	492	1	5	99
53	2	0	52	1639	5	17	52
54	1	0	52.5	1311	7	36	2
55	1	2		1148	1	5	126
56	1	2	53	984	19	25	77
57	4	2	53	1475	19	1	81

Appendix 3c (1992) and 3d(1993): Summary of data collected for each male.

male # is the individual number assigned to each male

status is the mating status of the male, 1=monogamy, 2=polygyny

weight is the weight of the male in grams

winglg is the wing length of the male in centimeters

nests is the total number of complete breeding nests built on a male's territory.

terr is the size of the male's territory in square meters

veg is the density of the emergent vegetation

dsedg is the minimum distance from the upland edge of the marsh to the boundary of a male marsh wren's territory

dsmw is the minimum distance between two adjacent marsh wren territories

dsrw is the minimum distance between a male marsh wren's territory boundary and an active redwing nest

Appendix 3c

male#	status	weight	winglg	nests	terr	veg	dsedg	dsmw	dsrw
1	2	51.5	11.5	7	248	46	80	18.82	61.18
2	2	53.5	11.5	17	1430	44.75	27.06	18.82	8.24
3	2	53	12	11	1708	45.33	0	36.47	42.35
4	1			6	280	41	67.06	28.24	9.41
5	1			14	938	55.67	123.5	16.47	42.35
6	2	57	12.5	10	499	59	175.3	22.35	74.12
7	1	52	12.5	8	269	56	122.4	16.47	23.53
8	1			5	317	60	177.7	22.35	82.35
9	1			12	446	54	123.5	5.88	51.76
10	1			10	162	29	101.2	17.65	71.76
11	1			19	825	56	95.29	5.88	23.53
12	1			13	507	44.8	1.18	32.94	20
13	1	52.5	12.5	16	270	49.33	18.82	5.88	14.12
14	1	53.5	15.5	11	364	44	0	5.88	30.59
15	0			18	346	48.33	96.47	10.59	54.12
16	1			16	299	45	124.7	12.94	81.18
17	1			13	285	45	118.8	2.35	68.24
18	1			10	103	40	165.9	25.88	82.35
19	1	51.5	12	17	376	45.3	103.5	2.35	60
20	1			28	870	47.4	76.47	15.29	21.18
21	1	58.5	12.5	17	473	40	52.94	22.35	14.12
22	1	55	13	11	204	55	14.12	15.29	8.24
23	2	54.5	14	14	603	42.25	0	11.76	28.24
24	1	51.5	11.5	17	448	34.67	0	10.59	7.06
25	1	52.5	14	7	435	53	0	10.59	30.59
26	1			8	74	47.5	54.12	22.35	17.65
27	2			18	506	44.33	104.7	20	25.88
28	1			4	138	46.5	64.71	22.35	10.59
29	1	51.5	12	20	789	36.33	0	10.59	30.59
30	1			16	220	35.5	28.24	10.59	11.76
31	1			10	382	35	5.88	11.76	17.65
32	0			4	72	52	87.06	18.82	20
33	1	50	12	13	213	29.5	124.7	10.59	25.88
34	0			3	92	43	149.4	11.76	31.76
35	1	52.5	12.5	11	141	25	178.8	5.88	64.71
36	1	54.5	13	3	76	25	181.2	5.88	61.18
37	1	50.5	12	15	208	34.5	109.4	7.06	5.88
38	1			8	152	40	89.41	7.06	11.76
39	2			7	534	42	152.9	8.24	82.35
40	1			13	463	40	110.6	8.24	51.76
41	1			5	106	35	103.5	4.71	23.53
42	0			8	66	38.33	63.53	4.71	21.18
43	1			8	139	39.67	50.59	4.71	25.88
44	1			10	685	33.4	0	1.18	38.82
45	1			14	244	40.67	96.47	4.71	15.29
46	1			15	184	39	118.8	5.88	37.65
47	1	53.5	12	16	596	39	112.9	3.53	32.94
48	2			21	530	37.67	77.65	3.53	27.06
49	2			20	703	38.5	130.6	2.35	29.41
50	2	53.5	13	23	348	45	161.2	2.35	47.06
51	1	52	11.5	20	481	43.75	96.47	9.41	9.41
52	1	53	12	17	194	31	94.12	9.41	7.06
53	1			15	847	42.83	23.53	12.94	0
54	0			4	314	44	3.53	12.94	7.06

Appendix 3d

male #	status	weight	winglg	nests	terr	veg	dsedg	dsmw	dsrw
1	2			17	2135	21.7	12.94	27.06	0
2	2	51	12	17	626	19.7	88.24	21.18	3.53
3	3			14	1095	33	171.8	7.06	54.15
4	2	52	13.5	13	808	31	132.4	7.06	17.06
5	2			8	598	9.7	54.12	34.12	22.35
6	2	54	12	7	873	26.7	36.47	23.53	2.94
7	4	52	12.5	18	2957	27.2	88.24	17.65	5.88
8	1	53	13	12	1277	23.4	2.35	24.71	21.18
9	2			9	1960	19.8	84.71	17.65	1.18
10	2	52	13	18	795	26.5	28.82	20	23.53
11	3	52.5	13	17	1179	26	90.59	20	9.41
12	1			9	516	29	152.9	17.65	23.53
13	1			9	604	17.5	120	15.29	4.71
14	2			3	382	29	14.71	63.53	25.88

Appendix 4a (1979) and 4b (1982): Summary of data collected for each nesting. The first column is the nest number.

status is the status of the breeding nest or male, 1=monogamy, 2=polygyny (harem of 2), 3=polygyny (harem of 3), 4=polygyny (harem of 4)

#fl is the number of young fledged per nest

veg is the vegetation density value for the area of the territory around the focal nest

dsrw is the minimum distance between a male marsh wren's territory boundary and an active redwing nest

dsmw is the minimum distance between two adjacent marsh wren territories

dsedg is the minimum distance from the upland edge of the marsh to the boundary of a male marsh wren's territory

date is the settlement date of the female for each breeding nest

Appendix 4a

	status	#fl	veg	dsrw	dsmw	dsedg	date
1	2	4	48	49.4	81	1	18
2	2	0	39	26.6	86.1	1	21
3	3	4	9	89.8	32.9	1	64
4	3	5	34	69.6	32.9	1	62
5	3	4	19	81	90.2	2	70
6	3	4	35	28.9	22.9	98	38
7	3	5	39	20.5	22.9	72	21
8	2	0	41	14.5	26.5	91	21
9	3	0	40	18.1	28.9	108	49
10	1	6	28	41	72.3	132	67
11	2	5	47	12.1	37.3	83	20
12	1	0	37	13.3	27.7	98	8
13	2	5	43	18.1	26.5	111	20
14	1	5	20	25.3	36.1	111	60
15	3	1	37	26.5	15.7	39	20
16	3	5	18	24.1	26.5	84	21
17	3	0	29	19.3	15.7	51	48
18	3	0	36	44.6	9.6	173	35
19	3	1	29	39.8	18.1	154	20
20	1	0	38	38.6	54.2	146	8
21	3	0	47	34.9	9.6	165	33
22	2	0	40	12.1	31.3	144	52
23	2	0	46	27.7	24.1	175	49
24	1	5	15	15.7	33.7	157	74
25	2	0	41	28.9	21.7	179	35
26	2	0	48	15.7	28	166	7
27	2	0	43	39.8	21.7	189	20
28	2	2	20	43.4	24.1	190	58
29	2	5	19	27.7	32.5	160	67
30	2	4	37	93.2	37.3	156	12
31	2	0	37	55.4	37.3	135	6
32	2	5	12	45.8	27.7	130	28
33	1	1	31	41	42.2	186	7
34	2	1	30	115	43.8	235	80
35	2	0	48	139.6	43.8	277	78
36	2	0	44	15.7	34.9	118	30
37	2	0	35	30.1	34.9	80	25
38	3	0	35	15.7	47	119	63
39	3	4	8	50.6	33.7	118	78
40	3	4	37	16.9	41	79	51
41	3	4	36	30.1	19.3	144	30
42	3	3	30	24.1	19.3	138	17
43	3	6	47	73.5	48.2	190	19
44	1	0	39	6.3	44.3	125	2
45	3	5	25	31.7	51.9	43	21
46	3	5	43	34.2	38	114	22
47	3	5	33	12.7	35.4	141	21
48	2	5	30	96.8	47	84	58
49	2	4	25	40.5	47	130	65
50	1	4	35	65.8	30.4	246	14
51	2	0	30	19	31.7	26	12
52	2	0	22	13.9	31.7	1	15
53	2	5	39	25.3	24.1	41	23
54	2	5	23	44.3	54.4	1	61
55	2	2	14	29.1	32.9	1	73
56	1	0	30	44.3	43	82	4
57	2	0	33	25.3	10.1	88	36

Appendix 4a

	status	#fl	veg	dsrw	dsmw	dsedg	date
59	3	3	35	31.7	24.1	171	35
60	3	1	42	21.5	24.1	157	18
61	3	5	45	40.5	17.7	182	8
62	3	5	36	21.5	27.9	171	58
63	3	0	49	24.1	15.2	171	25
64	3	6	45	16.5	11.4	181	50
65	2	0	37	58.2	45.6	160	18
66	2	5	38	41.8	22.8	159	21
67	2	3	37	83.5	51.9	139	65
68	2	6	31	25.3	39.2	160	64
69	4	3	26	53.2	36.7	132	20
70	4	4	25	53.2	19	91	23
71	4	5	35	30.4	10.1	70	23
72	4	3	36	38	10.1	74	36
73	2	4	30	60.8	12.7	101	62
74	2	4	28	73.4	12.7	100	65
75	2	4	37	48.1	20.3	220	18
76	2	3	49	40.5	20.3	221	30
77	2	5	42	36.7	27.9	220	59
78	2	6	35	13.9	27.9	204	64
79	2	4	40	25.3	25.3	118	18
80	2	4	44	44.3	25.3	134	23
81	1	5	45	32.9	19	69	22
82	1	5	28	48.1	19	57	62
83	3	0	18	11.4	7.6	24	34
84	3	4	34	16.5	7.6	23	18
85	3	5	27	25.3	36.7	1	24
86	1	5	29	72.4	59.5	140	7
87	1	0	52	99.8	57	140	49
88	1	0	41	38	46.8	199	1
89	2	0	51	35.4	21.5	218	22
90	2	5	38	12.7	21.5	198	24
91	3	6	46	16.5	21.5	223	52
92	3	0	16	72.2	36.7	282	56
93	3	0	14	38	22.8	245	65
94	2	6	19	55.7	39.2	264	76
95	3	6	35	65.8	34.2	77	10
96	3	5	31	59.5	17.7	53	20
97	3	0	29	40.5	17.7	42	31
98	3	5	32	44.3	38	70	52
99	2	3	26	20.3	35.4	37	68
100	1	3	43	21.7	49.4	61	6
101	1	0	47	19.3	38.6	59	49
102	1	0	35	12.1	38.6	62	58
103	1	4	34	15.7	21.7	1	17
104	1	4	16	41	32.9	1	60
105	1	0	34	53	38.6	85	3
106	2	5	45	38.6	25.3	71	21
107	2	4	38	38.6	25.3	79	22
108	1	3	26	32.5	43.4	90	72
109	2	0	23	33.7	36.1	92	17
110	2	4	46	62.7	33.7	121	34
111	3	4	41	37.3	25.3	83	49
112	3	3	13	44.6	25.3	100	73
113	3	5	13	30.1	39.8	60	66
114	2	5	23	18.1	36.1	29	17
115	2	5		14.5	36.1	1	22

Appendix 4a

	status	#fl	veg	dsrw	dsmw	dsedg	date
117	1	4	39	26.5	31.3	49	6
118	1	5	38	39.8	30.1	57	52
119	2	0	33	26.5	19.3	11	14
120	2	0	35	36.1	19.3	1	35
121	1	5	21	21.7	81.9	1	65
122	1	3	46	33.7	41	48	52
123	1	0	38	9.6	45.8	39	22
124	1	0	24	48.2	32.5	90	2
125	2	5	28	50.6	22.9	95	17
126	2	0	22	60.2	16.9	112	50
127	2	5	30	45.8	10.8	99	59
128	2	5	13	69.9	10.8	106	71
129	1	5	10	22.9	24.1	46	2
130	1	4	40	22.9	24.1	45	52
131	1	4	33	45.8	15.7	95	17
132	2	5	32	31.3	18.1	80	58
133	2	0	32	32.5	14.5	69	54
134	1	0	41	68.7	31.3	82	3
135	2	4	37	48.2	16.9	91	21
136	2	2	44	55.4	15.7	89	22
137	2	0	13	44.6	20.5	88	61
138	2	5	7	49.4	14.5	72	59
139	2	4	44	85	30.1	109	68
140	2	0	29	8.4	21.7	58	8
141	2	1	25	20.5	18.1	79	23
142	2	4	22	22.9	19.3	58	38
143	2	5	25	26.5	24.1	69	60
144	2	5	51	42.9	34.5	1	21
145	2	6	27	19.3	33.7	19	44
146	3	4	43	36.1	12.1	80	6
147	3	0	25	25.3	12.1	80	23
148	3	0	33	22.9	21.7	60	23
149	3	3	41	26.5	27.7	73	36
150	3	4	41	28.9	24.1	93	48
151	3	5	33	127.1	24.1	91	64
152	3	5	19	101.6	22.9	70	77
153	1	0	28	36.1	57.8	1	57
154	1	0	47	27.4	33.3	47	19
155	1	0	29	53	27.7	22	60
156	1	0	48	80.7	28.9	127	45
157	2	0	33	41	24.1	61	3
158	3	5	41	19.3	10.8	52	37
159	3	0	32	24.1	20.5	74	22
160	3	0	30	25.3	10.8	42	46
161	2	0	27	20.5	22.9	76	67
162	1	3	11	36.1	21.7	73	70
163	1	5	45	27.7	48.2	1	22
164	1	0	23	69.9	44.6	24	68
165	1	2	35	53	16.9	104	17
166	1	5	30	33.7	20.5	87	56
167	4	4	25	22.6	25	80	10
168	4	4	39	22.6	19.1	38	18
169	4	3	27	9.5	19.1	56	34
170	4	5	36	34.5	29.8	118	22
171	1	1	37	26.2	23.8	51	22
172	1	4	23	21.4	27.4	47	63
173	1	5	36	22.6	33.3	1	22

Appendix 4a

	status	#fl	veg	dsrw	dsmw	dsedg	date
175	1	0	44	21.4	84	71	3
176	2	0	23	23.8	23.8	71	18
177	2	6	44	44.1	27.4	104	21
178	2	2	31	9.5	17.9	73	36
179	1	0	16	44.1	31	104	69
180	1	0	27	35.7	84	1	4
181	1	0	22	34.5	33.3	1	25
182	2	5		40.5	29.8	1	38
183	2	4	20	31	29.8	4	64
184	4	3	37	15.5	21.4	74	10
185	4	4	36	59.5	13.1	87	21
186	4	1	42	22.6	25	61	39
187	4	0	33	29.8	20.2	69	38
188	4	5	32	10.7	11.9	118	43
189	4	0	36	29.8	14.3	108	50
190	4	5	10	17.9	31	97	61
191	4	5	18	13.1	35.7	90	63
192	2	0	26	42.9	29.8	114	19
193	2	0	33	22.6	20.2	94	18
194	2	0	32	19.1	20.2	98	36
195	2	0	16	47.6	36.9	127	69
196	2	4	14	71.4	36.9	92	71
197	2	0		28.6	11.9	59	31
198	2	0		21.4	11.9	57	23
199	2	5	49	29.8	17.9	70	46
200	1	0	32	52.4	11.9	124	43
201	1	0	22	35.7	29.8	116	21
202	1	5	8	8.3	32.1	22	57
203	1	0	37	22.5	44.1	1	23
204	1	6	26	42.9	50	1	63

Appendix 4b

	status	#fled	dsrw	dsmw	dsedg	date
1	1	0	36	90	2	91
2	1	0	27	90	43	30
3	1	0	46	6	167	25
4	2	0	31	8	178	45
5	2	0	51	3	163	45
6	3	0	38	6	166	54
7	3	0	53	3	164	54
8	3	0	24	26	183	72
9	1	0	44	20	92	37
10	2	4	30	20	79	54
11	2	0	6	32	59	72
12	1	0	27	7	107	31
13	1	3	23	7	116	58
14	3	0	92	8	1	27
15	3	2	59	12	18	34
16	3	0	58	23	10	32
17	2	0	86	8	1	52
18	3	4	52	29	27	57
19	2	0	48	9	22	80
20	1	0	34	61	223	65
21	1	0	44	4	63	39
22	2	4	46	4	63	59
23	2	0	32	21	86	62
24	1	0	73	31	137	27
25	1	0	25	8	145	83
26	1	0	18	10	176	31
27	1	0	23	10	163	48
28	1	0	54	23	112	29
29	1	0	34	23	96	40
30	1	0	62	45	22	26
31	2	0	23	23	137	34
32	2	0	30	23	161	55
33	2	0	38	20	243	24
34	2	0	55	6	264	35
35	2	0	66	8	277	49
36	1	3	61	5	271	67
37	1	0	25	4	139	28
38	1	0	22	4	154	69
39	1	0	93	23	301	36
40	1	5	33	6	111	21
41	1	0	25	6	102	57
42	2	0	5	42	198	23
43	2	2	34	13	118	23
44	1	0	39	13	130	64
45	1	0	3	11	72	12
46	2	0	20	7	92	29
47	2	0	35	14	52	47
48	2	4	13	7	88	73
49	2	0	16	14	60	72
50	2	3	13	27	53	30
51	2	0	18	18	62	36
52	4	0	7	23	87	59
53	4	0	20	18	66	57
54	3	3	37	16	117	28
55	3	0	29	26	119	59
56	3	0	38	40	101	55
57	3	3	37	16	143	69

Appendix 4b

	status	#fled	dsrw	dsmw	dsedg	date
59	1	0	44	6	1	39
60	1	4	49	7	206	31
61	1	4	48	7	199	73
62	2	4	26	22	4	32
63	2	0	24	22	29	50
64	1	0	26	33	80	28
65	2	0	49	12	123	29
66	2	5	61	14	138	44
67	2	4	60	14	136	54
68	2	0	47	16	122	83
69	1	4	35	32	8	27
70	2	5	58	15	96	52
71	2	0	46	15	85	76
72	1	0	37	6	103	30
73	1	0	37	6	103	51
74	1	0	37	6	103	66
75	2	0	56	1	72	17
76	3	2	33	20	39	25
77	3	0	34	21	60	37
78	3	0	56	2	83	37
79	3	0	55	2	82	48
80	2	0	63	5	90	63
81	2	0	17	21	43	67
82	1	0	39	1	120	15
83	2	4	50	18	131	31
84	2	4	40	1	119	39
85	2	4	61	18	141	78
86	2	0	39	1	119	91
87	1	0	37	32	1	19
88	1	0	15	38	63	32
89	1	0	30	19	62	52
90	1	5	13	19	45	70
91	1	0	63	38	3	61
92	1	0	18	1	112	16
93	1	2	18	1	113	20
94	2	0	25	9	123	56
95	2	0	9	3	108	70
96	1	4	17	45	12	17
97	2	0	27	12	73	30
98	2	0	4	13	103	33
99	1	1	28	1	82	49
100	1	0	27	1	81	79
101	1	4	21	32	23	28
102	2	0	46	40	1	60
103	2	0	25	27	1	64
104	1	5	44	28	7	11
105	1	0	34	31	38	57
106	2	0	5	1	102	16
107	2	2	22	24	122	21
108	1	0	5	1	104	64
109	1	5	64	24	1	31
110	1	3	22	31	129	39
111	2	1	18	6	63	33
112	2	0	19	24	114	56
113	1	0	18	6	69	20
114	1	0	20	17	56	19
115	2	0	20	22	60	42

Appendix 4b

	status	#fled	dsrw	dsmw	dsedg	date
117	1	5	42	15	121	28
118	1	3	41	17	105	70
119	1	3	12	22	102	18
120	3	1	6	13	22	26
121	3	1	30	14	1	31
122	3	0	32	14	1	52
123	2	1	9	21	18	61
124	2	0	4	21	8	70
125	2	1	24	11	63	17
126	2	0	18	7	97	30
127	2	0	16	7	83	55
128	2	0	21	14	59	61
129	2	0	21	20	99	1
130	2	0	22	10	119	25
131	1	1	35	10	119	60
132	2	0	6	1	43	29
133	2	0	42	11	1	36
134	2	0	6	1	43	52
135	2	0	42	9	1	52
136	2	3	6	1	43	71
137	2	4	37	9	1	65
138	1	0	21	5	121	20
139	2	2	1	22	99	40
140	2	1	24	5	124	61
141	2	0	6	17	61	17
142	2	0	5	26	52	33
143	2	0	13	18	63	49
144	1	0	28	36	12	26
145	1	0	7	36	2	62
146	1	0	1	5	126	18
147	1	0	6	5	131	51
148	1	2	18	9	142	67
149	1	2	19	25	77	35
150	2	0	29	1	102	17
151	3	2	29	14	128	32
152	3	0	28	14	122	41
153	3	0	21	2	82	40
154	4	0	19	2	81	51
155	4	0	29	1	103	53
156	3	0	62	36	158	71

Appendix 4c (1992) and 4d (1993):Summary of data collected for each nesting attempt including status of nest and number of young fledged per nest.

nest # is the number of the breeding nest

status is the status of the breeding nest or male, 1=monogamy, 2=polygyny (harem of 2), 3=polygyny (harem of 3), 4=polygyny (harem of 4)

male # is the number of the individual male

date is the settlement date of the female for each breeding nest

 # fled is the number of young fledged from each breeding nest

nest #	status	male #	status	date	# fled
1	2	1	2	42	5
2	2	1	2	57	4
3	2	2	2	17	2
4	2	2	2	23	0
5	2	2	2	59	0
6	2	3	2	14	3
7	2	3	2	60	5
8	2	3	2	33	0
9	1	4	1	11	0
10	1	5	1	24	0
11	1	5	1	55	0
12	2	6	2	20	5
13	2	6	2	43	3
14	1	8	1	76	0
15	1	9	1	23	0
16	1	10	1	16	0
17	1	10	1	43	0
18	1	11	1	19	0
19	1	11	1	49	0
20	1	12	1	24	0
21	1	13	1	21	0
22	1	13	1	36	0
23	1	14	1	17	0
24	1	14	1	47	0
25	1	14	1	60	0
26	1	16	1	20	0
27	1	17	1	27	0
28	1	17	1	47	0
29	1	18	1	25	0
30	1	19	1	18	0
31	1	19	1	42	1
32	1	19	1	53	0
33	1	20	1	23	0
34	1	20	1	50	0
35	1	21	1	23	3
36	1	22	1	20	0
37	1	22	1	42	3
38	2	23	2	12	0
39	2	23	2	17	0
40	1	24	1	21	3
41	1	24	1	65	0
42	1	25	1	22	0
43	1	26	1	13	0
44	1	26	1	60	0
45	2	27	2	18	0
46	2	27	2	22	0
47	1	28	1	14	0
48	1	29	1	19	0
49	1	29	1	23	5
50	1	30	1	23	0
51	1	31	1	23	0
52	1	33	1	12	0
53	1	33	1	42	6
54	1	35	1	23	4
55	1	35	1	61	0
56	1	36	1	62	2
57	1	37	1	19	0
58	1	38	1	11	0
59	2	39	2	19	4

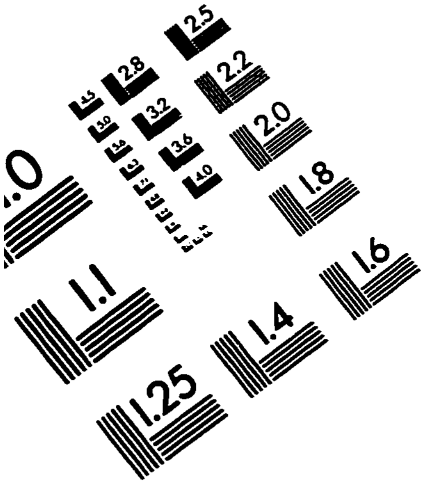
nest #	status	male #	status	date	# fled
61	2	39	2	42	0
62	1	40	1	24	0
63	1	41	1	11	4
64	1	43	1	50	0
65	1	44	1	20	0
66	1	44	1	47	0
67	1	45	1	19	5
68	1	45	1	60	5
69	1	46	1	58	0
70	1	47	1	35	5
71	1	47	1	65	0
72	2	48	2	20	0
73	2	48	2	47	0
74	2	48	2	26	3
75	2	48	2	62	0
76	1	49	2	12	4
77	2	49	2	49	5
78	2	49	2	34	0
79	2	49	2	69	0
80	2	50	2	8	2
81	2	50	2	53	0
82	2	50	2	36	0
83	2	50	2	58	5
84	2	50	2	60	0
85	1	51	1	17	5
86	1	51	1	61	0
87	1	51	1	82	0
88	1	52	1	31	2
89	1	52	1	51	0
90	1	53	1	54	0
91	1	5	1	68	0
92	1	20	1	18	0
93	2	49	2	62	0

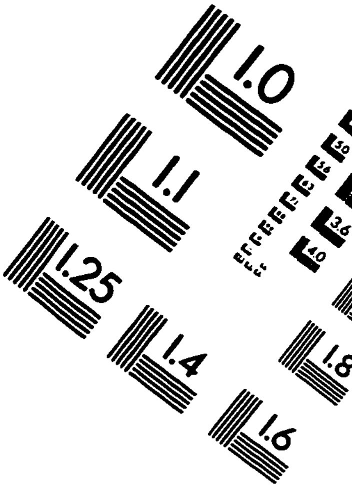
nest #	status	male #	status	date	# fled
1	2	55	2	11	0
2	2	55	2	16	0
3	1	55	2	13	0
4	1	55	2	67	0
5	2	56	2	16	0
6	2	56	2	46	0
7	2	56	2	4	3
8	2	56	2	56	0
9	3	57	3	17	3
10	3	57	3	53	0
11	3	57	3	28	0
12	3	57	3	62	0
13	3	57	3	40	0
14	2	58	2	10	0
15	2	58	2	59	2
16	2	58	2	50	0
17	2	58	2	67	2
18	2	59	2	18	2
19	2	59	2	1	0
20	2	59	2	44	0
21	2	60	2	11	2
22	2	60	2	15	3
23	4	61	4	12	2
24	4	61	4	15	0
25	4	61	4	51	0
26	4	61	4	36	0
27	4	61	4	27	0
28	4	61	4	35	0
29	1	62	1	5	0
30	1	62	1	56	0
31	1	62	1	59	5
32	2	63	2	17	0
33	2	63	2	42	4
34	2	64	2	22	6
35	2	64	2	44	4
36	3	65	3	8	0
37	1	65	3	42	0
38	3	65	3	9	0
39	3	65	3	25	0
40	1	66	1	39	0
41	1	66	1	66	0
42	1	67	1	16	0
43	1	68	2	26	0
44	2	68	2	46	0
45	2	68	2	39	0

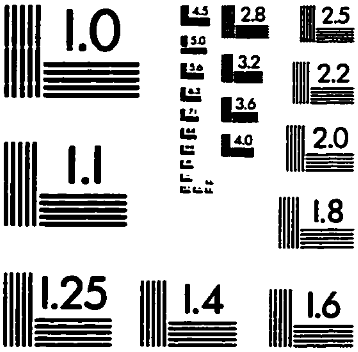
Appendix 5: Weight of marsh wren nestlings for each active nest that fledged young for the 1992 and 1993 breeding seasons.

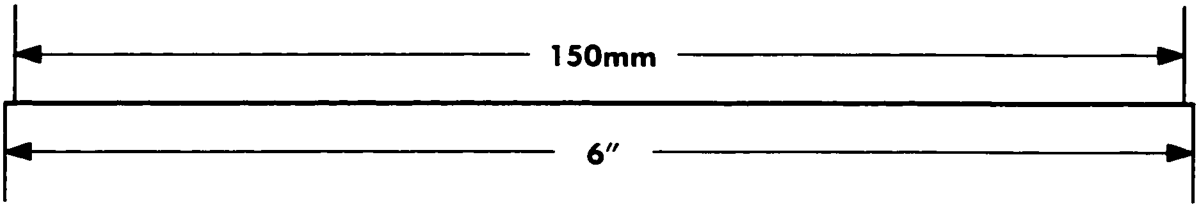
Nest #	Mean	Nestlings Weight (g)
1992		
1	10.5	11.5,10,10.5,9,11.5
2	9.0	9.5,10,8.5,8
3	10.5	9.5, 11.5
6	10.2	11.5,10,10.5,9.5,9.5
7	11.5	10,11.5,11.5,11,11.5
12	10.3	11,11,9.5,11,9
13	9.5	8.0,11.5,9.0
22	11.3	10.5,11.5,12
32	10.5	10.5
35	9.8	9.5,11.9
37	10.3	10,10,10,11,10.5
40	10.7	10.5,11.5,10
44	10.4	9.5,10.5,11,11,10
49	10.5	11,10
53	8.9	8.5,10,8.5,9,9,8.5
54	10.5	11.5,10.5,9.5,10.5
56	9.8	9,10.5
57	11	11
68	9.8	10,10,10.5,9.0,9.5
70	10	9.5,11,9,10.5,10
78	9.5	10,9.5,9.0,9.0,10
85	10.1	10,9.5,9.5,9.5,12
86	10	10,10,10,10,10
90	8.5	8.0,9.0
1993		
5	9.3	9,9.5,9.5
7	10.3	11,10,10
14	11.3	10.5,12
17	11.3	11.5,11
20	10.5	11,10
21	10.7	10,11.5,10.5
22	9.9	10,10,10,9.5
24	9.3	9,9.5,9.5
27	9.5	10.5,8.5,9,10
30	9.0	10,9,9,8,9
32	10.8	11.5,11.5,11,9
33	9.9	11,10,10,10,9.5,9
34	10.6	11.5,10.5,9.5,11

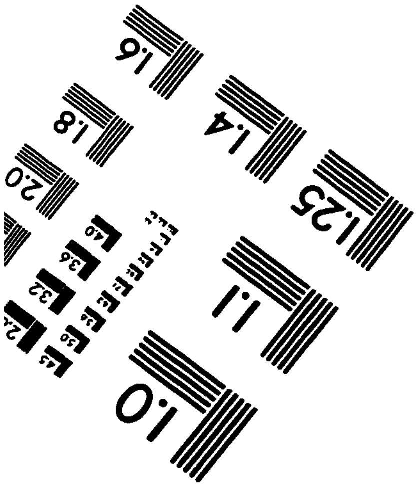
IMAGE EVALUATION
TEST TARGET (QA-3)

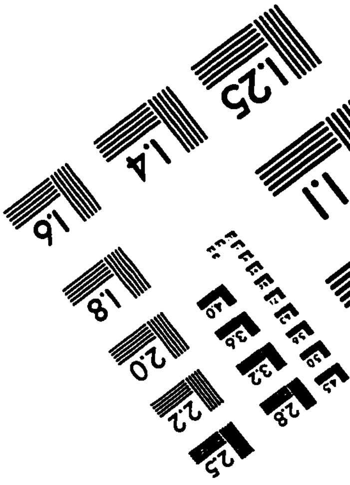












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