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REPLACEMENT BEHAVIOR OF MALE SONG SPARROWS AND YELLOW WARBLERS AS DETERMINED FROM REMOVAL EXPERIMENTS

By

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ABSTRACT

REPLACEMENT BEHAVIOR OF MALE SONG SPARROWS AND YELLOW WARBLERS AS DETERMINED FROM REMOVAL EXPERIMENTS

By

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This study examines the effect that brood number has on the frequency of replacement and the subsequent level of investment by the consorts. Territorial males were removed from nine Song Sparrow (multiple brooded) and seven Yellow Warbler (single brooded) territories after the nest had reached the three egg stage. Two classes of data were collected for comparison between the two species. These included: frequency of replacement, and whether or not the replacements fed the young of the original male.

Complete replacement in the Yellow Warbler and in all but one of the territories for the Song Sparrow indicated that brood number was not a major factor in the bird's decision on whether to replace or not. Complete failure of my sample of Song Sparrow nests precluded the determination of investment level for that species. Four out of the seven Yellow Warbler replacements were known to feed the young of the original male. Possible explanations for the high level of investment on the part of the replacement male Yellow Warblers are discussed.

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INTRODUCTION

Due to predation and other factors causing mortality during reproduction, birds are often faced with the problem of raising a brood without the help of a mate. According to Trivers (1972) a female bird in such a situation has three choices: 1) she can desert the eggs and attempt to breed again; 2) she can try to raise the young by herself; or 3) she can try to induce another male to help raise the young. Attracting another male to help raise the young would be the most advantageous because it would give her the best chance for genetic return on her current investment. This is assuming that she does not have to spend a lot of time and energy, normally spent on her offspring, attracting a new mate. The male should avoid investing his efforts in the genes of another male's offspring unless it somehow improves his own genetic fitness.

For a female to attract a new male depends on several factors. First there must be males ("floaters") in the habitat. By floaters I am referring to either non-breeding males who are moving through the territories searching for one that is unoccupied, or territorial males who occupy suboptimal habitat and are searching for better territories (Krebs 1971). That these "floating" males exist for many species of birds has been shown by removal experiments (Orians 1961, Watson and Jenkins 1956, Stewart and Aldrich 1951, Hensley and Cope 1951, Power 1975). Probably the most well known of these experiments was conducted by Stewart and Aldrich (1951) and later continued by Hensley and Cope (1951).

Therefore, with "floating" males available, a female who loses a mate may be able to induce a replacement into investing in her former mate's offspring, a process called cuckoldry. Cuckoldry can be defined as raising another male's offspring (Trivers 1972). That birds are sometimes fooled into raising another male's offspring is evidenced in the literature by cases where they are observed to feed the nestlings of another species (Carr and Goin 1965, Mannan 1979). The classic example of birds being fooled is when they are parasitized by other species such as the Brown-headed Cowbird (Molothrus ater). In these cases the faster maturing cowbird nestling is often fed more frequently to the detriment of the pair's own nestlings.

In spite of the problem of cuckoldry there are seven ways a potential replacement could improve his own genetic fitness by replacing even when the female has already mated. These include: 1) gaining experience for future nestings; 2) investing in one's close relatives or kin selection; 3) gaining access to a limited resource such as food or cover; 4) mating with the female to fertilize the unlaid portion of the clutch; 5) mating with the female during a subsequent brood; 6) mating with the female in the event that the first nest fails; and 7) obtaining a mate or territory for the following season.

In terms of genetic fitness the possibility of mating with the female for a subsequent brood in a multiple brooded species is the most adaptive for a replacement male in that it provides the highest potential for current genetic return on investment. It is for this reason that I chose to compare a single brooded species versus a multiple brooded species in a replacement study. Barash (1975) concluded in reference to the avoidance of cuckoldry "... this characteristic would be especially well developed among single-brooded, monogamous species and those in which males make a substantial investment in the success of their offspring." For comparison I chose a classic multiple brooded species, the Song Sparrow (*Melospiza melodia*), and a single brooded species, the Yellow Warbler (*Dendroica petechia*), based on their overall similarities in breeding biology and at the same time their difference in brood number. According to genetic investment theory then, the Yellow Warbler, without the advantage of second broods, should exhibit a lower frequency of replacement than the Song Sparrow. This is the hypothesis I set out to test.

NATURAL HISTORY

Song Sparrows and Yellow Warblers were chosen as the subjects for my study based on their similarities in breeding biology along with a difference in the number of broods raised in a single season. Below I will summarize the relevant aspects of their breeding biology and point out the differences and similarities between the two species that are pertinent to my research.

The Song Sparrow nests commonly in readily accessible habitats such as gardens, hedgerows, and oldfields. Breeding lasts from 3.5 to 5 months during which a pair will raise up to four broods (Nice 1937). The number of broods and length of the breeding season depend on the latitude and weather conditions, but in most if not all parts of the Song Sparrow's range, including Michigan, they can be classified as a multiple brooded species. The Yellow Warbler differs in this last respect which is the main variable in my study. Their breeding season is much shorter, i.e., 1.5 to 2 months, during which they raise only one brood (Goosen 1978). Breeding pairs of Song Sparrows remain on the territory throughout the breeding season and often remain in the vicinity at other times of the year (Nice 1937). Song Sparrows are easily caught and banded on their territories using recordings, mist nets, and seed traps (personal experience). Song Sparrows are partially migratory in that some of the males and females overwinter while the rest migrate south. This is in contrast to the Yellow Warbler in which the entire population moves south during the non-breeding season (McWhirter and Beaver 1977). Both Song Sparrows and Yellow Warblers occupy a type "A" territory which includes mating, nesting and feeding (Nice 1937, Song Sparrow and Frydendall 1967, Yellow Warbler). In both species the male sets up a territory and attracts a female, while the female does all of the nest building, incubating and brooding of the young. In both species the male and female feed the young while they are in the nest, but in the case of the Song Sparrow, the male takes over feeding the young after they have fledged so that the female can begin another clutch (Nice 1937, Song Sparrow and Bigglestone 1913, Goosen 1978, Smith 1943, Schrantz 1943, Mousley 1926, Yellow Warbler).

Although Song Sparrow pairs usually remain together during the breeding season, they rarely remate the following year. Nice (1937) found only eight pairs out of over 200 possibilities that remated the following year. As far as replacements occurring during a breeding season are concerned, Tompa (1964) found that when 30% of the Song Sparrow population on Mandarte Island, B.C., was killed, 21 males replaced the 14 dead males within 10 to 14 days. Nice (1937) found only two cases where a male who had disappeared was replaced by another male. Unfortunately, Nice does not give a sample size in relation to this figure. In both cases the male came from another nonadjacent territory from which it had been driven or which it had abandoned. She also noted four cases where one male had two females. These cases were apparently the result of a female losing her mate and a neighboring male expanding his territory to include both females (Nice 1937).

Two of the factors that effect nest failure and ultimately the chance for renesting are predation and nest parasitism. Nice (1937) recorded an average of 48% nest success in a sample of 223 nests. The Song Sparrow is a favorite host for the Brown-headed Cowbird and according to Barrows (1912) probably raises more cowbirds than any other species in the state of Michigan. Even though the presence of a cowbird egg in the nest decreases the number of Song Sparrow young produced, the nest is rarely abandoned for this reason. This is in contrast to the Yellow Warbler which is considered to be a poorer host relative to the Song Sparrow and often will abandon the nest due to the presence of a cowbird egg (Goosen 1978). McGeen (1972) found a success rate of 42% for cowbirds in Song Sparrow nests while the same figure for Yellow Warbler nests was 18%. Cowbird parasitism, at least in the case of the Yellow Warbler, increases the chance that the nest will fail and a renesting will occur.

The Yellow Warbler is an ideal subject for study. Although it is not as common as the Song Sparrow in Michigan, its nests are easily found and its sexual chromatism makes it an easy species to keep track of males and females. Below I will describe the relevant aspects of breeding biology that were not covered in the previous section.

The Yellow Warbler is a summer resident in Michigan (McWhirter and Beaver 1977) migrating to South America for the fall and winter. Although the Yellow Warbler is considered to be a single brooded species, Goosen (1978) found six attempts at second broods out of a sample of 260 pairs (~ 2%), only one of which was successful. This appears to be the exception.

Although second broods are extremely rare, renestings due to the failure of the first nest are a common occurrence. Goosen (1978), while studying over 333 nests over a period of three years, found that an average of 47% of the nests were successful in that at least one of the young survived to the fledging stage.

Like the Song Sparrow the Yellow Warbler is also a favorite host for the Brown-headed Cowbird. Goosen (1978) blamed parasitism for 8.9% of the nests that failed. Goosen also categorized the response of Yellow Warbler to the presence of a cowbird egg as follows: 40.3% accepted the egg; 43% buried it or built a new nest on top of the eggs; and 16.7% deserted the nest. Rates of parasitism for the Yellow Warbler in the literature are: 24.8% (Goosen 1978); 29.5% (Robertson and Norman 1976); and 40.9% (Berger 1951). Rothstein (1975) considers the Yellow Warbler to be an acceptor species in that his experimental birds accepted 16 out of the 16 simulated cowbird eggs that he placed in their nests. He felt that desertion and the burial of eggs was due to several possible factors such as: human disturbance, the presence of adult cowbirds at the nest, and/or a change in clutch size due to parasitism. The relevant factor to this study is the high frequency of renesting due to disturbance of any kind related to cowbird activity.

DESCRIPTION OF STUDY AREA

My study was conducted at four sites in Ingham County, Michigan. The sites were chosen based on the presence of suitable habitat for the species studied. The first area was the Doby Road Research Area owned and maintained by Michigan State University. My study took place on a 15.61 ha. portion of this area and consisted of oldfields surrounded by deciduous woods, low shrubs, and trees. The Red Cedar River bisects the property. Several old brush piles are located in the oldfield portion of the study area. These brush piles offered excellent habitat for the Song Sparrow and were the focus of my study at this site. The density of Song Sparrow at this location was approximately .94 pairs per hectare. There were no Yellow Warblers found at this location.

The second site was 9.44 ha. in size and consisted of several oldfields and hedgerows which bordered a railroad track. I will refer to this area as the Holt site. *Cornus* spp. (dogwood) and *Crataegeus* spp. (hawthorn) made up most of the larger species of plants at this site and served as abundant nesting habitat for the Yellow Warbler. Interspersed with these shrubs were various species of grasses that made up the bulk of the Song Sparrow nesting habitat. Densities for the two species at this location were .85 Yellow Warbler pairs per hectare and 1.0 Song Sparrow pairs per hectare.

The third site was 52.4 ha. in size and was located in East Lansing. This area consisted of oldfields and small patches of woodland. I will refer to this area as the Hudson site. The oldfields there consisted of clumps of *Cornus* and *Crataegus* spp. along with small islands of *Populus* spp. (cottonwood). The bulk of the habitat was made up of various species of grasses. The density of Yellow Warblers at this site was .1 pairs per hectare. The low density here was probably due to the fact that the nesting habitat for the Yellow Warbler was present in the form of small islands of shrubs. Song Sparrows from this area were not used in this study.

The fourth site was used only briefly and consisted of deciduous woods located in the Red Cedar Natural Area on the Michigan State University campus. This area was chosen because a fellow researcher had located an active Song Sparrow nest there. No density measurements were made at this site.

EXPERIMENTAL PROCEDURE AND MATERIALS

Song Sparrows began nesting in April both years, while Yellow Warblers returned in early May and nesting began shortly thereafter. When I located a territory of either species, I spent several hours observing the male to determine the boundaries of the territory and also if a female was present. After determining that there was a female present I began my search for nests. It was important to know the stage of the nesting cycle prior to removal of the male since I wished to ascertain that the female had in fact laid eggs fertilized by her first mate.

Nests of the Song Sparrows were extremely hard to locate. During the 1978 field season I searched for nests by sitting and observing the territories to determine the focus of the female's activities. Due to their secretive behavior in the vicinity of the nest, this proved unproductive. Only one nest was found during the 1978 season. Even though I failed to locate more nests during 1978, I was able to determine the stage of the nesting cycle by the female's behavior. If the female was seen carrying nesting material, I assumed that she was still in the process of building. If she was visible only for short periods of time during which she fed, I assumed that she was incubating. If the female began carrying food repeatedly, I assumed she was feeding young. These assumptions are supported by

Nice's (1937) observations and by my own observations on the one territory in 1978 and the three territories in 1979 where I had located the nest. In all of these cases the behaviors mentioned above were clear indicators of the stage of the nesting cycle.

During the 1979 season I employed a new tactic for locating Song Sparrow nests. This consisted of rapidly moving through each territory systematically covering the entire area. This method of search gave the female little warning of my approach. If the female was incubating and I approached to within a few feet of her she would flush directly from the nest. A careful search of the vegetation usually revealed the well-camouflaged nest.

Locating Yellow Warbler nests was considerably easier because they are built higher up in shrubby vegetation. Nests were found by moving underneath the vegetation and looking up.

Once I had located a nest of either species, I examined it daily to determine its stage and whether or not it had been parasitized by the cowbird. I then waited until there were at least three eggs present before removing the male. The three egg stage was chosen because it represented not only an indication to potential replacements that the female has already mated, but it also represented a large investment by the female. It was also hoped that this level of investment would act as an incentive for the female to remain with the nest. Removal of the male was done by two different methods. The first method consisted of placing a mist net in the territory along with a model of the bird placed in close proximity to the net. With the aid of recordings of the male's territorial calls played on a

Sony TC 110 A tape recorder, the males were lured into the net. This method was especially effective with the Song Sparrow. However, if they escaped from the net during the first attempt, they were extremely hard to catch a second time. Males removed using this method were maintained in captivity for the duration of the study and then released.

Yellow Warblers proved to be hard to catch using the above method and difficult to maintain in captivity once captured. Because they were hard to maintain in captivity I tried transporting males that I was able to catch a sufficient distance from the study area and releasing them. When a male returned the day after removal from a distance of 20 miles, this procedure was abandoned. I then began removing the males by shooting them with a Beeman .177 cal. pellet gun with a telescopic sight. This method proved efficient and caused little disturbance on the territory. After a male was removed from a territory I returned to observe for one hour each day to watch for the appearance of replacement males. A new male was classified as a replacement when he was observed to sing within the territory on at least two separate days. This criterion excluded birds who were just moving through the territory. These observations were made either in the early morning or late afternoon, at times when the birds were normally active. Short observations were continued for one week after removal or until a replacement male was observed on the territory. When the eggs hatched in the nest, replacement males were observed for up to two hours a day for three days to determine their level of investment toward the female and her offspring.

Two types of investment were recorded. These were: 1) feeding the young; and 2) defense of the territory. Only in those cases where the male defended against a potential threat to the female or her offspring, such as defending against cowbirds, was the behavior classified as parental investment. Other cases such as when males defended the territory against conspecifics may have been related only to the defense of a feeding territory for the male and not to the potential survival of the young.

To test for differences in the frequency of replacement between the two species the data was analyzed using Fisher's exact test (Siegel 1956).

RESULTS

A total of 16 removals were made during the 1978 and 1979 breeding seasons, seven for the Yellow Warbler and nine for the Song Sparrow. Because of the difficulty of locating Song Sparrow nests, five out of the nine removals were made on territories where I was unable to locate the nest. In these cases the stage of the nesting cycle was judged based on the behavior of the female.

All of the Yellow Warbler removals were done on territories where I had located the nest. On one territory I attempted to shoot the male but was unsuccessful for two days. The male then disappeared and no males were seen on the territory for four days. On the fifth day a male appeared and began singing on the territory. Because this male's song was noticeably different from the first male's and also that he sang from a different set of perches, I classified him as a replacement. I assumed that the first male had been driven from the territory or had died.

Eight out of the nine removal territories for the Song Sparrow had replacement males singing on the territory between zero and three days after removal. The average time to replacement was 1.63 days. Each replacement was observed on the territory on at least two occasions and was noted singing well within the territorial boundaries (Table 1). At least two of the Song Sparrow replacements were males who had

Table 1. Frequency of replacement and the time interval between removal and replacement on territories of Yellow Warblers and Song Sparrow.

Species	Removal Date	Replacement Date	Time to Replace
Song Sparrow	5/11/78	5/11/78	0
	5/12/78	5/14/78	2
	5/18/78	5/20/78	2
	6/19/78	6/21/78	2
	6/20/78	6/22/78	2
	6/20/78	--	--
	5/04/79	5/05/79	1
	5/04/79	5/07/79	3
	5/05/79	5/06/79	1
Yellow Warbler	5/28/78	5/29/78	1
	5/24/79	5/26/79	2
	5/26/79	5/28/79	2
	5/28/79	5/29/79	1
	5/29/79	6/02/79	4
	6/03/79	6/04/79	1
	6/03/79	6/04/79	1

Total: Song Sparrow replaced 8/9 times or 89% while the Yellow Warbler replaced 7/7 or 100% of the time. The average time to replacement for the Song Sparrow was 1.63 days and the average time to replacement for the Yellow Warbler was 1.71 days.

expanded their own territories to include the territory of the removed male.

All of the Yellow Warbler removals had replacement males singing on the territories between one and four days after removal. The average time to replacement was 1.71 days (Table 1).

The difference in frequency of replacement between the two species was found to be insignificant at the .05 level of significance using Fisher's exact test. The calculated probability of obtaining the observed distribution of frequencies was .56.

Determining the level of investment for Song Sparrows was impossible because all of the nests that I was observing failed. Out of the four nests three of them failed during the nestling stage and one during the egg stage. In all four cases nest failure occurred after a replacement had been on the territory for at least two days. It appeared that nest failure was due to predation because eggs and young had disappeared from each nest. In three out of the nine removal territories copulation was observed between the resident female and the replacement male. In all of these cases the nest was still active at the time of copulation.

Due to the greater visibility and higher success of the Yellow Warbler nests, the level of investment was easier to determine. In three out of the seven nests replacement males were observed feeding young belonging to the resident male which had been removed. A fourth male was presumed, but not actually seen, to feed the young due to his repeated appearance in the vicinity of the nest with food in his bill. In this case my view of the nest was obscured by dense vegetation. It is unlikely that he was feeding the female because she was out foraging for the young herself a large amount of the time.

On one Yellow Warbler territory, where feeding of the young was not observed, a replacement male chased a female cowbird out of the territory. This same male was also observed to feed the female.

As mentioned above, all of the Song Sparrow nests that I was observing failed. Two out of the seven Yellow Warbler nests where I made removals failed due to predation.

Another cause of nest failure, especially in the Yellow Warbler, is that of nest parasitism. Three out of the seven Yellow Warbler nests contained one cowbird egg each. Two out of the four Song Sparrow nests that were observed contained one cowbird egg each. These figures are based only on the nests where removals were made. There were several nests that I found that had been abandoned prior to the three egg stage, presumably due in some cases to the presence of cowbird eggs in the nest.

DISCUSSION

The high frequency of replacement (89%) for the Song Sparrow was an expected result due to the advantage of the replacement being able to breed with the female for subsequent broods. Unfortunately, due to the failure of all of the Song Sparrow nests that I was observing, I was not able to determine the level of investment on the part of the replacement males. In the four cases where the nest had been located, replacement, and in three cases copulation, occurred with the replacement male while the nest was still active.

The reason for complete failure of my sample of nests could be due to several factors such as human disturbance, high levels of predation, or low levels of investment on the part of the replacement male. It is possible that my activities allowed predators to find the nests because I visited the nests daily, but it is unlikely that this would be responsible for the loss of all the nests. Gottfried and Thompson (1978) found no significant difference in predation between experimental open-cup nests that were visited daily and those that were checked only once at the end of the exposure period. In their experiment the nests were placed in low shrubs and on the ground similar to places where Song Sparrows nest.

Still, high levels of predation may have been responsible for the failure of all of the Song Sparrow nests. Shortly after my 1978 study season began, the two large fields on either side of the railroad tracks at the Holt site were plowed for planting. This could have focused predation pressure on the strips of habitat along the tracks where the majority of my nests were located. This does not explain the failure of the two nests that were located at other sites, or the high level of success for the Yellow Warbler at the Holt site.

Without further study I can only speculate on the possibility that the lack of observed investment on the part of the replacements caused the high frequency of failure of Song Sparrow nests. Pinkowski (1978) found that replacement male bluebirds did not give alarm notes and fed the nestlings fewer times when compared with later broods in which the replacement male mated with the female. A similar result was found by Rutberg and Rohwer (1980) with Yellow-headed Blackbirds (Xanthocephalus xanthocephalus). It is possible that a lack of investment on the part of the replacement male Song Sparrows caused the female to either abandon or to become more conspicuous by increasing the demands on her time and investment. This could have increased the vulnerability of the nest to predation. As mentioned earlier, Song Sparrows are normally very secretive and approach the nest indirectly out of sight in the vegetation. One female, after removal of her mate, began approaching the nest directly. She repeatedly perched within several inches of the nest giving loud chip notes. Her nest became an obvious focus of her attention and was destroyed several days after the young had hatched. This was one of the two territories where the replacement male expanded his own territory to include that of the removal territory.

Because Song Sparrows are normally tolerant of cowbird eggs and only two out of the four nests contained cowbird eggs, it is assumed that nest parasitism did not play a major role in nest failure.

Due to the fact that the high frequency of replacement on the part of the Song Sparrow was expected because of the advantage of second broods, the rest of the discussion will concentrate on the results for the Yellow Warbler for which replacement was not expected. Replacement of removed Yellow Warbler males occurred as rapidly as for the Song Sparrow. Even more surprising was the high level of investment on the part of the replacement males.

Erickson and Zenone (1976) found that male ring doves court sexually unstimulated females more vigorously than they court females that are close to ovulation as a result of prior exposure to other males. Power (1979) attributed the close following behavior of female Mountain Bluebirds (_Sialia currucoides_) by males to the avoidance of cuckoldry.

If elaborate behaviors such as the ones mentioned above have evolved to keep males from investing in the genes of another male's offspring, then it would seem only logical that a replacement would be able to tell that the eggs present in the nest at the time of replacement were not the result of his own copulations. The possibility that males do not see the nest and its contents is unlikely because they are often observed in close proximity to the nest (personal observation) and several authors have noted that the male Yellow Warbler feeds the female on the nest during incubation (Kammeraad 1964, Schrantz 1943, Smith 1943, Bigglestone 1913, Mousley 1926). In his work on the Mountain Bluebird, Power (1975) concluded that the one replacement (a female) out of ten, that actually fed the young, had made a reproductive error. He hypothesized that the replacement may have been at the same stage of the nesting cycle and thus responded to the young as if they were her own. That the replacement Yellow Warblers in the present study were committing reproductive errors seems unlikely because of the high frequency of replacement, 100%, and the high frequency of birds that fed young, 57%. For such a high frequency of investment to be attributed to reproductive error would require that the situation where a male is lost during the nesting cycle had not occurred at a high enough frequency naturally to allow the potential replacements to evolve the necessary anti-cuckoldry behaviors.

Assuming that Yellow Warblers are not committing a reproductive error by investing in another male's offspring, there are seven possible advantages to be gained from this behavior. These possible advantages include: 1) gaining experience for future nestings; 2) investing in one's close relatives or kin selection; 3) gaining access to a limited resource such as food or cover; 4) mating with the female to fertilize the unlayed portion of the clutch; 5) mating with the female during a subsequent brood during the same season; 6) mating with the female in the event that the first nest fails; and 7) obtaining a mate or territory for the following season. Each one of these possible advantages will be considered below.

Studies on the effects of experience on nesting success have emphasized the age of the bird and in some cases whether it had raised a successful brood or not (Pinkowski 1977, Coulson 1966). Coulson (1966) found that pairs of the Kittiwake Gull (Rissa tridactylla) were more likely to remate the following year if the pair had raised a successful brood. Pinkowski (1977) found that all of the adult Eastern Bluebirds (Sialia sialis) that returned to breed in his study area for a second consecutive year had nested successfully the previous season. With the Yellow Warbler it is a different situation because the replacement is entering the cycle at the egg stage. It is difficult to determine whether experience alone in assisting the female improves a replacement's chances for raising a successful brood in the future. To determine the effects of experience, one would have to compare the following year's nesting success of birds whose only experience is from replacement to those birds that are nesting for the first time. Even with this type of study it would be difficult to separate out the effects of experience alone, and the advantages due to the possibility of mating with the same female for the following season. Whatever benefits are gained from experience, there is a cost to the individual involved. A replacement must expend energy defending the territory and feeding the young. If a replacement is closely related to the female and her offspring then the energy spent could increase his own inclusive fitness.

Kin selection is defined by Wilson (1975) as "the selection of genes due to one or more individuals favoring or disfavoring the survival and reproduction of relatives (other than offspring) who possess the same genes by common descent." Woolfenden (1974) found that in the Florida Scrub Jay (Aphelocoma coerulescens) when a territorial male dies, he is most likely to be replaced by the dominant male helper at the nest. Helpers at the nest are usually closely related to the resident pair.

For the Yellow Warbler there is no documentation of helpers at the nest, but it is possible that the young from the previous year return to the vicinity of their parent's nest. This pattern has been shown for Great Tits (Parus major) where approximately 25% of the males banded in the nest settled either in the natal territory when the male disappeared or in the adjacent territory. Female Great Tits settled a further distance from the natal territory (Greenwood, Harvey and Perrins 1979). Great Tits, unlike Yellow Warblers, are year-round residents. It is possible that this year-round residency allows the young birds to become familiar enough with a specific area to make it advantageous to return. In young Yellow Warblers, who migrate soon after independence, experience with a certain habitat may not be as important. Unfortunately, the data, including return rate of young and winter mortality for Yellow Warblers, are not currently available.

It is possible that replacements are obtaining access to limited resources by moving onto territories. Limited resources for the Yellow Warbler could include such things as food and roosting sites. Both the Hudson and Holt study sites contained abundant habitat that was unsettled by Yellow Warblers. Much of this habitat appeared to be identical to that in use by the warblers. It is possible that the territories differed in some important aspect, such as prey availability, that was not evident in my observations. That this unsettled habitat can support floating males is evident because they must subsist in these areas until a territory becomes available. Floating males are not tolerated within the territory and are chased out by the resident males. Even if the territories do contain some limiting resources, a replacement must pay in energy for them. All of the Yellow Warbler replacements defended territories and four of them fed young. This would seem to be a considerable investment and may outweigh any of the advantages due to gaining access to limiting resources. It would also seem that if territories contained abundant resources that family groups would remain in the area later in the season. This is not the case because as soon as a brood is independent they move out of the area. If the female is considered the limiting resource, then the only way a floating male can obtain a female is by replacing. Under these circumstances replacement would be advantageous if subsequent broods are attempted and also if the female has not already been inseminated.

It is possible that a replacement male could improve his genetic fitness by fertilizing the unlayed portion of the female's clutch. Although this may have influenced the behavior of the Song Sparrows in this study, it does not explain the replacement or investment patterns of the Yellow Warbler replacements. In all seven of the Yellow Warbler territories the clutch was complete at the time of removal.

For the Song Sparrow the advantage of being able to mate with the female during subsequent broods during the same season gives the replacement a chance for current genetic return on investment.

Because second broods appear to be the exception for the Yellow Warbler (Smith 1943, Goosen 1978) they would offer little incentive to a replacement. While second broods are extremely rare, renestings due to the failure of the first nest are quite common.

Yellow Warbler nests fail for a variety of reasons such as weather damage, predation, and nest parasitism. Goosen (1978) found that in a sample of 227 nests 54.2% failed; 62% of these failures were due to predation and 15.4% were due to desertion. Of the nests that were deserted (N = 19) 47% were due to nest parasitism by the cowbird. Rates of parasitism in the literature for the Yellow Warbler range from 24.8% to 40.9%. Kammeraad (1966) found that out of the nine nests that he studied all four pairs that were parasitized built new nests. It is at this point that a replacement male could mate with the female and obtain genetic input for that season. This could explain the high observed rate of replacement. The problem with this argument is that why should a replacement feed the young of the former male thus improving their chances for survival and decreasing his own chances for genetic input during the current season since only one brood will be raised?

It is possible that a female will accept a male only after determining that he is willing to invest in her offspring. Pinkowski (1977) felt that a replacement male improved his chances for a second brood by assisting with the first brood. This view is also supported by the evidence that pairs remain together for subsequent broods during the same or following years at a higher frequency when a successful brood has been raised (Pinkowski 1977, Coulson 1966). A female at the beginning of the nesting season may choose a mate using a variety of criteria such as male appearance, song, territory quality, and courtship behaviors. Whereas a female who has lost her mate is confronted with a replacement male who has not had to go through territorial establishment or the earlier courtship behaviors. Her judgment of the replacement may be based entirely on his behavior at that point in the nesting cycle; i.e., does he drive away competitors or does he bring food to the young. If a female judges a potential mate from these criteria, it would seem to her advantage to choose the one whose level of investment is the same or greater than her original mate. A replacement who does not live up to her expectations may not be tolerated on the territory because he represents a competitor for resources. While there is a high chance that a nest will fail and renestings will occur, there is also nearly equal chance that a nest will succeed and a replacement will end up investing in another male's genes without the benefit of any genetic input during the current season. This occurred for five out of the seven Yellow Warbler nests studied. A replacement male in this position may have a better chance of retaining either the territory and/or the female for the following season.

Unfortunately the data for the Yellow Warbler concerning return rates, site tenacity, and the frequency that pairs renest in the following season is not currently available. Again Pinkowski (1977) and Coulson's (1966) data suggest that pairs with successful broods are more likely to return to the same area to breed the following season. Sixty-four percent (64%) of the Kittiwake Gulls in Coulson's study remated with the same individual for the following year. A replacement male Yellow Warbler may improve his chance of retaining the female for breeding during the following year by demonstrating a high level of investment to the female.

There is always the possibility that the high level of investment of the part of the replacement male Yellow Warblers is not adaptive on the individual level and is maintained by group selection or as an epiphenomenon. Unfortunately, due to the scope of this study, I was unable to address these possibilities.

A floating male who does not replace has no chance for genetic input during the current season. By replacing and assisting the female there is a good chance that he will be able to mate with the female for a renest during the current season or perhaps improve his chances of mating with the female for the following year.

Thus, it seems that the distinction between single and multiple brooded species is not as useful in terms of predicting replacement behavior as is the probability of further nesting attempts for whatever reason. The obvious next step will be to compare replacement behavior within a species over the breeding season to see what happens as the probability of new nesting attempts decline.

SUMMARY

During 1978 and 1979 removal experiments were conducted to test for differences in replacement behavior between a multiple brooded species, the Song Sparrow, and a single brooded species, the Yellow Warbler. Results showed an equal frequency of replacement between the two species. The complete failure of the Song Sparrow nests during the study made it impossible to determine the level of investment of the replacements for that species. Yellow Warbler replacements showed a high level of investment with four out of the seven replacements actually feeding the young of the original male.

Benefits of replacing, such as the possibilities for a renesting in the event that the first nest fails, are discussed. Compared to the lack of genetic input during the current season in the case of a male who does not replace, the potential for genetic input by a male who does replace is felt to be a sufficient incentive for replacement.

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