

EXPERIMENTAL EVIDENCE FOR THE FUNCTION OF MATE REPLACEMENT AND INFANTICIDE BY MALES IN A NORTH-TEMPERATE POPULATION OF HOUSE WRENS¹

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Abstract. Male birds who replace other males on territories may kill, care for, or act indifferently towards offspring of the previous resident. In short-lived species, selection should favor adoption or indifference over infanticide only when the resident female is the only mate the replacement male is likely to obtain, and when this female will desert the male if her offspring are killed. We tested this hypothesis by removing 29 male House Wrens (*Troglodytes aedon*) from territories in a population in which unpaired females are readily available as mates. Ten of 16 males that were subsequently observed on experimental territories removed offspring from nests as predicted. At least four resident females bred with these males. All infanticidal males paired within 72 hr of replacement and most subsequently fledged young of their own. An eleventh replacement male fed young after eggs hatched but disappeared before nestlings fledged. The five remaining males appeared indifferent to resident offspring. Unlike infanticidal males, however, indifferent males did not remain on territories continuously, court resident females, or attempt to attract a mate to the territory. No indifferent male bred on the territory. Our observations suggest that selection should strongly favor a "replacement-then-infanticide" strategy among unsettled male House Wrens in this population. However, for reasons yet unknown, some males fail to complete this sequence of behaviors.

Key words: *Infanticide; mate replacement; brood adoption; House Wren; Troglodytes aedon; intraspecific differences.*

INTRODUCTION

Infanticide is recognized as an adaptive behavior which may increase the reproductive success of the perpetrator in many animal species (Hrdy 1979, Hrdy and Hausfater 1984). Among birds, infanticide is often committed by individuals who replace other individuals on territories containing offspring of the previous resident (reviewed in Rohwer 1986, Kermott and Johnson 1990). Replacement can occur after one member of a pair dies or deserts the territory, or through physical eviction of one member of a pair by a non-resident bird (Freed 1986a, Arcese 1989, John-

son and Kermott 1990). Two hypotheses for the adaptive value of infanticide in this context have been proposed (cf. Hrdy 1979). First, by eliminating dependent offspring, the perpetrator may shorten the interval between replacement and the time that the resident is capable of starting a new breeding attempt (Freed 1986a, Emlen et al. 1989). Second, destruction of offspring may provide the perpetrator access to a resource that is critical for attracting a mate, such as a nest site (Robertson and Stutchbury 1988). Despite these potential benefits, replacements do not always commit infanticide. In some species, replacements have been observed to act indifferently towards resident offspring (e.g., Bowman and Bird 1987) or provide them with some form of parental care (Dunn and Hannon 1989, Martin 1989).

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Rohwer (1986) outlined conditions under which infanticide, adoption or indifference would maximize the future reproductive success of a replacement male (i.e., by rapid acquisition of a mate). We summarize these conditions briefly here, restricting our attention to short-lived species for which the potential benefits of a response are not likely to be realized in subsequent breeding seasons. Infanticide should be favored when only enough time remains in the breeding season to complete either the resident female's current breeding attempt or one new attempt. Infanticide will also be favored, regardless of the number of broods that can be raised that breeding season, when there is a high probability that the resident female will pair with the replacement male following infanticide, or if there is a high probability that the replacement male can attract a new mate to the territory if the resident female deserts. Indifference or adoption will only be favored over infanticide if the resident female represents the only mate a replacement male is likely to obtain that year. Thus, there must be a high probability that the resident female will desert the replacement male if he kills her offspring, and a low probability that the male will attract a new mate if the resident female deserts. In addition, enough time must remain in the breeding season to complete both the resident female's breeding attempt and at least one additional attempt.

We tested Rohwer's predictions by removing males from breeding pairs of House Wrens (*Troglodytes aedon*), a short-lived songbird (see Drilling and Thompson 1988 for data on longevity in this species). House Wrens are well known for their habit of destroying the offspring of other birds including conspecifics (Kendeigh 1941, Quinn and Holroyd 1989, Finch 1990; also see Belles-Isles and Picman 1986). However, in almost all reported cases, perpetrators have been "floaters" or territorial neighbors that were not resident on the territories where infanticide occurred. The behavior of actual replacement birds is more equivocal. Kendeigh (1941) identified two cases of infanticide by males following replacement in an Ohio population. In our own population, we have observed one case each of infanticide, adoption, and indifference by males following natural replacements (Kermott and Johnson 1990, Johnson and Kermott 1990). Indeed, this variation in behavior stimulated this study.

In this report, we first provide evidence that

replacement males in this population should quickly be able to attract a mate after replacement. Thus, selection should favor infanticide over indifference or adoption in response to resident young. We then report results of the removal experiment designed to test this prediction.

METHODS

This study was conducted on the Gallatin and Canyon Ranches near Big Horn, Wyoming, USA (44°40'N, 106°56'W). Wrens in this area occupy woodlands along the Little Goose Creek and its small tributaries which flow through large expanses of pasture, hayfields and prairie. All wrens in this study nested in wooden nest boxes which were mounted on greased poles to eliminate predation on eggs and nestlings. Between 100 and 150 breeding attempts were made in boxes each year. Boxes were patchily distributed and were not placed in much of the suitable habitat. Thus, the majority of wrens in this population nested in natural cavities.

To determine the frequency and speed with which unpaired males obtain mates in this population, we surveyed each of 22 territories in one area of our study site each day during the 1988, 1989 and 1990 breeding seasons. Our objective was to determine the day that each territory was settled, and the day that each settled male paired. A territory was considered settled if a male was singing loud spontaneous song and/or had constructed a partial nest in the box on the territory. We considered a male to be paired the first day that we observed a female carrying nesting material to nest box. Observations were facilitated by distinct and dramatic changes in song output following territory establishment and pairing (Johnson and Kermott 1991).

To determine the response of replacement males to offspring (hereafter "offspring" refers either to eggs or nestlings) on territories at the time of replacement, 9 and 20 males were removed from territories during the second half of their incubation stages in 1989 and 1990, respectively. In three cases, two males were removed from the same territory and the same female, the second male being an earlier replacement. Males were individually color-banded and transported to a distant patch of woods from which they did not return. In some cases females were captured and color-banded at the same time that males were removed. We visited each ter-

ritory on the day following male removal and every 1–4 days thereafter. During these visits we noted the nest contents and condition of any eggs or young present, and the identity and behavior of wrens on the territory. In five cases where we suspected males were acting indifferently towards resident offspring, we observed nests on the territories involved for 75–120 min on 2–4 different days to determine whether males were feeding young.

RESULTS

PAIRING SUCCESS OF NON-REPLACEMENT MALES

In the three years of surveys, 24 males became established on unoccupied territories between 7 June and 9 July, the period encompassed by the removal experiment. Twenty-one (88%) males attracted a mate, in an average of 3.8 ± 3.0 (SD) days after establishing a territory. The three males who did not attract a mate disappeared from their territories after four, six, and seven days. These data suggest that unpaired females are readily available as mates in this population.

MALE BEHAVIOR ON TERRITORIES FROM WHICH RESIDENT MALES WERE REMOVED

“New” males were observed on experimental territories after 6 of 9 male removals in 1989 and 8 of 20 removals in 1990. With one exception (discussed below), all replacements occurred between 7 and 24 June (Table 1). The temporal pattern of breeding attempts in the population suggested that enough time remained when each of these replacements occurred for the completion of one and probably only one complete breeding cycle. The last females who attempted two cycles in 1989 and 1990 had begun laying eggs for their first cycles earlier than the time of all replacements (on 5 and 4 June in the two years, respectively). However, the last females to successfully complete a breeding attempt in each year did not begin laying until 8 and 19 July, respectively.

We suspect that we observed a total of 16 males on territories after residents were removed. However, in four cases, males were not present on territories each day that we made observations and because the males were unbanded, we cannot be certain that just four males were involved. Two of the 16 males observed were banded. One male (case 89-5) was a bird banded as a nestling in the previous year. The second

banded male was the only male known to hold another territory while present on an experimental territory. This male made several trips/hr to the experimental territory from his own neighboring territory on which he and his mate were feeding nestlings. Because almost all territorial males in the vicinity of experimental territories were color-banded, we suspect that most of the 14 unbanded males did not hold territories elsewhere when they appeared on experimental territories.

Ten of 16 males observed on experimental territories appeared to destroy resident offspring (Table 1). We observed one male take eggs from the box and drop them <1 m away. In two cases, we found either eggs with beak-sized punctures or dead nestlings below nest boxes. In two other nests, we observed nestlings with several small bleeding wounds that could have been caused by blows from a wren's sharp bill. These nestlings later disappeared from the nest. Direct evidence of infanticide was lacking in remaining cases and could only be presumed from the disappearance of offspring from otherwise undisturbed nests. In nine of the ten cases where infanticide occurred, all offspring were removed within 24 hr of replacement. In one case, a male appeared to kill only five of seven nestlings within the first 24 hr. Females did not vigorously attack infanticidal replacements but in some cases they sat in nest box entrances and appeared to resist male entry inside. No female was observed to solicit copulation from a replacement male, a behavior previously observed among widowed females in the Pied Flycatcher (*Ficedula hypoleuca*; Gjershaug et al. 1989).

In the nine cases where infanticide was immediate and complete, males were present on territories continuously during our observations, sang loudly and constantly, and vigorously courted resident females. Four of the nine resident females who were color-banded paired with infanticidal males. All other males were paired within 72 hr. The one exception (Case 89-6) was the male who replaced in July of 1989, about the time that the last breeding attempt of that year began. This male remained unpaired for four days at which point his box was removed. Infanticidal replacements who did pair fledged at least one nestling in three of the four cases for which breeding success data were available (Table 1).

We observed one case of temporary brood adoption. The male involved fed nestlings three times in 30 min when observed two days after

TABLE 1. Summary of events associated with mate replacement in the study population of House Wrens. Under the category of "Nest contents when replaced," Eggs → Nestlings indicates that the nest box contained eggs and then nestlings during replacement male's tenure on territory, and Eggs/Nestlings indicates that the nest may have contained eggs, nestlings, or both eggs and nestlings during the male's tenure on territory (i.e., replacement occurred when eggs were due to hatch). N/A = data not available.

Case	Date male removed	Days to replacement	Nest contents when replaced	Replacement male response	Replacement pairs with resident female?	Days to obtain new mate	Subsequent breeding success: young fledged
89-1	7 June	2	Eggs	Infanticide	No	3	N/A ^a
89-2	9 June	1	Eggs	Infanticide	Yes	—	0
89-3	15 June	1	Eggs	Infanticide	No	3	N/A ^a
89-4	23 June	1	Eggs	Infanticide	Uncertain	—	—
89-5	24 June	3	Eggs/Nestlings	Infanticide	No	1	1
89-6	9 July	2	Eggs/Nestlings	Infanticide	No	N/A ^b	—
90-1	9 June	6–8	Nestlings	Infanticide	Yes	—	3
90-2	11 June	2–3	Eggs/Nestlings	Infanticide	Yes	—	N/A ^a
90-3	13 June	4	Eggs/Nestlings	Infanticide	No	1–2	N/A ^c
90-4	13 June	1	Eggs → Nestlings	Temporary adoption	—	— ^d	—
		7–12 ^e	Nestlings	Indifference	No	— ^f	—
90-5	14 June	1	Eggs → Nestlings	Indifference	No	— ^d	—
		8–11	Nestlings	Infanticide	Yes	—	5
90-6	15 June	1	Eggs → Nestlings	Indifference	No	— ^d	—
90-7	15 June	5–8	Nestlings	Indifference	— ^g	—	—
90-8	22 June	3–5	Nestlings	Indifference	No	— ^d	—

^a Replacement male removed from territory.

^b Nest box removed after four days (male remained unpaired).

^c Nestlings were collected as part of another study.

^d Male disappears from territory before new breeding cycle could commence.

^e Second replacement male is a paired neighbor with nestlings on his territory.

^f Replacement male already possessed a mate on a neighboring territory.

^g Female deserted brood after she was banded later in the nestling stage.

eggs hatched. Although this male sang, he did not court the resident female. This male occasionally moved near an unoccupied nest box 40 m from the focal nest and sang loudly. This male had disappeared by the time the territory was visited four days later.

The remaining five males appeared to act differently towards resident offspring. No eggs or healthy nestlings disappeared from nests on these territories. These males did not feed young, nor did they approach or give alarm calls when we inspected nest contents. Indifferent males differed from infanticidal males in that they were not always on the territory during observations, they did not sing loudly or continuously, and they did not court resident females. Some of these males occasionally sang near unoccupied nest boxes in adjacent areas. One male may have attracted a mate to an adjacent area but we cannot be certain because this male was unbanded.

DISCUSSION

Unpaired males in this population of House Wrens quickly attract mates. Because resident females do not represent the only or even most

likely mate a replacement male can acquire, there should not be strong selection on replacement males to encourage resident females to remain on territories by allowing, or assisting them in completing a breeding attempt. Selection should favor replacement males who remove offspring from nest sites in preparation for their own breeding attempt. Most male House Wrens in this study who claimed territories from which resident males were removed behaved as predicted and immediately destroyed offspring fathered by the previous resident. Approximately half of resident females paired with infanticidal males. Because most resident females were captured, handled and banded a day or two before replacement, the actual frequency with which resident females pair with replacement males may be higher than observed in this study. The other infanticidal males who were deserted by resident females all paired within three days of replacement. Our results support the hypothesis that infanticide by replacement males is adaptive because it increases access to a resource (the nest site) needed to attract a mate for breeding. If under natural conditions resident females typically pair with replacements, this will also

strengthen the selection for infanticide. However, because unpaired females are readily available in this population, access to a mate (i.e., the resident female) is probably not the primary factor that favors infanticide.

One male fed nestlings on at least one day before disappearing. The most parsimonious explanation for the two cases of brood adoption now observed in this population is that the males involved were simply committing "reproductive error." Plissner and Gowaty (1988) observed a pair of Eastern Bluebirds (*Sialia sialis*) adopt young in a neighbor's nest immediately after their own young were depredated. Unfortunately, we do not know the recent breeding history of males in either case of adoption that we observed. We cannot rule out the possibility that the adopting males were related to the young that they fed. Adopting males may have been feeding kin but such cooperative breeding has not been observed in temperate House Wrens to date. It is also possible that the males were feeding young that they sired through extra-pair copulations (Johnson and Kermott 1989).

Five males observed were present on territories only intermittently and did not court resident females. Because these males did not "claim" experimental territories, we hesitate to consider them "true" replacements. These males clearly had access to active nests on the territories but were apparently indifferent to the offspring within. Because most infanticidal replacements paired and subsequently fledged young of their own, we do not believe that indifferent males were behaving in a manner that would maximize their reproductive output. Even if indifferent males held active territories elsewhere (and at least one indifferent male did), it could still benefit the male to claim the territory, remove the offspring from the nest site, and attempt to pair with the resident or other female. A number of males are successfully polygynous in our study population each year. Freed (1986b) described six instances in a Panamanian population of House Wrens in which paired males obtained second mates by replacing males on neighboring territories. In sum, the behavior of indifferent males remains puzzling.

WHY REPLACE?

Infanticide increases a replacement male's opportunity to reproduce only on one specific territory. We must still ask why replacement, either

passive replacement or replacement through usurpation (Johnson and Kermott 1990), occurs at all. To breed, a male House Wren must control a cavity suitable for nesting. However, we do not believe that replacement occurs because suitable cavities are in limited supply. Since 1987, we have monitored pairing and breeding success of many males on our study area who utilized natural nest sites and have found that not all suitable nest sites are used each year. Also, unoccupied nest boxes were present within 30–200 m of all territories on which replacement occurred. We therefore suspect that it is the presence of an *active* nest that favors replacement. Such territories may be attractive because they contain potential mates but again, there is no evidence of mate limitation in this population. Rather, we suspect that males prefer active nest sites because they are "proven" attractive to females. Many late-settling males, including most replacements, are probably first-time breeders (unpubl. data). Because males in this population tend to return to the territory that they held in the previous year, selection should favor those males who obtain high-quality nest sites and territories early in life. Males should judge nest sites currently in use by breeding females to be of higher quality than those that are unoccupied, especially after most older birds have settled.

COMPARISON WITH TROPICAL HOUSE WRENS

Freed (1986a) reported that in one Panamanian population of House Wrens, males usurp territories of other males during 10% of all breeding attempts, and that destruction of resident offspring then follows in almost all cases. However, in contrast to our temperate population, the primary factor favoring replacement by tropical males appears to be a scarcity of unpaired females in breeding condition. Furthermore, because of the scarcity of alternative mates, infanticide is probably favored over adoption or indifference primarily because resident females rarely desert infanticidal males (Freed 1986a). These two studies provide an example of how different demographic conditions can select for an identical suite of behaviors in two populations of the same species.

CONCLUSION

Our study is the third of four removal experiments which support Rohwer's (1986) hypoth-

eses concerning selection on the response of replacement birds to offspring of previous residents (Robertson and Stutchbury 1988, Emlen et al. 1989, Martin 1989). This is only the second removal experiment using a population in which adoption or indifference after natural replacement has been reported (see also Martin 1989). We provide evidence that the benefits of adoptive or indifferent behavior are probably far less than the benefits of infanticide in this population. Strong selection for infanticide after replacement will be nearly universal in all short-lived bird species and it is questionable whether adoption or indifference will be adaptive in any short-lived species. To confirm this, additional removal experiments must be made using species in which adoption or indifference after natural replacement is known to occur. For example, more than one incident of adoption is reported for Eastern Bluebirds (*Sialia sialis*; Rohwer 1986, Plissner and Gowaty 1988), Prairie Warblers (*Dendroica discolor*; Nolan 1978), Black-capped Chickadees (*Parus atricapillus*; Odum 1941, Howitz 1986), and Song Sparrows (*Melospiza melodia*; Rohwer 1986). Studies on these species would be especially valuable because each species' natural history is unusually well-known. Removal experiments on these species may also identify conditions not previously considered which would favor indifference or adoption among replacements.

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