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Possible Causes of Territory Takeovers in a North-temperate Population of House Wrens

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In most animal species, residents defeat nonresident challengers in a high proportion of contests over territories and other resources (summary in Leimar and Enquist 1984; see also Krebs 1982, Walton and Nolan 1986, Jakobsson 1988). Three explanations are generally suggested for this observation. First, residents may be stronger or larger, or have larger weapons, greater energy reserves, more experience in fighting, etc., which gives them greater "resource holding potential" (Parker 1974). Second, residents may assign a greater value to the disputed resource than do challengers, and may therefore fight harder or longer for that resource. The relative value of a territory should increase as the resident gains knowledge of its resources (i.e. food sources, areas of cover, and potential nest sites). Challengers are presumably less familiar with the resident's territory and thus should not value it more than any other territory.

Third, under certain conditions, the simple convention of "owner wins" may be used to settle contests (Maynard Smith and Parker 1976). Conflicts should be settled in this manner only if the cost of an escalated contest is high relative to the value of the resource, if individuals have little control over the risk of injury in escalated contests, or if resources are readily available elsewhere (Krebs 1982).

Recent reports have indicated that, in populations of several species of birds, challengers regularly evict residents from territories (Freed 1986, Ueda 1986, Eckert and Weatherhead 1987, Arcese 1989). Because such results run counter to the frequently observed outcome of resident-challenger contests, they may provide unique insights into the nature and evolution of animal conflict behavior. We report observations of territory takeover attempts in a north-temperate population of House Wrens (*Troglodytes aedon*). We outline several hypotheses to explain the occurrence of territory takeover attempts in birds, and we discuss the success of some challengers in evicting residents in a game-theoretical framework.

Observations were conducted from 1985 to 1989 on

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TABLE 1. Breeding stage of resident when territory takeover attempt occurred vs. the success of the takeover attempt. In the one case where a challenger attempted to take over both the primary and secondary areas of a polygynous resident's territory, the success in each area is tallied separately.

Resident's breeding stage	Outcome of attempt			Total
	Suc-cess	Fail-ure	Incom-plete	
Premating	2	1	0	3
Prelying	6	3	2	11
Laying	0	0	0	0
Incubation	0	1	0	1
Nestling	1	5	0	6
Unknown	1	0	0	1
Total	10	10	2	22

the Helen Brinton Bird Reserve at the Quarter-circle A Ranch, and on the neighboring Gallatin Ranch near Big Horn, Sheridan County, Wyoming, USA. We monitored the breeding progress of 206 pairs of wrens nesting in boxes and 75 pairs in natural cavities. Most males on the study area were marked individually with colored leg bands shortly after settling on a territory. Most females were unbanded. On most territories, we recorded the identity and behavior of resident wrens, and contents of nests (those in boxes only) during 0.25–1.5 h observation sessions every 1–6 days in conjunction with other studies. This report concerns only cases in which one male challenged another male for a territory. We observed a single takeover attempt (unsuccessful) between a resident and a nonresident female. This takeover attempt is discussed elsewhere (Johnson and Kermott 1990).

We observed 21 cases in which 19 different resident males were in conflict with nonresident challengers within their territories. Thus, males were challenged for territories during approximately 7% of breeding attempts. The actual frequency of takeover attempts was probably greater because we did not observe each territory daily for extended periods of time. Significantly more takeover attempts occurred on territories with boxes (20/206, 9.7%) than on territories with nest sites in natural cavities (1/75, 1.3%; $G = 7.43$, $P < 0.01$).

We estimate that 17 different males were challengers. One banded male tried twice to take over territories of the same resident male. The challenger first attempted, unsuccessfully, to recover the territory that he had occupied the year before from the current resident, who was unpaired at the time. The next day the same resident was found ca. 100 m away on a new territory and was now paired. The challenger attempted, again unsuccessfully, to obtain the resident's new territory. In another situation, we suspect that a single unbanded male was involved in four takeover attempts that occurred over a 4-day period

on four neighboring territories. In all remaining cases, we either knew that challengers were different males because they were banded, or assumed that they were different males because the attempts were widely separated in distance and time.

In ten cases, challengers evicted residents and obtained the entire territory if residents were unpaired or monogamous, or obtained the area around either the primary or the secondary nest site if residents were polygynous. In nine other cases, residents held their territories. In the remaining two cases, both challenger and resident were mist-netted during the takeover attempt, and the conflict did not resume after the birds were released. Although our data suggest that challengers are successful in obtaining territories in more than 50% of attempts, it is possible that we were more likely to observe successful attempts if such attempts involve more prolonged contests than unsuccessful attempts.

Residents and challengers behaved essentially the same in each takeover attempt. Residents repeatedly pursued challengers in tight circles around the territory in chase sequences that usually lasted 20–60 s. Each chase sequence commenced immediately after a challenger began to sing. Residents appeared to quit chases first. Challengers would then land 2–10 m from residents. After a pause of 5–30 s, they would sing and chasing resumed immediately. In a few instances we observed contestants come together and fight briefly (for 5 s or less). Occasionally, contests stopped for 5–20 min, and the challenger was not visible. Most contests lasted at least several hours, but less than a day. One contest lasted eight days.

Takeover attempts occurred during all stages of resident males' breeding cycles except egg laying. A disproportionate number of takeover attempts were made during the relatively short pre-mating and pre-laying stages compared with the longer incubation and nestling stages (Table 1). This difference did not result from our spending more time observing birds in the pre-mating and pre-laying stages. Of the 19 resident males, 16 were observed at regular intervals throughout their breeding cycles, and the longest observations were made during the incubation and nestling stages. We also found that the success rate of takeover attempts was higher during the pre-mating and pre-laying stages (75%, $n = 12$) than during the incubation and nestling stages (14%, $n = 7$). This difference is significant ($G = 5.25$, $P < 0.03$; we excluded two takeover attempts made by one challenger on the same resident male because the outcomes of these attempts were probably not independent of one another). The challenger that we suspect attempted four takeovers failed in his first three attempts when resident females were incubating or feeding young. He succeeded in obtaining part of a fourth resident male's territory in which the resident had a second mate who had not yet laid eggs. In the one successful takeover of a territory that occurred when the resident

female was feeding nestlings, the contest for the territory was extremely prolonged, lasting eight days.

Six challengers obtained a territory or part of a territory on which there was a female who had not yet laid eggs. In two cases the resident female was color-banded and was known to pair with the challenger. We strongly suspect challengers paired with resident females in the remaining four cases as well, although all four females were unbanded. On the morning following takeovers, each of the four challengers had a female on his territory who was working on a nearly completed nest, which suggests that the resident female was involved. In five cases, females began to lay eggs one to three mornings after the takeover. Despite the chance that some eggs were fertilized by previous mates of these females, no eggs were destroyed (see Freed 1987a). In the remaining case, the box was removed from the territory before the female began to lay.

At least three hypotheses may explain the occurrence of territory takeover attempts. The "previous resident" hypothesis proposes that takeover attempts occur because challengers had occupied the disputed territories during a previous breeding attempt. Challengers may therefore place a high value on the territory and be willing to engage in a long contest to regain it. Walton and Nolan (1986) and Jakobsson (1988) found that, when male Prairie Warblers (*Dendroica discolor*) and Willow Warblers (*Phylloscopus trochilus*) return in spring, they often evict newcomers from their territories of the previous year. In our study, the identity of the previous resident was known in 13 takeover attempts. In only one case was the challenger the previous resident on the territory. We conclude that previous residence cannot explain the occurrence of most takeover attempts in our population.

The "territory limitation" hypothesis proposes that takeover attempts occur because no suitable habitat is available. Challenging an established male for his territory may therefore be a better strategy than becoming a nonbreeding "floater" and waiting for an established male to disappear. Arcese (1989) suggested that this may explain the frequency of territory takeover attempts in an isolated population of 30-70 Song Sparrows (*Melospiza melodia*) on Mandarte Island, British Columbia. We reject this hypothesis for this wren population because apparently suitable habitat with natural cavities and unoccupied nest boxes was available to unsettled males when takeovers occurred.

The "territory quality" hypothesis proposes that takeover attempts will occur if the *net value* of an occupied territory (resource benefits minus expected takeover costs) exceeds the value of any unoccupied territory. Food resources or nest sites on occupied territories may be superior to those on unoccupied territories. We recorded significantly more takeover attempts on territories with boxes than on those with natural cavities. Wrens prefer boxes over most natural

cavities, and thus they may consider nest boxes to be a higher quality resource than natural cavities. Although we have conducted no formal choice experiments to prove this preference, in more than 100 instances we have erected boxes on territories containing natural cavities used by wrens in previous years when no boxes were present. Wrens used boxes rather than natural cavities in more than 90% of these cases.

Territory value can also be based on the presence of a female. Freed (1986) proposed that House Wrens in Panama frequently usurp territories because territories contain potential mates. In Panama, House Wrens are permanently monogamous and maintain territories throughout the year. Territories and nest sites were not in short supply, but opportunities for finding a mate may have been extremely limited for unpaired birds (see also Freed 1987b). In 13% of all breeding attempts, a male or female floater replaced its counterpart on a territory, often by physical takeover. When males were challengers, more than 90% of resident females remained and bred with challengers. In our study of House Wrens, resident males were paired in 17 of 20 (85%) takeovers for which resident pairing status was known. Challengers apparently obtained females in 6 of 7 successful takeovers. Mate limitation may therefore explain some takeovers in our population, but we currently do not have evidence to demonstrate whether females are a limited resource. Note that two unpaired residents also lost their territories, and challengers could not have directly gained a mate in these situations.

One hypothesis for the success of challengers in some takeover attempts can be derived from game theory. The contest between a resident and a challenger in House Wrens resembles a "war of attrition" (Maynard Smith 1974) in which escalated fighting is rare, and the winner is that bird which persists the longest. If we denote V as the value of the resource to a contestant and c as the rate at which the contestant accumulates costs during a contest, then persistence time for a contestant will be determined by V/c (Hammerstein and Parker 1982). The contestant with the highest V/c ratio should be able to persist longer than his opponent and thus win the contest. For territorial species, the perceived value of a territory is unlikely ever to be higher for challengers than for residents. Even if the value of the territory is based on the presence of a female, V should be equal for residents and challengers. Thus, challengers should win only if the rate at which they accumulate costs in a contest is much less than that of residents. We hypothesize that this is possible because challengers may take the opportunity to accumulate a large store of energy through intensive foraging before challenging a resident. Presumably residents cannot do the same because they are busy with territorial maintenance and mating activities. Challengers could also interrupt contests intermittently for additional foraging,

whereas residents must engage in other activities. One could test this hypothesis by comparing either fat levels or body mass per unit size of challengers and residents during takeover attempts.

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Measures of Wing Area and Wing Span from Wing Formula Data

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The modification of wing shape is an important feature of many avian adaptive radiations, whether the differences are among major taxa (Saville 1957) or within a group of closely related species (Gaston 1974,

Fitzpatrick 1985). An accurate and convenient description of wing-shape variation is relevant to many systematic and comparative studies of birds.

Wing shape is often described by means of tracing or photographing the outline of the extended wing. However, wing formulae, long recognized as useful descriptors of wing shape (Johnson 1963, Svensson 1975), have several important advantages. For example, measuring the distance between successive

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