

Territorial song in the Anna's hummingbird, *Calypte anna*: costs of attraction and benefits of deterrence

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Abstract. Playback of territorial song of Anna's hummingbirds near newly available feeders attracted intruders to the feeders and hastened territory establishment. The first feeding by intruders was not significantly earlier in the presence of playback, apparently because intruders were tentative about feeding in the presence of playback. Playback of song on established territories benefited owners by deterring potential intruders.

Virtually all territorial animals rely on some form of communication, whether it is scent, sound or vision, to advertise their presence. Because of its pervasiveness and aesthetic appeal, territorial bird-song has long been one of the most intensely studied examples of such communication (Howard 1920; Kroodsmma & Miller 1982). Studies of the agonistic functions of birdsong (e.g. Yasukawa 1981a, b; Falls 1988) generally focus on the benefits of announcement as a deterrent to potential intruders.

Several experiments support the idea that announcement song deters potential intruders. Surgical muting adversely affects abilities of birds to acquire and maintain territories (Peek 1972; Smith 1979; McDonald 1989). Broadcasting song from territories after the removal of owners can deter intruders. In red-winged blackbirds, *Agelaius phoeniceus*, fly-through rate, but not trespass rate, was lower where such playback was present (Yasukawa 1981b). In white-throated sparrows, *Zonotrichia albicollis*, intrusions were fewer and delayed compared with controls (Falls 1988), and in great tits, *Parus major*, playback delayed recolonization (Krebs et al. 1978). Announcement song might deter intruders by advertising the owner's presence on the territory, thereby communicating that the intruder will have little chance of stealing resources.

Singing may entail costs such as increased energy expenditure (Eberhardt 1990), increased predation (e.g. Tuttle & Ryan 1981), and the preclusion of

other activities necessary for survival or reproduction (Ydenberg 1984; Radesater et al. 1987). Singing might also be costly because it informs competitors that a rich resource is present. If so, announcement might attract intruders that seek resources or information about owners. Owners might then have to spend time and energy chasing these intruders, or they might lose resources or even control of their territories.

In this study we attempt to determine whether such attractive costs of territorial announcement song exist and, if so, whether any deterrent benefits outweigh them. We chose to study Anna's hummingbirds because of their observability and rapid territorial responses to manipulations of nectar (Ewald 1985).

MATERIALS AND METHODS

We conducted the study in the Santa Lucia Mountains of central California at Hastings Natural History Reservation, administered by the University of California, Berkeley. We attracted a population of approximately 100 hummingbirds by providing 20% sucrose solution (weight/weight) from unrestricted feeders several weeks prior to the beginning of the experiment. Because natural flowers were extremely rare during our study, the attracted population was almost completely dependent on our feeders. We placed feeders at the edge of the vegetation so that they could be observed without obstruction while vegetation similar in structure to that in natural territories was readily available to birds visiting the feeders.

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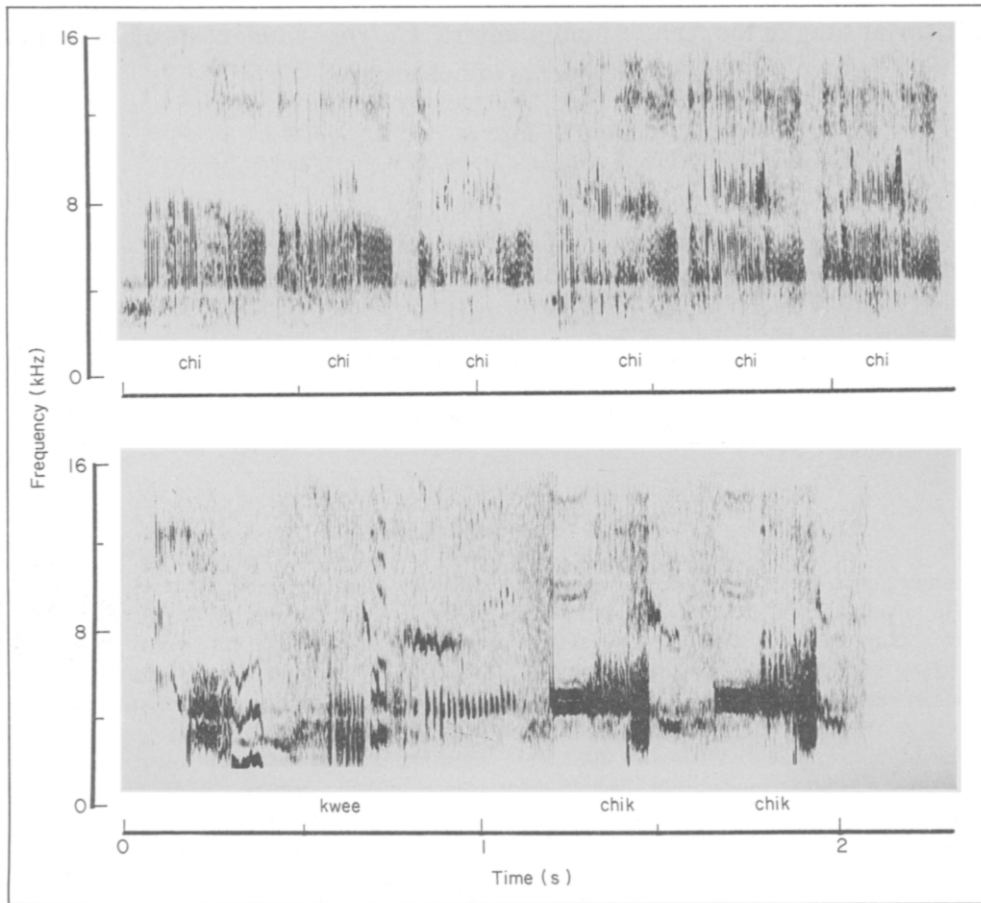


Figure 1. Sonagram of the representative cycle of the Anna's hummingbird territorial announcement song that was used in the experiment. The sonagram was made using a Kay Model 5500 sonagraph.

During the non-breeding season, male Anna's hummingbirds use announcement song apparently to aid in their defence of flowers. A full cycle of song typically consists of two or more sets of 'chi chi chi' followed by 'kwee chik chik'. We recorded this song from an adult male Anna's hummingbird using an R.D. Systems parabolic microphone and Marantz PMD430 cassette recorder (Fig. 1). We copied the recording onto another tape to create a continuous cycle of 15 s of song followed by 30 s of silence. We played this recording for all playbacks through a Realistic CD 3301 stereo system.

Experiment 1: the Costs of Attraction

For each replicate, we placed two feeders containing green sucrose solution (20% by weight) in

two locations in which there had not previously been any food. We paired locations for similarity in vegetation, sunlight and distance from other food sources. The distance between each pair of feeder locations was generally about 50 m. To select locations with similar characteristics, however, we sometimes placed feeders as close as 25 m or as far as 100 m apart. Each feeder consisted of two stoppered, inverted test tubes mounted on either side of a ring stand so that birds approaching from any direction could see at least one of the two red-tipped feeding holes. Although song was played only next to experimental feeders, we placed a silent speaker the same distance from control feeders (0.3 m) to control for visual effects. At approximately 1000 hours, the experimental observer and the control observer removed paper envelopes

covering the feeders; the experimental observer immediately began playback.

We recorded verbally on microcassette recorders the time, identity, feeding activity and aggression for any hummingbirds within 10 m of the feeder. We identified individuals on the basis of plumage characteristics and dyes applied by perch feeders (see Ewald & Rohwer 1980). We terminated observations when a bird had successfully established territorial defence as indicated by fulfillment of all of the following criteria: (1) residency, a bird had to spend at least 50% of any 30-min period within 10 m of the area of the feeder; (2) feeding, a bird had to feed at the feeder; and (3) chasing, a bird had to chase at least 80% of at least five intruders. To quantify time until ownership, we calculated the interval between the first exposure of the feeder and the beginning of the residency period. We also recorded times and durations of song, and aborted feedings (defined as an approach within 0.5 m of the feeder followed by sudden movement away from the feeder).

After the first replicate in a location, we reversed the sites of control and experimental treatments. After each pair of replicates, a new pair of sites was selected and the process was repeated until 10 replicates were obtained.

Experiment 2: Announcement as a Deterrent

Two unlimited feeders were placed on established territories, which had previously contained only artificial food. The owners were then allowed to equilibrate for at least 1 week before experimental manipulation, during which time the territory contained no flowers visited by hummingbirds. On the day of manipulation, the feeders on each territory were replaced by one of the feeders described in experiment 1. Owners began feeding from and defending these feeders within minutes. As in experiment 1, we paired territories according to locational similarity, and treatments were reversed on successive replicates, after which we selected a new pair of sites. Distances between experimental and control feeders averaged about 30 m (range = 20–70 m).

We began observations at approximately 0900 hours, using one observer per territory. Using laptop computers, we noted simultaneously on experimental and control territories the birds entering the area bounded by the owner's chases (i.e. intrusions) and the territorial behaviour of the

owner over a 3-h period. During the first hour no song was played on either site. During the second and third hours, song was played on the experimental site. We used the second hour to allow for any adjustment period in the response of birds to playback.

This protocol created a double control design; intrusion rates subsequent to playback on experimental sites could be compared not only with intrusion rates before playback, but also with intrusion rates on control sites. Any natural changes in intrusion rate (due to time of day, changing weather conditions, etc.) would influence control and experimental data similarly; changes in experimental intrusion rates relative to controls would thus reflect the influence of playback.

RESULTS

Experiment 1: the Costs of Attraction

On the basis of plumage characteristics and marks from dyes, we could determine that most of the visitors to the feeders and all the eventual defenders were not defending any of the approximately 10 territories elsewhere in our study site. All of our eventual defenders were different birds. Prior to defence, most of these birds were meeting their energy requirements by feeding at an undefended patch in the centre of the study site. This patch was at least 40 m away from the experimental feeders, and was undefendable because it lacked perches suitable for defence.

Birds discovered feeders more than an order of magnitude quicker when playback was present than when playback was absent (Table I). The visiting birds sometimes responded visibly to playback. On one occasion, five birds appeared from five different directions at the experimental feeder within 1 min of the beginning of playback. Birds initiated defence of playback feeders more than twice as soon as control feeders (Table I). Although birds tended to feed sooner on experimental feeders, the trend fell slightly short of significance (Table I). This probably reflects the greater tentativeness of birds attempting to feed when song was being played; in the presence of playback, aborted feedings occurred over an order of magnitude more frequently than in the absence of playback (Table I).

Table I. Means \pm SE for times until discovery, defence and feeding and for tentativeness at newly available feeders

	Control \pm SE	Experimental \pm SE	<i>P</i> *
Time until discovery of feeder (min)	223.8 \pm 86.0	7.8 \pm 2.2	0.003
Time until initiation of defence (min)	410.8 \pm 106.0	147.3 \pm 65.0	0.005
Time until first feeding (min)	238.3 \pm 87.0	70.6 \pm 33.3	0.08
Tentativeness (no. of aborted feeding attempts)	0.5 \pm 0.2	6.1 \pm 1.2	0.004

For each mean, *N* = 10 replicates on different sites.

*Two-tailed matched-pairs randomization tests.

Table II. Mean intrusion rates in defended territories before and during playback

Site	Intrusions per hour of observation (\pm SE)			
	Before playback		During playback	
	Hour 1	Hour 2	Hour 3	Mean*
Control	15.9 \pm 4.1	22.2 \pm 5.2	20.2 \pm 8.2	21.2 \pm 6.7
Experimental	22.8 \pm 4.8	16.4 \pm 3.5	11.1 \pm 2.0	13.7 \pm 2.5

For each mean, *N* = 10 different territories defended by 10 different owners.

*Mean of hours 2 and 3.

Experiment 2: Announcement as a Deterrent

Song played from established territories had the opposite effect. While intrusion rate increased by an average of 5.3 intrusions per hour in control territories (perhaps because of natural daily cycles of intrusion), it decreased by an average of 9.1 intrusions per hour where playback was present (Table II; two-tailed matched pairs randomization test, $P = 0.004$, Siegel 1956; the *i*th data point represents the following quantity: $(E_{si} - E_{bi}) - (C_{si} - C_{bi})$, where *E* is the intrusion rate on experimental territories, *C* is the intrusion rate on control territories, *s* is the playback period, and *b* is the observation period before playback). Data from the second and third hours were combined because there was no statistically significant difference in intrusion rate between these two periods ($P = 0.23$, two-tailed matched-pairs randomization test, Table II).

The results of playback on established territories draw attention to the importance of the double control design. A paired design without double control would not have yielded a statistically significant deterrent effect: intrusion rates on experimental

and control territories were not significantly different when the pre-manipulation observations were omitted from calculations (two-tailed matched-pairs randomization test, $P = 0.08$).

Playback on the owners' territories did not influence territorial behaviour of owners perceptibly. Nearly every owner spent all of the observation time on its territory and chased all encountered intruders. Song rates of owners did not change significantly in response to playback of song on the owner's territory; the change in song rate (\pm SD) from hour 1 to hours 2 and 3 of the observation period (percentage of time spent singing by owners during playback minus pre-playback) was $0.2 \pm 14.0\%$ on control territories and $-4.4 \pm 7.2\%$ on experimental territories (matched-pairs randomization test, $P = 0.33$). Song rates of owners during these periods ranged from zero to the song rate broadcast from the recording.

DISCUSSION

The results of experiment 1 show that territorial announcement song of Anna's hummingbirds has an attractive element. Attractive costs should be

relatively high in environments characterized by high turnover within the intruder population, high turnover of territory ownership (assuming songs of individuals can be distinguished) or a high rate of new territory establishment. In each of these situations intruders might be evaluating owners or resources.

Birds finding newly available resources defended only by the empty threat of announcement song tended to initiate defence of their own. An unseen owner of a new resource singing but not defending would thus incur two costs: intruders would be more likely to locate and consume some of the resource, and successful intruders would be more likely to begin defending the resource. These results suggest that hummingbird song is an honest advertisement (Clutton-Brock & Albon 1979) of intent to defend. A cheater that sings without actively defending would probably attract rather than repel competitors.

Our results are noteworthy with reference to data from Alatalo et al. (1982) on pied flycatchers, *Ficedula hypoleuca*. They found that breeding pairs settled in three out of four nestboxes with playback of male song whereas no birds settled in four boxes without playback. The small sample size and lack of statistical significance (two-tailed $P=0.14$), however, make these results ambiguous, as does the alternative hypothesis that the females rather than males were attracted by the song. Mountjoy & Lemon (1991) conducted a similar experiment on starlings, *Sturnus vulgaris*, during the breeding season. Contrary to their prediction, male song attracted both males and females. Presumably, during the breeding season, male song geared towards attracting mates has the unavoidable consequence of attracting competing males as well.

When defenders use song principally to deter competitors, it may still attract them. Aggressive song of female red-winged blackbirds played from male breeding territories lacking females decreased the time until female settlement but did not increase the number of females settling or the total rate of female visitation (Yasukawa 1990). These findings are consistent with our results from hummingbird territories; defending individuals apparently vocalize to deter competitors, but vocalization attracts competitors when it emanates from areas without a singer already in residence.

Song of Anna's hummingbirds apparently benefits owners by making intruders more tentative. Birds in the presence of playback aborted more

feeding attempts than birds at control feeders. This effect probably accounted for the fact that playback from undefended feeders did not significantly advance the timing of first feeding relative to controls. Several of the birds discovering playback feeders fulfilled the chasing criterion for initiation of territoriality before they even fed from the feeders (four out of 10 experimentals versus zero out of 10 controls). The timing of first feeding might have been significantly advanced by playback had patches of flowers been used instead of the experimental feeders, which forced birds to come very close to the speaker (i.e. the apparent defender, from the intruder's point of view) to steal nectar.

The results of experiment 2 show that song backed by defence benefits the owner. In an area of established territories, intruders have probably had prior experience with territory owners. Song emanating from established territories probably communicates to potential intruders the presence of an actively defending owner. Under such circumstances, one would expect intruders often to pass up these defended resources to find new resources or temporarily vacant territories.

Previous studies demonstrating a deterrent effect of announcement have involved manipulations of fully established territories (e.g. Smith 1979; Yasukawa 1981b; Falls 1988). One would expect the deterrent aspects of song to outweigh the attractive ones in such areas. We are aware of no studies demonstrating deterrence in an area that had not previously been defended; indeed, on the basis of this study, one might expect this effect to be rare or absent in nature.

The playback and muting studies collectively account for alternative explanations that are not accounted for by any single study. Muting studies (Smith 1979; McDonald 1989) control for the visual presence of the territory owner unlike the experiments in which songs are played from unoccupied areas (e.g. experiment 1 and Yasukawa 1990). The muting experiments also did not increase the overall song rates, unlike experiments in which song is played from occupied territories (e.g. experiment 2). The protocol of muting studies controlled for physical trauma of surgery, but not for other correlates of muting; for example, birds attempting but unable to sing might be less motivated to defend their territories because of psychological stress.

In nature, owners may enforce song by fighting. By eliminating this enforcement, playback after removal of owners (Yasukawa 1981b; Falls 1988)

may not deter intruders as much as playback in the presence of owners (experiment 2). This reduced deterrence may be especially relevant to data from red-winged blackbirds (Yasukawa 1981b), which showed a deterrent effect of song on fly-throughs but not on intrusions.

Our results show that the recorded song used in our experiment had both deterrent and attractive components. The tendency for song to attract competitors may be especially pronounced in Anna's hummingbirds, which have evolved to defend ephemeral resources that become available unpredictably. It would be interesting to determine whether attractive components of song generally tend to be associated with species that defend such resources.

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