A TEST OF THE ADAPTIVENESS OF INTERSPECIFIC TERRITORIALITY IN THE BLUE-THROATED HUMMINGBIRD

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ABSTRACT.—Interspecific territoriality in birds has generally been regarded as adaptive, but Murray (1969, 1971) proposed a nonadaptive model in which interspecific aggression is explained as mistaken misdirected intraspecific aggression. Gradually increasing the size of an artificially induced territory of a male Blue-throated Hummingbird, *Lampornis clemenciae*, permitted a test of the two hypotheses. The male ejected all hummingbirds except female conspecifics from a small space around an initial clustered grouping of 10 hummingbird feeders, but as feeders were dispersed outward radially in 3 subsequent treatments, thus necessitating defense of an increasingly larger area, first Black-chinned Hummingbirds, *Archilochus alexandri* (treatment 2), then Rivoli's Hummingbird, *Eugenes fulgens* (early in treatment 3), and finally male conspecifics (late in treatment 3) were permitted to forage. This shows that the male was able to make clear distinctions between species and contradicts the basic assumption of the Murray model. Character convergence (Cody, 1969) and the adaptive model of Orians and Willson (1964) are discussed as alternative explanations of these findings.—*Department of Biology, Cornell College, Mt. Vernon, Iowa 52314.* Accepted 31 October 1975.

MOST investigators (e.g. Simmons 1951; Orians and Willson 1964; Cody 1969, 1974) have regarded interspecific territoriality in birds as adaptive, i. e. individuals that exclude other species as well as conspecifics from an area restrict access to some common resource, thereby enhancing their own reproduction and survival. Murray (1969, 1971) has proposed a nonadaptive model for which the basic assumption is that interspecific territoriality is derived from mistaken and misdirected intraspecific aggression, but apparently no direct tests of this assumption or the predictions of the model have occurred since the model was first proposed. The purpose of this paper is to test the basic Murray assumption that interspecific territoriality results from misdirected intraspecific territoriality, by manipulating the size of an artificially induced "territory" of a male Blue-throated Hummingbird (*Lampornis clemenciae*).

Wolf (1970) and Stiles and Wolf (1970) indicated the important variables that determine the presence or absence of hummingbord territoriality: (1) distribution of the nectar resource in space and time, (2) the richness and degree of localization of nectar relative to alternative nectar sources, and (3) the abundance of intraspecific and interspecific competitors. Thus if a single nectar source were divided into subunits of equal richness which then became increasingly dispersed with time, it is predicted that the nectar would become more difficult to protect from thieving by other hummingbirds, and a territorial bird would have to expend more time and energy guarding it. If dispersion is continued, at some point the advantage gained by excluding thieving birds will be nullified by the increased energy used in defense, and the territorial bird will have to make a "decision" about which species of hummingbirds to continue to exclude, if any.

In the present study the second variable above was held constant—nectar richness did not vary throughout the experimental period and no naturally occurring alternative nectar sources were available within the study area because of a prolonged drought. The third variable, the number of competitors, could not be controlled, but was readily measurable. The first variable was manipulated experimentally. Thus any changes in territorial behavior that occurred during the study period could be

TABLE 1

COMPARISON OF TIME BUDGETS (%) FOR THE MALE BLUE-THROATED, *CALYPTE ANNA*, AND *EULAMPIS JUGULARIS*[1]

Species	Perching	Chasing	Insect foraging	Nectar foraging	Absent	C/F
L. clemenciae						
Treatment 1	80.0	14.2	0.2	0.8	4.5	18.4
Treatment 2	75.0	19.5	0.5	0.9	4.3	20.3
Treatment 3	76.0	20.0	0.9	1.1	1.9	18.2
Mean	78.0	17.5	0.5	.9	3.7	20.2
C. anna						
21 January	81.0	5.9	1.2	8.4	3.5	0.7
22 March	79.9	7.9	1.1	8.2	2.8	1.0
E. jugularis (flower type = *Inga*)	79.3	5.9	1.2	4.4	8.3	1.3

[1] Percentages for *C. anna* taken from Stiles (1971) and for *E. jugularis* from Wolf and Hainsworth (1971). C/F = chasing/foraging. C/F for both *C. anna* and *E. jugularis* calculated from authors' data. *C. anna* data from a single male. Number of *E. jugularis* unknown.

attributed to the manipulated dispersion of the nectar resource or change in number of competitors, and such changes could then be used as a device to test the Murray hypothesis.

The study was carried out in early June 1974 in Cave Creek Canyon, Chiricahua Mountains, Arizona at approximately 1550 m elevation. In addition to the Blue-throated, Rivoli's Hummingbird (*Eugenes fulgens*) and Black-chinned Hummingbird (*Archilochus alexandri*) were the most abundant hummingbirds in the canyon and in addition to conspecifics, were the individuals towards which the male's aggression was most commonly directed.

METHODS AND MATERIALS

Ten commercial hummingbird feeders filled with 20% (1.11 M) sucrose solution were set up on a 120-cm-high linear rack, 20 cm separating adjacent feeders. A male Blue-throated, identified by a distinctive tail coloration pattern, quickly took up residence and defended the rack from all hummingbirds. Three days later an experimental period covering 4 days was begun during which 3 different dispersion patterns circumscribing areas of 13 (treatment 1), 41 (treatment 2), and 85 m^2 (treatment 3) were established consecutively around the rack. Each area described an approximate circle with two feeders on the rack at the center and the remaining eight feeders spaced equidistantly along the periphery. The following schedule of treatments was carried out: the first on 4 June, the second on 5 June, and the third on 6 and 7 June. For each treatment the number and species of hummingbirds entering and chased from the territory or allowed to feed, and the approximate distance of each chase, was recorded. A time budget of the male's activities was also kept throughout the experimental period. Activities were recorded in the following categories: perching, chasing, nectar foraging, and insect foraging. Perching was the time the bird was actually on the perch. Chasing included flying toward and threatening an intruder as well as active chasing. Nectar foraging was total time spent at the feeders and included time flying between feeders and to and from the perch. Insect foraging included all time spent hawking insects from the perch and gleaning from foliage.

RESULTS

The area the male defended in each treatment was approximately that within the periphery of the circle defined by the outer feeders. Much of the male's time was spent at one of several perches in trees within the area defended from which all feeders could be seen. Prior to the experimental period (all feeders on the rack), all Blue-throated males, Rivoli's, and Black-chins coming within 1 m of the rack were

TABLE 2

NUMBER PER HOUR OF OBSERVATION TIME OF EACH SPECIES OF HUMMINGBIRD TRESPASSING AND CHASED FROM THE TERRITORY[1]

	Treatments					
	1		2		3	
	No.	%	No.	%	No.	%
Trespassing/hour						
Black-chin	80	69.6	122	56.2	171	59.7
Rivoli's	11	9.6	31	14.3	34	11.9
Blue-throated ♂	19	16.5	56	25.8	72	25.0
Blue-throated ♀	5	4.3	8	3.7	10	3.5
Total[2]	115		217		287	
Chased/hour						
Black-chin	69	69.7	55	38.7	2	2.7
Rivoli's	11	11.1	31	21.8	13	17.8
Blue-throated ♂	19	19.2	56	39.4	58	79.5
Blue-throated ♀	0	0.0	0	0.0	0	0.0
Total	99		142		73	

[1] Observation time in treatments 1 and 2 consisted of five 30-min periods each. Treatment 3 consisted of a total of 6 hours of observation time.

[2] $\chi^2 = 72.4$, $P < 0.001$ that total numbers trespassing/hour is the same in all treatments.

chased, generally for less than 10 m, but most Blue-throated females were allowed to feed unmolested. Infrequently, apparent displays by the male toward trespassing females occurred in which the male hovered in front of females but did not chase them. Some birds, particularly Black-chins, the smallest and most abundant species, foraged at the feeders while the male was involved in other chases. Hummingbirds flying through the area or perching above the perched male were not chased.

Results of the time budget study show only small changes across treatments (Table 1). As size of the territory was increased the proportion of time spent perching decreased slightly. Time chasing and foraging (insects and nectar) increased slightly.

Except for Blue-throated females, which were seldom chased, the number and species chased or allowed to forage differed markedly across treatments. During treatment 1, similar to when all feeders were on the rack, all trespassing Blue-throated males, Rivoli's, and most Black-chins believed noticed by the male were chased. During treatment 2, Blue-throated males and Rivoli's intruders again were chased, but most Black-chins were allowed to feed unmolested (Table 2).

In treatment 3 the number and species of hummingbirds chased from the territory (Table 3) differed markedly from treatments 1 and 2. For two 1-hour observation periods beginning at 0830 and 1030, respectively on 6 June, few trespassing Black-chins and Blue-throated females were chased and of those ejected most were pursued only a short distance (Table 3). No Rivoli's or male Blue-throateds were allowed to forage and these were chased greater distances than Black-chins and Blue-throated females. During a third 1-hour period beginning at 1430, again all Black-chings and female Blue-throateds were allowed to forage, but all trespassing Blue-throated males were chased, most for long distances. A large number of trespassing Rivoli's (58%) were allowed to forage during this same period and those ejected were chased shorter distances than Blue-throated males (Table 3). During a fourth 45-min period beginning at 1600 all Rivoli's as well as Black-chins were allowed to forage unmolested. The only birds chased were male Blue-throateds, but even 37% of these were allowed to forage. An additional 2¼ hour of observation on 7 June again showed that

TABLE 3

REACTION OF THE MALE *L. CLEMENCIAE* TO INVADING HUMMINGBIRDS IN TREATMENT 3

Time period	Species[1]	Not chased		Threatened[2]		Total not chased or threatened	Distance chased[3]						Total chased	Grand total (N)
							S		M		L			
		No.	%[4]	No.	%		No.	%	No.	%	No.	%		
0830–0930	Aa	297	90.6	20	6.1	317	8	2.4	3	0.9	0	0.0	11	328
1030–1130	Ef	0	0.0	14	16.9	14	17	20.5	29	34.9	23	27.7	69	83
6 June	Lcm	0	0.0	15	10.1	15	28	18.8	46	30.9	60	40.2	134	149
	Lcf	18	81.8	2	9.1	20	2	9.1	0	0.0	0	0.0	2	22
1430–1530	Aa	184	97.9	3	1.6	187	1	0.5	0	0.0	0	0.0	1	188
6 June	Ef	15	57.7	5	19.2	20	4	15.4	2	7.7	0	0.0	6	26
	Lcm	0	0.0	3	6.7	3	15	33.3	12	26.7	15	33.3	42	45
	Lcf	12	100.0	0	0.0	12	0	0.0	0	0.0	0	0.0	0	12
1600–1645	Aa	115	100.0	0	0.0	115	0	0.0	0	0.0	0	0.0	0	115
6 June	Ef	12	100.0	0	0.0	12	0	0.0	0	0.0	0	0.0	0	12
	Lcm	19	37.3	13	25.5	32	4	7.8	8	15.7	7	13.7	19	51
	Lcf	8	100.0	0	0.0	8	0	0.0	0	0.0	0	0.0	0	8
0830–1045	Aa	379	99.5	2	0.5	381	0	0.0	0	0.0	0	0.0	0	381
7 June	Ef	68	85.0	8	10.0	76	3	3.7	0	0.0	1	1.3	4	80
	Lcm	9	5.0	21	11.7	30	56	31.3	32	17.9	61	34.3	149	179
	Lcf	14	100.0	0	0.0	14	0	0.0	0	0.0	0	0.0	0	14

[1] Aa = *Archilochus alexandri*; Ef = *Eugenes fulgens*; Lcm = *Lampornis clemenciae* male; Lcf = *L. clemenciae* female.
[2] Threatened = flew toward intruder but did not chase or chased only to territory boundary.
[3] S = short: chased to within 3 m of territory boundary; M = medium: within 3–6 m outside territory boundary; L = long: > 6 m.
[4] All percentages based on grand totals.

a large percentage of trespassing Rivoli's and Black-chins were not chased, but only 5% of the trespassing male Blue-throateds were permitted to feed and most were chased long distances (Table 3). On the afternoon of 6 June the male was absent for increasingly frequent periods. Though he returned on the morning of 7 June and defended the territory (treatment 3) for several hours, during the afternoon he was absent most of the time and returned only for a few short periods during which he defended the area only against Blue-throated males. On 8 June the territory was abandoned. Thus during treatment 1 all individuals except Blue-throated females were excluded from the territory, and all but Black-chins and Blue-throated females were excluded in treatment 2. All but male conspecifics were allowed to forage during the latter stages of treatment 3. Throughout treatments the number of competitors per hour of observation time increased, but number of birds chased per hour first increased then decreased in treatment 3 (Table 2).

DISCUSSION

Comparison of time budgets of the male Blue-throated, *E. jugularis* (Wolf and Hainsworth 1971) and *C. anna* (Stiles 1971) show similar proportions of time spent in flying and perching for the three species, but a much higher chase/foraging (C/F) ratio for the Blue-throated (Table 1), probably because of the relatively great number of competitors (Table 2). The great and immediate influx of birds upon establishment of the feeders was undoubtedly encouraged by the richness, localization, and stability of the food source and the absence of floral sources at alternative locations. Nectar foraging increased slightly throughout treatments, but the proportion of time spent in chasing leveled off in treatment 2 (Table 1) even though the number of trespassing birds entering the territory and the number of species and individuals permitted to forage at the feeders increased throughout the experimental period.

As nectar foraging constituted such a small proportion of the time budget relative to other activities, it is not clear why a slight increase in time spent nectar-foraging could not have accommodated continued defense despite an increase in competitors. It may have been that the critical factors influencing the energetic "decision" to abandon territorial behavior were the frequent short periods of intense chasing activity and that time budget data averaged over longer periods masked the importance of these bursts of activity. In addition, factors other than energetic considerations alone may influence the breakdown of territories, particularly breeding territories where attraction of females (Stiles 1973) and not only protection of a food source may be an important function of the territory. We noted active nests of Blue-throateds in Cave Creek Canyon during the period of the study and for as long as 1 month after the termination of the study period, both in 1975 and in previous years. Thus for territorial breeding males time spent simply watching for receptive females may increase fitness while time spent excluding intruders may actually lower it, especially in situations such as in this study, where food resources are superabundant.

Whatever the factors leading to abandonment, it is clear that as both territory size and the number of competitors increased, first Black-chins, then Rivoli's were permitted to forage, and finally many Blue-throated males as well. Thus an ability to discriminate among species on the basis of increasingly subtle criteria was demonstrated, and this is in direct contradiction to the basic assumption and predictions of the Murray model, because if interspecific territoriality is derived from misdirected intraspecific aggression, all trespassing species should have been treated with equal aggressiveness up to the time of abandonment. It might be argued that ignoring trespassing Black-chins was a learned behavior based on a obvious difference in body size between Black-chins and the much larger Blue-throated and Rivoli's, i.e. that an innate tendency to act aggressively toward all hummingbirds regardless of size was present, but that faced with the great numbers and persistence of Black-chins, all small hummingbirds were eventually tolerated, an interpretation that could be consistent with the model. The ability to discriminate between individual Rivoli's and Blue-throateds (even females), species of equal size, indicates that finer distinctions were made, probably on the basis of behavior, plumage, or body profile differences.

The demonstrated ability to distinguish male from female conspecifics is also consistent with the argument that interspecific territoriality is adaptive and not due to mistaken intraspecific identification. Female conspecifics constitute vehicles for gene perpetuation and increased fitness, hence their presence in the territory should be encouraged, even if it results in some resource depletion. Males are not only competitors for resources, but also genetic threats and should be persistently excluded under even high levels of resource availability.

Though these conclusions are based on the activities of a single bird, additional observations of another male Blue-throated induced to behave territorially at a similar feeder rack operating simultaneously near by indicated that initially, when feeders were clumped on or near the rack all hummingbirds except female conspecifics were chased from around the rack, but as feeders were then systematically dispersed outward, progressively greater numbers of Black-chins were permitted to feed at one or more feeders while at the same time most trespassing Blue-throated males and Rivoli's of both sexes continued to be chased. Further, observations at feeders in other parts of the canyon indicated that early in the spring when migrant hummingbirds first began to arrive and numbers of all species were low, male Blue-

throateds successfully defended feeders against all hummingbirds, including Black-chins. As the influx of migrants continued, first Black-chins, but eventually also Rivoli's and Blue-throateds were able to thieve successfully until finally attempts by dominant male Blue-throateds to defend the area around feeders ceased.

We consider that the nonadaptive Murray model fails to explain the maintenance of Blue-throated male interspecific territoriality in this particular hummingbird territorial system, but our findings are compatible with the adaptive Orians and Willson (1964) model. Orians and Willson argue that interspecific territoriality should be selected against, unless the distribution of food resources is such that species divergence in behavior or in utilization of space or time is not possible, viz. in very simple habitats, where food resources are stratified in more complex habitats, or where other species exploiting similar resources are already present in an area into which a species is extending its range. Implicit in the Orians and Willson model is the assumption that interspecifically territorial species recognize one another, yet still interact aggressively.

Cody (1969) extended the Orians and Willson argument to suggest that under certain circumstances it is to the advantage of two or more closely competing sympatric species to come to look more like each other (i.e. character convergence), thus presumably assuring more efficient interspecific territorial defense. The assumption of the Cody model is not necessarily that, as in the Murray (1971) model, all cases of interspecific territoriality stem from mistaken intraspecific territoriality, but that efficiency of excluding interspecific competitors is enhanced if the visual and behavior cues each species uses in identifying conspecifics is mimicked by closely competing sympatric species.

Interpreted in terms of character convergence it might be suggested that the closer size approximation of Rivoli's than Black-chins to Blue-throateds accounts for the more persistent aggressiveness of territorial male Blue-throateds toward Rivoli's than toward Black-chins, but even though male Rivoli's are approximately the same size as Blue-throateds, plumage coloration and patterns are distinctly different. In addition, as Blue-throated females are allowed to forage during all treatments, one would predict that because Rivoli's females closely resemble Blue-throated females, any hesitancy by the male in ejecting trespassing hummingbirds should be most evident in interactions with Rivoli's females, yet in the pre-experimental period when all feeders were on the rack and in treatments 1 and 2, all intruding Rivoli's females were quickly chased. It therefore appears that the concept of character convergence is also inadequate to explain the maintenance of interspecific territoriality in this system.

When the feeders were on the rack and in treatment 1, all species of hummingbirds were excluded from the territory circumscribed by the feeders, and only when the number of competitors doubled in treatment 2 (Tables 2 and 3) and the area to be defended trebled did the territorial male make distinctions between species. This suggests that in nature under normal dispersion patterns of the nectar resource probably all species of hummingbirds are excluded from Blue-throated territories with equal efficiency. Lyon (1976) showed that in an interspecific hummingbird territorial system in Oaxaca, Mexico involving six species ranging widely in size and plumage and in which the Blue-throated was also the dominant territorial species, all hummingbirds were chased from Blue-throated territories with equal frequency.

The behavior the territorial Blue-throated showed in our study may therefore represent an artifact in the sense that we devised experimental conditions allowing us

to determine if the male could distinguish hummingbird species, but in doing so manufactured a condition of great food localization and concentration that probably seldom occurs in nature. This suggests that though character convergence apparently occurs in certain interspecific territorial systems (Cody 1969, Cody and Brown 1970), in at least some hummingbird systems effective adaptive interspecific territoriality can occur despite fairly large differences in size and plumage characteristics of the interacting species.

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