

Interference asymmetries among age-sex classes of rufous hummingbirds during migratory stopovers

F. Lynn Carpenter¹, Mark A. Hixon², Robert W. Russell¹, David C. Paton³, Ethan J. Temeles⁴

¹ Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92717, USA

² Department of Zoology, Oregon State University, Corvallis, OR 97331, USA

³ Department of Zoology, University of Adelaide, GPO Box 498, Adelaide, SA 5001, Australia

⁴ National Zoological Park, Smithsonian Institution, Washington, DC 20008, USA

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Summary. Three age-sex classes of rufous hummingbirds (*Selasphorus rufus*) overlap temporally and defend feeding territories during migratory stopovers in the Sierra Nevada of California. We demonstrate that these classes differ in their ability to secure and maintain high-quality feeding territories for refueling, and that these differences result in differences in resource use. Data on acquisition of territories, territory characteristics, and responses of territory owners to intruders suggest that several mechanisms are involved in determining dominance, involving sex- and age-related differences in wing disc loading, coloration, and experience. We discuss the implications of these results for understanding intraspecific variation in migration strategies.

Key words: Intraspecific dominance – Territoriality – Migration – Stopovers – Hummingbirds

Introduction

Many studies of nonbreeding birds have documented differences among sex and age classes in resource use (e.g., reviews by Selander 1966; Morse 1980; Grubb and Woodrey 1990; Wunderle 1991). Sometimes these differences may arise from the superior ability of one age or sex class in interference competition. This “interference hypothesis” maintains that age-sex classes differ in resource use because of differential behavioral dominance, which may be conferred by differences in size or morphology. One age-sex class displaces the other from mutually preferred resources through interference competition, i.e., aggressive and/or territorial behaviors (Miller 1967; Gauthreaux 1978; Morse 1980; Peters and Grubb 1983). As a consequence, the subordinate classes subsist on resources outside their preference or adopt other behaviors to exploit the dominants’ resources.

Considerable indirect evidence exists for the interference hypothesis (e.g., Murton et al. 1971; Glase 1973; Kodric-Brown and Brown 1978; Kuban et al. 1983; Hepp and Hair 1984; Temeles 1986). Furthermore, experimental studies have demonstrated that male downy woodpeckers (*Picoides pubescens*) exclude females from more productive foraging sites (Peters and Grubb 1983), and that adult willow tits (*Parus montanus*) do the same to young birds (Hogstad 1988). Natural selection on body sizes of males and females in at least one species has been attributed in part to interference competition (Fleischer and Johnston 1984).

During our 11-year study of migrant rufous hummingbirds (*Selasphorus rufus*) at a stopover site in the California Sierra Nevada, we noted differences in the responses of different age-sex classes to experimental and natural reductions in the number of flowers on their feeding territories. Males were more likely than females to expand their territory boundaries upon flower reduction, thereby maintaining constant the total number of flowers defended (Hixon et al. 1983; Carpenter et al. 1991). We therefore suspected that although all age-sex classes vigorously defend territories, asymmetries might exist among the different classes in interference abilities.

In studies of multi-species hummingbird assemblages, asymmetries among species in interference abilities have often been attributed to morphological characters thought to underlie flight performance and energetics (e.g., Feinsinger and Chaplin 1975; Feinsinger and Colwell 1978; Feinsinger et al. 1979; Snow and Snow 1980). Kodric-Brown and Brown (1978) applied the same reasoning to explain their observation that short-winged male rufous hummingbirds defended territories with higher densities of flowers than did females. In this paper, we present data on the ability to acquire and maintain territories and the resulting patterns of resource use by different age-sex classes of rufous hummingbirds. We also examine potential mechanisms underlying relative territorial abilities by using morphological and plumage color differences among the classes to predict their positions in a dominance hierarchy.

Methods

Study species. Rufous hummingbirds migrate during the summer along the Cascade-Sierra Nevada and Rocky Mountain ranges to their wintering grounds in Mexico (Grant and Grant 1967; Phillips 1975; Calder 1987). They stop periodically in mountain meadows, establish territories around patches of flowers, and require from several days to 3 weeks to reach an appropriate migratory mass before resuming their journey (Gass 1979; Carpenter et al. 1983, 1993a; Hixon et al. 1983). They often compete intensely for food at these stopover sites (Kodric-Brown and Brown 1978).

We have argued previously (Carpenter et al. 1983; Hixon et al. 1983; Paton and Carpenter 1984; Hixon and Carpenter 1988) that this species is selected to minimize the time spent on migratory stopovers, and therefore to maximize the rate at which refatting occurs on feeding territories. Our birds act in ways consistent with maximization of energy gain, in terms of territory size (Carpenter et al. 1983; Hixon et al. 1983), time budgeting (Hixon and Carpenter 1988), foraging patterns (Paton and Carpenter 1984), and meal size (Hixon et al. unpublished data). The selection pressures for maximization of daily net energy gain in rufous hummingbirds should operate equally on males and females. It is not surprising, then, that both sexes defend feeding territories during migratory stopovers.

Adult males migrate 3–4 weeks before females and immatures (Phillips 1975; Calder 1976; personal observations), so adult and immature females often contend only with immature males during most of the summer migration. This pattern usually occurred at our study site. Thus, we have limited data on adult males, and our study focuses primarily on adult females and immatures of both sexes, in contrast to studies conducted along other migratory routes in Colorado and Arizona (Kodric-Brown and Brown 1978; Calder 1987).

Study site. Our study site is a 2-ha meadow in sagebrush scrub desert at the eastern base of the Sierra Nevada, 27 km northwest of the town of Bishop, California (37° 30' N, 118° 30' W, 1700 m elevation). Associated with a stream are willows and a grassy zone supporting the hummingbird-visited plant *Castilleja linariaefolia* (Scrophulariaceae). The habitat is open, facilitating continuous observation of bird behavior from 2-m ladders placed outside territories.

Procedures. We collected data at this site for 11 summers from 1976 to 1986, standardizing our techniques for studying rufous hummingbirds in 1980. Most of the data reported here were collected during the latter 7 years.

Hummingbirds usually arrived at our site between late July and early August. At any one time up to 50 exclusive territories were established in the 2 ha of *Castilleja* (Carpenter 1987). We captured the birds with mist-nets, weighed them, identified their species, sex, and age class using keys (Stiles 1972; Johnsgard 1983), and color-marked them with narrow strips of colored surveyor's flagging glued to the skin of the back. These strips did not seem to bother the birds and did not add detectably to their mass. In most years we caught 200–400 individuals over the summer, 3–35% of these established territories, and on any one day up to 80% of the territory owners were marked, as determined by subsequent daily mapping of marked and unmarked territory owners.

Our netting, marking, and mapping allowed us to compare the proportions of each age-sex class in the overall netted population (including floaters) to those in the population that successfully established territories in the meadow. In addition, we collected detailed data on several territorial individuals each summer. For these birds, we determined territory boundaries daily, counted flowers within territories, and measured standing crops of nectar at the end of the foraging day. For the standing crop measurements, we sampled nectar of flowers in the evening using microcapillary tubes to measure volume and a Bausch and Lomb sucrose refractometer to measure sugar concentration (Carpenter 1976, 1983).

One to four times each summer we counted flowers along two permanent 2-m wide transects through the *Castilleja*, one 36 m long

and one 50 m long, set up in the flower-dense and flower-sparse parts of the meadow, respectively.

Predictions. Several studies of different hummingbird species have noted sexual differences in territorial behavior and resource use. In direct territorial encounters between the two sexes during the non-breeding season, males typically dominate females (e.g., Feinsinger and Colwell 1978; Kodric-Brown and Brown 1978; Kuban et al. 1983). Similarly, males tend to defend territories in areas of high flower density, whereas females tend to defend territories in areas of low flower density, or are nonterritorial (e.g., Kodric-Brown and Brown 1978). All age-sex classes should prefer dense patches of flowers, because territories are then smaller and easier to monitor and travel costs are thereby reduced. Monopolization of the densest flower patches by one sector of a population can therefore be interpreted as an indication of behavioral dominance or territorial superiority.

Sexual differences in dominance and territorial abilities of hummingbirds are thought to result from differences in wing disc loading, the ratio of body mass to area swept out by the wings, hereafter denoted as WDL (Feinsinger and Chaplin 1975; Feinsinger and Colwell 1978). In hummingbird species with male dominance, males have higher WDL than females (Feinsinger and Chaplin 1975; Feinsinger and Colwell 1978; Kodric-Brown and Brown 1978; Kuban et al. 1983). High WDL is thought to improve agility (Feinsinger and Chaplin 1975). Because territorial defense in many hummingbird species requires quick acceleration, high WDL should be associated with superior territorial ability.

In addition, sexual differences in territorial abilities of hummingbirds may be related in part to differences in coloration. In many species, males are more brightly colored than females (Johnsgard 1983). Ewald and Rohrer (1980) demonstrated that drab individuals of another color-polymorphic hummingbird are disadvantaged in territorial disputes, and have to chase intruders more frequently and for longer periods than more brightly colored individuals.

The four age-sex classes of rufous hummingbirds differ in WDL and coloration, which allowed us to make predictions based on the earlier studies. All four age-sex classes differ in wing length (Kodric-Brown and Brown 1978; Carpenter et al. 1993b), and therefore in WDL, and birds with a given body mass may be arranged by WDL from highest to lowest as follows: adult males > immature males > adult females > immature females (Fig. 1). Moreover, the

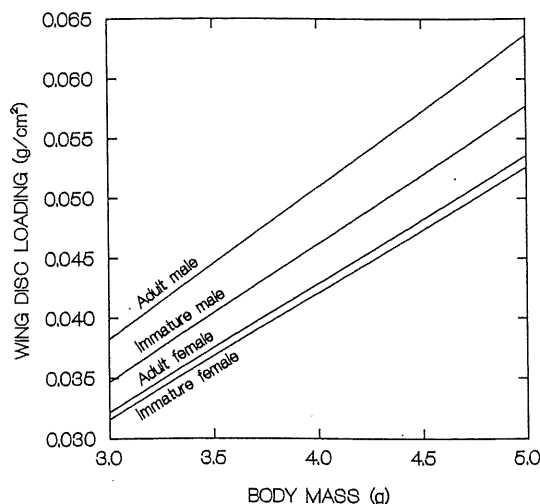


Fig. 1. Differences in wing disc loading (WDL) among the age-sex classes in relation to variation in body mass (BM). WDL is calculated as $WDL = BM / [\pi(b/2)^2]$, where b , the wing span (cm), is calculated from the regression $b = 2L + 0.809(L^{0.6})$, and L is the wing length (cm) (Greenewalt 1975). The wing length data on which the figure is based are from Table 1 in Carpenter et al. (1993b)

age-sex classes differ in coloration: adult males are the most brightly colored with a brilliant red gorget and extensive rufous coloration on the body, especially the dorsal surface. Immature females are the duller, with immaculate white throats and little rufous coloration on the body. Immature males and adult females are intermediate in brightness and similar in appearance: both have some iridescent red feathers on the throat and considerable rufous coloration at the base of the tail (Stiles 1972; personal observations).

In all cases, adult males should be dominant and immature females subordinate, so we can predict the following dominance order: adult males > immature males ≥ adult females > immature females. The position of adult females relative to immature males is potentially diagnostic for separating the effects of color from effects of WDL. If color is more important than WDL, immature males and adult females should be about equal in territorial ability. In contrast, if WDL is more important than color, immature males should dominate adult females.

Effect of color-marking. As noted above, we color-marked birds to facilitate individual identification. Color marks may influence the social behavior of birds both in captivity and in the wild (reviewed by Calvo and Furness 1992). We used our color-marking scheme for an additional analysis of the possible influence of coloration on territory acquisition. The colors we used fell into "hot" (red, orange, and pink) and "cool" (green, yellow, white, and blue) categories. The tags lie flat along the back of a bird, and the hot colors resemble the bright rufous coloration of the back of adult males. If back coloration is important in mediating interference interactions, we would expect color marks to influence the perceived dominance of their bearers (Brodsky 1988), and consequently influence the outcome of territorial disputes.

Statistical analyses. In order to test for associations between age-sex class, year, color mark ("hot" tag versus "cool" tag), and territory acquisition, we used a four-way log-linear model of the form

$$\ln f_{ijklm} = u + a_i + b_j + c_k + d_m + ab_{ij} + ac_{ik} + ad_{im} + bc_{jk} + bd_{jm} + cd_{km} + abc_{ijk} + abd_{ijm} + acd_{ikm} + bcd_{jkm} + abcd_{ijklm}$$

where f_{ijklm} is the expected frequency in cell $ijklm$ of the associated four-way contingency table, u is the mean of the logarithms of the expected frequencies, a_i , b_j , c_k , and d_m are the effects of categories i , j , k , and m of the four respective factors, and the other terms express interactions between the factors (Sokal and Rohlf 1981). We also applied three-way log-linear analysis to several other sets of data on age-sex class and other qualitative variables of interest.

Because of the large numbers of factors and categories in our log-linear analyses, some of the cells in our contingency tables have relatively low expected frequencies. However, Haberman (1977) showed that asymptotic properties of χ^2 statistics are still applicable when individual expected cell frequencies are small, providing that the overall sample size and the number of cells in the table are both large.

In these analyses, a significant three-factor interaction between year, age-sex class, and another variable of interest indicates that the degree of association between age-sex class and the variable of interest varied among years. Consequently, when this occurred we did not attempt to fit simpler models, and instead used separate two-way tests for independence between age-sex class and the variable of interest within years (Sokal and Rohlf 1981).

For quantitative data we used parametric analyses of variance (ANOVAs). Because both year and age-sex class were potentially important effects, analysis of the two-way classification would be most appropriate. However, sample sizes for quantitative data were small in most years and we had no data for some year/age-sex class combinations, precluding the use of full two-way ANOVAs. To circumvent this problem, we used the means model ANOVA (Milliken and Johnson 1984). The null hypothesis for this test is that the means of non-empty cells are equal. If a means model ANOVA did not detect significant differences among cell means, we then lumped

years to improve sample sizes and used a one-way ANOVA to look for differences among the age-sex classes. On the other hand, if a means model ANOVA did indicate significant differences among means of non-empty cells in the two-way classification, we then conducted separate one-way ANOVAs for the three years in which we had data on all three age-sex classes (1980, 1981, 1985).

If variances were heterogeneous or normality did not hold approximately, quantitative data were transformed prior to analysis. Significant F -tests in ANOVAs were followed by multiple comparisons using Fisher's least significant difference (LSD) procedure (Milliken and Johnson 1984). Unless stated otherwise, all sample sizes reported refer to numbers of different individuals. When multiple measurements were made on the same individual, the mean of these measurements was used as one replicate in statistical analyses.

Results

The proportions of birds in each age-sex class that successfully established territories in each year are shown in Table 1. Log-linear analysis indicated that color-marking had no effect on the tendency for a bird to acquire a territory (Table 2). The significant three-factor interac-

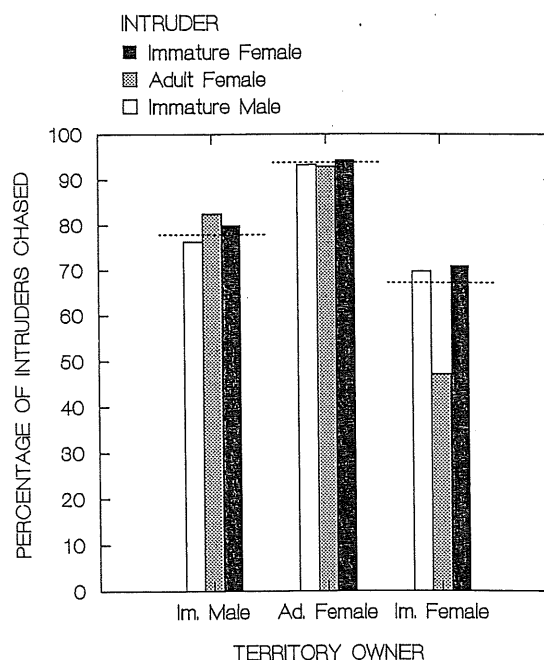


Fig. 2. Percentages of intruders that were chased by territory owners, in relation to age-sex class of both owner and intruder. Dotted lines indicate the overall percentages of intruders chased by territory owners of each age-sex class (likelihood of chase did not depend on the age-sex class of the intruder; Table 3). Sample sizes (numbers of intrusions onto territories held by immature males, adult females, and immature females, respectively) are as follows: intruder = immature male (152,30,33); intruder = adult female (40,14,17); intruder = immature female (30,36,69). Intrusions that occurred while a territory owner was temporarily absent are not included. Intrusion data from 1980 and 1982 are also excluded: data from 1980 were not taken in the same manner as the other years, and 1982 was a territorially anomalous year in which intrusions were difficult to score because territory boundaries were difficult to determine (Carpenter 1987). Data from all other years are pooled for analysis. These data include both marked and unmarked individuals, so the total number of individuals involved is not known. Also observed but not shown in the figure were six intrusions by adult males onto territories of immature males; all six adult males were chased

Table 1. Numbers of marked birds that eventually established territories and those that did not, in 7 years of study

Year	Number (%) of marked individuals		
	Territorial	Nonterritorial	
1980			
Immature male	33 (26)	94	$\chi^2 = 19.16$ $df = 2$ $P < 0.0001$
Adult female	9 (64)	5	
Immature female	17 (14)	101	
TOTALS	59	200	
1981			
Adult male	11 (79)	3	$\chi^2 = 11.23$ $df = 2^a$ $P = 0.004$
Immature male	41 (42)	56	
Adult female	27 (36)	49	
Immature female	18 (20)	73	
TOTALS	97	181	
1982			
Immature male	10 (4)	228	$\chi^2 = 3.67$ $df = 2$ $P = 0.16$
Adult female	0 (0)	18	
Immature female	3 (1)	206	
TOTALS	13	452	
1983			
Immature male	8 (5)	155	$\chi^2 = 1.76$ $df = 2$ $P = 0.41$
Adult female	5 (8)	54	
Immature female	5 (4)	123	
TOTALS	18 ^b	332	
1984			
Immature male	12 (19)	51	$\chi^2 = 0.77$ $df = 2$ $P = 0.68$
Adult female	4 (24)	13	
Immature female	9 (15)	51	
TOTALS	25	115	
1985			
Immature male	11 (20)	44	$\chi^2 = 1.78$ $df = 2$ $P = 0.41$
Adult female	9 (32)	19	
Immature female	13 (29)	32	
TOTALS	33 ^c	95 ^d	
1986			
Immature male	9 (13)	58	$\chi^2 = 1.01$ $df = 2$ $P = 0.60$
Adult female	4 (11)	33	
Immature female	17 (17)	82	
TOTALS	30	173 ^e	

The percentages of marked birds establishing territories are indicated in parentheses. Several hummingbirds that were injured during capture or that looked unhealthy upon release are not included in totals or analyses

^a The adult males are excluded from the analysis to ensure comparability among years. Statistics when the adult males are included: $\chi^2 = 23.24$, $df = 3$, $P < 0.0001$

^b One marked adult male that established a territory is not included in totals or analyses

^c Three marked birds of unknown age-sex class that established territories are not included in totals or analyses

^d Two marked birds of unknown age-sex class that did not establish territories are not included in totals or analyses

^e Two marked adult males that did not establish territories are not included in totals or analyses

Table 2. Summary of the log-linear analysis of the data in Table 1

Model	df	χ^2	P^a
YAT, YAC, YTC, ATC	10	10.16	ns
difference due to deleting ATC	2	1.20	ns
YAT, YAC, YTC	12	11.36	ns
difference due to deleting YAC	14	16.30	ns
YAT, YTC	26	27.66	ns
difference due to deleting YAT	28	157.75	<0.0001
YTC, A	54	185.41	<0.0001
difference due to deleting YTC	13	21.38	ns
YAT, C ^b	39	49.04	ns

Adult males are not included in the analysis. Effects are symbolized as follows: Y = year; A = age-sex class; T = territorial status; C = color mark. Interacting effects are listed together, not separated by commas; noninteractive model components are separated by commas. For example, YAT,C represents a model with a three-way interaction between year, age-sex class, and territory acquisition, and with a nonuniform distribution of color marks (e.g., more individuals marked with "hot" colors than with "cool" colors), but with no interaction between color mark and the other effects

^a "ns" = data do not differ significantly from model predictions ($P > 0.05$)

^b All lower-order models were rejected ($P < 0.05$)

Table 3. Summary of the log-linear analysis of the data shown in Fig. 2.

Model	df	χ^2	P
IO, IM, OM	4	3.25	ns
difference due to deleting IM	2	1.28	ns
IO, OM	6	4.53	ns
difference due to deleting IO	4	82.25	<0.0001
OM, I	10	86.78	<0.0001
difference due to deleting OM	2	20.54	<0.0001
IO, M	8	25.07	<0.01

Effects are symbolized as follows: I = age-sex class of intruder; O = age-sex class of owner; M = outcome of intrusion (i.e., whether or not the intruder was chased). See Table 2 for more details on interpretation

tion between year, age-sex class, and territorial status indicates that the relative proportions of birds in different age-sex classes that eventually established territories differed among years. Separate χ^2 tests showed highly significant differences in two years, 1980 and 1981 (Table 1). These were two of the most nectar-limited years during the study (Carpenter et al. unpublished data).

We observed 12 naturally occurring displacements of one bird by another from territories. Six immature males were displaced, three by adult males and three by other immature males. Six immature females were displaced, four by immature males, one by an adult female, and one by another immature female. All displacements were consistent with the order of dominance predicted by WDL and color hypotheses.

Figure 2 shows the frequency with which different age-sex classes chased intruders, and the frequency with which they were chased when they intruded onto others' territories. Log-linear analysis indicated associations between the age-sex classes of owners and intruders, and

Table 4. Numbers of birds that established territories in an area of low flower density and an area of high flower density during 7 years

Year	Flower density	(flrs/m ²)	Age-sex class			
			Adult male	Immature male	Adult female	Immature female
1980	low	(5.2)	0	12	4	13
	high	(20.8)	0	13	1	8
1981	low	(3.2)	1	8	11	11
	high	(13.3)	6	16	3	5
1982	low	(7.8)	0	6	0	6
	high	(31.0)	0	8	0	8
1983	low	(8.0)	1	6	2	7
	high	(30.6)	0	7	1	5
1984	low	(9.8)	0	9	2	5
	high	(14.6)	0	12	0	13
1985	low	(7.2)	0	3	7	12
	high	(11.4)	0	14	6	9
1986	low	(6.9)	0	7	3	16
	high	(18.2)	0	13	5	17

These data include unmarked as well as marked birds, so sample sizes exceed those reported in a preliminary analysis (Carpenter et al. 1991). Also shown for each year are mean flower densities, which were measured at the time of peak flowering along two transects (one in the area of low and one in the area of high flower abundance). χ^2 goodness-of-fit tests indicated that the densities of flowers in the two areas differed significantly from expectations under an assumption of uniformity ($P < 0.001$ in all years)

between the owner's age-sex class and the outcome of the intrusion (Table 3). The first interaction reflects the fact that the majority of observed intrusions by immature males and adult females were onto territories held by immature males, whereas the majority of intrusions by immature females were onto other immature females' territories (see sample sizes in legend of Fig. 2). The second interaction indicates that the likelihood of an intruder being chased depended on the age-sex class of the territory owner, with adult females most likely to chase, immature females least likely to chase, and immature males intermediate in position (Fig. 2). However, intruders of all age-sex classes were equally chased (Fig. 2, Table 3).

The different age-sex classes tended to establish territories in different parts of the meadow (Table 4). Log-linear analysis indicated significant associations between year and age-sex class, and between age-sex class and location of territories in the meadow (Table 5). The

former interaction reflects the fact that relative numbers of the different age-sex classes establishing territories varied among years (Table 1). The latter interaction indicates that immature males tended to hold territories in the more densely flowering part of the meadow, whereas females tended to hold theirs in the more sparsely flowering area (Table 4). Although the log-linear analysis did not detect a significant influence of year on the distribution of the age-sex classes in the meadow, some trends are suggested in Table 4. The most striking differences were evident in 1981 and 1985, the two years when peak flower density in the meadow was lowest (Carpenter et al. unpublished data). In contrast, differences between the age-sex classes were less obvious in the other years when resource availability was comparatively higher.

Differences among the age-sex classes were also apparent from direct measurements of flower density on territories, although sample sizes were small in most years and we had no data for some combinations of year and age-sex class. A means model ANOVA on log-transformed data did not detect significant differences among means of cells for which we had data ($F_{13,43} = 1.61$, $P = 0.12$). However, when we lumped years, improving sample sizes, a highly significant difference emerged among the classes (one-way ANOVA: $F_{2,54} = 5.89$, $P = 0.005$). On average, territories of immature males were the most densely flowered, those of immature females were the least densely flowered, and those of adult females were intermediate (Fig. 3A). Multiple comparisons indicated a significant difference between immature males and immature females ($P = 0.001$), but not between immature males and adult females ($P = 0.29$) or between adult and immature females ($P = 0.38$).

Immature females tended to defend fewer flowers than immature males or adult females, but again, some of the

Table 5. Summary of the log-linear analysis of the data in Table 4

Model	df	χ^2	P
YA, YD, AD	10	12.36	ns
difference due to deleting YD	6	6.63	ns
YA, AD	16	18.99	ns
difference due to deleting YA	14	25.16	<0.05
AD, Y	30	44.15	<0.05
difference due to deleting AD	2	10.22	<0.01
YA, D	18	29.21	<0.05

Adult males are not included in the analysis. Effects are symbolized as follows: Y = year; A = age-sex class; D = territory site (section of the meadow with high or low flower density). See Table 2 for more details on interpretation

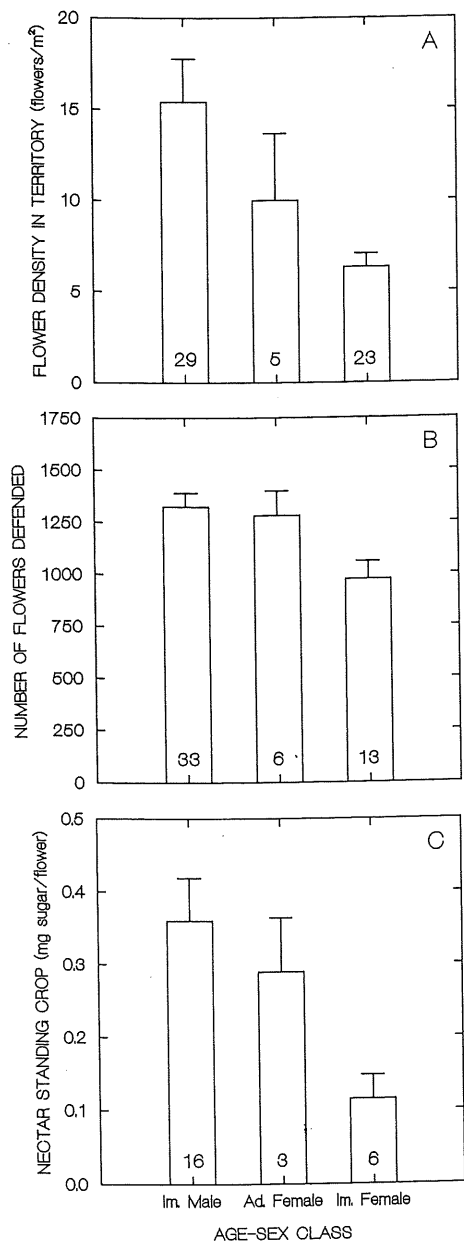


Fig. 3A-C. Variation in measures of territory quality among the age-sex classes. Means and SEs of untransformed data are shown, with sample sizes inside the bars. **A** Average flower densities in territories pooled across all years. **B** Numbers of flowers defended on territories in 1980, the year with the largest samples. **C** Nectar standing crops measured on territories in the evening (1930–2030 hours Pacific Daylight Time) in 1980

cells in our year \times age-sex classification were empty. A means model ANOVA on log-transformed data indicated significant differences among means of cells for which we had data ($F_{14,75} = 9.26$, $P < 0.0001$). Separate one-way ANOVAs for the years in which we had data on all three age-sex classes showed significant differences among the age-sex classes in 1980, the year with our only large sample ($F_{2,49} = 7.00$, $P = 0.002$; Fig. 3B). Multiple comparisons indicated significant differences between immature males and immature females ($P < 0.001$) and between adult and immature females ($P = 0.028$), but not

between immature males and adult females ($P = 0.83$). Differences were not detected in 1981 or 1985, but sample sizes were very small in those years (1981: $F_{2,6} = 0.21$, $P = 0.82$; 1985: $F_{2,4} = 0.66$, $P = 0.57$).

Standing crops of nectar remaining in flowers by the end of the foraging day were highly variable but reflected the trends in number of flowers defended. A means model ANOVA on log-transformed data showed significant differences among means of cells for which we had data ($F_{14,48} = 4.19$, $P < 0.0001$). Separate one-way ANOVAs for the years in which we had data on all three age-sex classes showed significant differences in 1980 ($F_{2,22} = 6.17$, $P = 0.008$; Fig. 3C). Multiple comparisons indicated significant differences in nectar standing crops between immature males and immature females ($P = 0.002$) and between adult and immature females ($P = 0.037$), but not between immature males and adult females ($P = 0.89$). Differences were not detected in 1981 or 1985, but again, sample sizes were small in those years (1981: $F_{2,6} = 0.70$, $P = 0.53$; 1985: $F_{2,6} = 0.18$, $P = 0.84$).

Discussion

Our results are consistent with reports of male dominance in hummingbird species (e.g., Feinsinger and Colwell 1978; Kodric-Brown and Brown 1978; Kuban et al. 1983) and the predicted order of dominance based upon considerations of WDL and coloration. At our study site, immature males acquired territories in less time than females (Carpenter et al. 1991), and these territories had higher resource densities than those of females, particularly immatures (Fig. 3). Moreover, immature males were more successful at expanding their territory boundaries following flower reductions (Carpenter et al. 1991); and they occasionally displaced females from their territories. Immature females defended territories having the lowest resource densities (Fig. 3), never displaced territorial males or adult females, and seemed reluctant even to attempt to chase intruders from their territories (Fig. 2). The position of adult females was variable, but in general seemed intermediate between immature males and immature females. This intermediate position, together with the absence of a detectable effect of color-marking on territory acquisition (Table 2), may indicate that WDL is more important than coloration in determining dominance. However, because we did not analyze WDL and coloration for specific individuals, we are unable to draw definitive conclusions concerning the relative contributions of WDL and coloration to interference abilities of the age-sex classes. Experiments comparing individuals of known WDL and coloration and defending territories identical in both resource and intrusion levels will be necessary to dissect this problem.

Two results from our study, however, are not consistent with predictions of dominance based on either WDL or coloration. First, adult females outperformed immature males by several measures of territorial ability. In at least one resource-limited year (1980), adult females held a disproportionate number of territories in comparison to both immature males and immature females (Table 1).

Moreover, adult females seemed to be superior in ability to detect and chase intruders (Fig. 2; see also Fig. 4 in Carpenter et al. 1993b). Possibly, territorial and detection abilities might improve with experience. Therefore, a third factor – the experience that comes with age – may be influential in territory dynamics, in addition to WDL and coloration.

Second, females acquired and maintained territories in the meadow in all years, despite annual surpluses of nonterritorial males (Table 1). State-dependency is one possible explanation for this observation. These hummingbirds can nearly double their body mass during migratory stopovers (Carpenter et al. 1993a), and consequently undergo tremendous individual changes in WDL. Fat immature females surpass lean immature males in WDL (Fig. 1), and might be able to defeat them in territory contests if WDL figures prominently in interference abilities. Prior residency (*sensu* Davies 1978; Krebs 1982) might then enable these territorial females to withstand later challenges by males (e.g., Cristol et al. 1990; Holberton et al. 1990). However, the fact that males occasionally were observed to displace females from their territories argues against this explanation.

On the other hand, territories defended by females had lower flower densities than territories defended by males, and may have lacked sufficient resources to permit economical defense by males. Such a tradeoff between the sexes in territory quality and interference versus exploitative abilities has been suggested as an explanation for sexual differences in resource use (e.g., Gauthreaux 1978; Kodric-Brown and Brown 1978; Morse 1980; Temeles 1986). We present data supporting this explanation in the accompanying paper (Carpenter et al. 1993b).

Implications for understanding migration strategies

Many species of migratory birds have sex- or age-specific migration routes or time schedules and/or spend the winter in largely different areas (reviewed by Gauthreaux 1982). Similarly, the age-sex classes of some species select different habitats during migratory stopovers (Hunt et al. 1975) or on the wintering grounds (e.g., Weeden 1964; Koplín 1973; Opat and Greenberg 1990).

Many of these patterns of sex- and age-related differences in migration and habitat use result in spatiotemporal resource partitioning, and may therefore represent the evolutionary consequences of intraspecific competition. However, in many species, including the rufous hummingbird, there is a relatively broad degree of overlap in the routes, time schedules, habitats, and behaviors used by different sectors of the population during migration and winter. In cases such as these, intense intraspecific competition is likely to occur during periods of high energy demand or low resource availability.

Although our results clearly show that females, especially immatures, are territorially disadvantaged in most respects relative to males, we show elsewhere (Carpenter et al. 1993b) that females are able to compensate energetically for their disadvantages. Although the exact mechanisms permitting compensation remain unresolved,

females defending their relatively poor territories gain mass at the same rate and in the same pattern as males, leave at the same body mass, and spend the same amount of time on stopovers. Furthermore, females can maintain or gain body mass even without a territory, whereas nonterritorial males lose body mass (Carpenter et al. 1993b).

Adult males do not make a direct contribution to feeding the young, and as soon as they finish mating they begin accumulating fat stores for the southward migration. In contrast, females must recover losses of internal reserves incurred during breeding and fledge their young before being able to depart. Thus, adult females and immatures are expected to leave later than adult males. This is the pattern that we have observed, as have workers in other parts of the western United States (e.g., Calder 1976, 1987; Kodric-Brown and Brown 1978). In most years, adult male rufous hummingbirds were temporally separated from the other age-sex classes at our study site; 1981 was the only year in which we captured behaviorally dominant adult males to any extent. Since this was a highly nectar-limited year (Carpenter et al. unpublished data), it seems probable that stopover durations might have been extended if sufficient resources were difficult to acquire. In fact, stopover durations were longer in 1981 than in any other year during our study (Russell et al. unpublished data). Thus, adult males, which normally would have already passed through our site, were apparently slowed enough by low availability of resources to force more overlap than usual with the other age-sex classes. Under such circumstances, interference can have important consequences for the ability of subordinate age-sex classes to secure and maintain high-quality territories for refueling. We suggest that the dual asymmetry between interference abilities (this study) and exploitation abilities (Carpenter et al. 1993b) in rufous hummingbirds, which might have originated in the context of reproductive role division (Kodric-Brown and Brown 1978), could be enforced and augmented through natural selection during migration, in response to unpredictable periods of severe competition that force more overlap than usual between the age-sex classes.

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References

- Brodsky LM (1988) Ornament size influences mating success in male rock ptarmigan. *Anim Behav* 36:662-667
- Calder WA III (1976) Energetics of small body size and high latitude: the rufous hummingbird in coastal Alaska. *Int J Biometeorol* 20:23-35

- Calder WA III (1987) Southbound through Colorado: migration of rufous hummingbirds. *Natl Geogr Res* 3:40-51
- Calvo B, Furness RW (1992) A review of the use and the effects of marks and devices on birds. *Ring Migr* 13:129-151
- Carpenter FL (1976) Plant-pollinator interactions in Hawaii: pollination energetics of *Metrosideros collina* (Myrtaceae). *Ecology* 57:1125-1144
- Carpenter FL (1983) Pollination energetics in avian communities: simple concepts and complex realities. In: Jones CE, Little RJ (eds) *Handbook of experimental pollination biology*. Van Nostrand Reinhold, New York, pp 215-234
- Carpenter FL (1987) Food abundance and territoriality: to defend or not to defend? *Am Zool* 27:387-399
- Carpenter FL, Paton DC, Hixon MA (1983) Weight gain and adjustment of feeding territory size in migrant hummingbirds. *Proc Natl Acad Sci USA* 80:7259-7263
- Carpenter FL, Hixon MA, Paton DC, Temeles EJ, Russell RW (1991) Sexual differences in resource acquisition by migrant hummingbirds. *Acta Congr Int Ornithol XX*:1156-1165
- Carpenter FL, Hixon MA, Beuchat CA, Russell RW, Paton DC (1993a) Biphase mass gain in migrant hummingbirds: body composition changes, torpor, and ecological significance. *Ecology* 74:1173-1182
- Carpenter FL, Hixon MA, Temeles EJ, Russell RW, Paton DC (1993b) Exploitative compensation by subordinate age-sex classes of migrant rufous hummingbirds. *Behav Ecol Sociobiol* 33:305-312
- Cristol DA, Nolan V, Ketterson ED (1990) Effect of prior residence on dominance status of dark-eyed juncos, *Junco hyemalis*. *Anim Behav* 40:580-586
- Davies NB (1978) Territorial defence in the speckled wood butterfly (*Pararge aegeria*), the resident always wins. *Anim Behav* 26:138-147
- Ewald PW, Rohwer S (1980) Age, coloration and dominance in nonbreeding hummingbirds: a test of the asymmetry hypothesis. *Behav Ecol Sociobiol* 7:273-279
- Feinsinger P, Chaplin SB (1975) On the relationship between wing disc loading and foraging strategy in hummingbirds. *Am Nat* 109:217-224
- Feinsinger P, Colwell RK (1978) Community organization among neotropical nectar-feeding birds. *Am Zool* 18:779-795
- Feinsinger P, Colwell RK, Terborgh J, Chaplin SB (1979) Elevation and the morphology, flight energetics, and foraging ecology of tropical hummingbirds. *Am Nat* 113:481-497
- Fleischer RC, Johnston RF (1984) The relationships between winter climate and selection on body size of house sparrows. *Can J Zool* 62:405-410
- Gass CL (1979) Territory regulation, tenure, and migration in rufous hummingbirds. *Can J Zool* 57:914-923
- Gauthreaux SA Jr (1978) The ecological significance of behavioral dominance. In: Bateson PPG, Klopfer PH (eds) *Perspectives in ethology*, vol 3. Plenum Press, New York, pp 17-54
- Gauthreaux SA Jr (1982) The ecology and evolution of avian migration systems. In: Farner DS, King JR, Parkes KC (eds) *Avian biology*, vol 6. Academic Press, New York, pp 93-168
- Glase JC (1973) Ecology of social organization in the black-capped chickadee. *Living Bird* 12:235-267
- Grant KA, Grant V (1967) Effects of hummingbird migration on plant speciation in the California flora. *Evolution* 21:457-465
- Greenewalt CH (1975) The flight of birds. *Trans Am Philos Soc* 65:1-67
- Grubb TC Jr, Woodrey MS (1990) Sex, age, intraspecific dominance status, and the use of food by birds wintering in temperate-deciduous and cold-coniferous woodlands: a review. *Stud Avian Biol* 13:270-279
- Haberman SJ (1977) Log-linear models and frequency tables with small expected cell counts. *Ann Statist* 5:1148-1169
- Hepp GR, Hair JD (1984) Dominance in wintering waterfowl (Anatini): effects on distribution of sexes. *Condor* 86:251-257
- Hixon MA, Carpenter FL (1988) Distinguishing energy maximizers from time minimizers: a comparative study of two hummingbird species. *Am Zool* 28:913-925
- Hixon MA, Carpenter FL, Paton DC (1983) Territory area, flower density, and time budgeting in hummingbirds: an experimental and theoretical analysis. *Am Nat* 122:366-391
- Hogstad O (1988) Rank-related resource access in winter flocks of willow tit *Parus montanus*. *Ornis Scand* 19:169-174
- Holberton RL, Hanano R, Able KP (1990) Age-related dominance in male dark-eyed juncos: effects of plumage and prior residence. *Anim Behav* 40:573-579
- Hunt WG, Rogers RR, Stowe DJ (1975) Migratory and foraging behavior of peregrine falcons on the Texas coast. *Can Field-Nat* 89:111-123
- Johnsgard PA (1983) *The hummingbirds of North America*. Smithsonian Institution Press, Washington, DC
- Kodric-Brown A, Brown JH (1978) Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant rufous hummingbirds. *Ecology* 59:285-296
- Koplin JR (1973) Differential habitat use by sexes of American kestrels wintering in northern California. *Raptor Res* 7:39-42
- Krebs JR (1982) Territorial defense in the great tit (*Parus major*): do residents always win? *Behav Ecol Sociobiol* 11:185-194
- Kuban JF, Lawley J, Neill RL (1983) The partitioning of flowering century plants by black-chinned and Lucifer hummingbirds. *Southwest Nat* 28:143-148
- Miller RS (1967) Pattern and process in competition. *Adv Ecol Res* 4:1-74
- Milliken GA, Johnson DE (1984) *Analysis of messy data. Vol 1: Designed experiments*. Lifetime Learning Publications, Belmont
- Morse DH (1980) *Behavioral mechanisms in ecology*. Harvard University Press, Cambridge
- Murton RK, Isaacson AJ, Westwood NJ (1971) The significance of gregarious feeding behaviour and adrenal stress in a population of wood-pigeons *Columba palumbus*. *J Zool* 165:53-84
- Ornat AL, Greenberg R (1990) Sexual segregation by habitat in migratory warblers in Quintana Roo, Mexico. *Auk* 107:539-543
- Paton DC, Carpenter FL (1984) Peripheral foraging by territorial rufous hummingbirds: defense by exploitation. *Ecology* 65:1808-1819
- Peters WD, Grubb TC Jr (1983) An experimental analysis of sex-specific foraging in the downy woodpecker, *Picoides pubescens*. *Ecology* 64:1437-1443
- Phillips AR (1975) The migrations of Allen's and other hummingbirds. *Condor* 77:196-205
- Selander RK (1966) Sexual dimorphism and differential niche utilization in birds. *Condor* 68:113-151
- Snow DW, Snow BK (1980) Relationships between hummingbirds and flowers in the Andes of Colombia. *Bull Br Mus Nat Hist (Zool)* 38:105-139
- Sokal RR, Rohlf FJ (1981) *Biometry*, 2nd edn. Freeman, New York
- Stiles FG (1972) Age and sex determination in rufous and Allen hummingbirds. *Condor* 74:25-32
- Temeles EJ (1986) Reversed sexual size dimorphism: effect on resource defense and foraging behaviors of nonbreeding northern harriers. *Auk* 103:70-78
- Weeden RB (1964) Spatial separation of sexes in rock and willow ptarmigan in winter. *Auk* 81:534-541
- Wunderle JM Jr (1991) Age-specific foraging proficiency in birds. In: Power DM (ed) *Current ornithology*, vol 8. Plenum Press, New York, pp 273-324