

1991. Proceedings of the 20th International Ornithological Congress 2:1156-1165. New Zealand Ornithological Congress Trust Board; Wellington, New Zealand.

SEXUAL DIFFERENCES IN RESOURCE ACQUISITION BY MIGRANT HUMMINGBIRDS

F. LYNN CARPENTER¹, MARK A. HIXON², DAVID C. PATON³, ETHAN J. TEMELES⁴
and ROBERT W. RUSSELL¹

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

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

³ Department of Zoology, University of Adelaide, G.P.O. Box 498, Adelaide, SA 5001, Australia

⁴ Department of Zoology, University of British Columbia, Vancouver, BC V6T 2A9, Canada

ABSTRACT. Data on migrant Rufous Hummingbirds *Selasphorus rufus* suggest that females, especially immatures, may be disadvantaged in obtaining and maintaining feeding territories in the presence of their immature male rivals. Males tended to secure a disproportionate number of territories more quickly and occupied areas of higher flower density. They also were more successful at expanding their territories aggressively upon flower reduction, and were displaced less often than females. Perhaps, in consequence, immature females lagged behind males and migrated through our study site toward the end of the flowering season. However, our data on whether females spent more time on refuelling stopovers or resumed migration later or at lower weight than males were inconsistent. The possibility that immature females compensate for their territorial disadvantage by greater foraging efficiency remains open.

Keywords: Hummingbirds, territoriality, feeding territories, sexual differences, female disadvantage, male advantage, resource acquisition, migratory stopover, flower reduction.

INTRODUCTION

Sexual differences in resource use have been reported for a variety of animal species (Selander 1966, Temeles 1986), yet the reasons for these differences remain poorly understood and controversial (Lewin 1985). Two hypotheses attempt to explain sexual differences in resource use during the non-breeding season. The "Exploitation Hypothesis" states that sexes use different resources because they differ in body size and/or morphology; each sex prefers resources most suited to it (Selander 1966, Peters & Grubb 1983, Temeles 1985). In contrast, the "Interference Hypothesis" maintains that sexes differ in resource use because of social dominance (sometimes conferred by differences in size or morphology). In this case, one sex aggressively displaces the other from mutually-preferred resources through interference competition (Gauthreaux 1978, Temeles 1986). As a result, the subordinate sex subsists on resources outside its preference.

To date, several studies provide indirect support for the Interference Hypothesis (Wolf 1975, Kodric-Brown & Brown 1978, Peters & Grubb 1983, Kuban et al. 1983, Hepp & Hair 1984, Temeles 1986). Two studies (Kodric-Brown & Brown 1978, Temeles 1986) suggest that the superior interference ability of the dominant sex in the acquisition of preferred resources may be offset by a superior exploitative ability of the subordinate sex in the utilization of less preferred resources. Thus, the Exploitation and Interference Hypotheses are not necessarily mutually exclusive.

Data are lacking on the relative abilities of males and females to acquire and exploit resources. Such data are necessary to test basic assumptions of the Exploitation and Interference Hypotheses, i.e. that sexes differ in foraging and/or territorial abilities. Here we offer some relevant data on migrant Rufous Hummingbirds *Selasphorus rufus*, which we studied in California for 11 summers (1976 - 1986).

Rufous Hummingbirds migrate during the summer from their breeding grounds in the Pacific Northwest to their wintering areas in Mexico (Phillips 1975). En route, both sexes stop periodically in mountain meadows, establish vigorously-defended territories around patches of flowers, and require one to two weeks to replenish their 1-2 gram migratory fat store from flower nectar before resuming their journey (Carpenter et al. 1983). Adult males migrate one to four weeks before females and immatures (Phillips 1975, Calder 1987), so females contend mainly with immature males during most of the summer migration. Because we captured significant numbers of adult males at our site in only one year, we are eliminating them from this analysis.

We have argued (Carpenter et al. 1983, Hixon et al. 1983, Paton & Carpenter 1984, Hixon & Carpenter 1988) that this species is selected to minimize the time spent on migratory stopovers, and thus to maximize the rate at which refattening occurs on feeding territories. Our birds act in ways consistent with energy maximization, in terms of territory size adjustments, time budgeting, foraging patterns, meal size, and mass gain (Carpenter et al. 1983, Hixon et al. 1983, Karasov et al. 1986, Hixon & Carpenter 1988, Carpenter & Hixon 1988). The selection pressures for maximization of daily net energy gain in Rufous Hummingbirds should operate equally on males and females, and consistent with this, both sexes defend feeding territories during migratory stopovers.

Body masses of the sexes are similar (male = 3.2 g, female = 3.4 g, Johnsgard 1983), but males have shorter wings and hence a 15% higher wing loading ($0.044 \text{ g}\cdot\text{mm}^{-2}$) than females ($0.038 \text{ g}\cdot\text{mm}^{-2}$). Wing lengths do not overlap (Johnsgard 1983, Temeles unpubl.). Feinsinger & Chaplin (1975) argued that higher wing loading increases the cost of flight but also improves agility and therefore enhances territorial ability, enabling monopolization of the densest flower patches. Dense flower patches should be preferred because travel costs among flowers would be reduced.

Indeed, Kodric-Brown & Brown (1978) noted that Rufous Hummingbird males defended territories of higher flower density than females. They suggested that the lower wing loading of females relegated them to sparser patches of flowers, but that their lower cost of flight compensated for the concomitantly longer foraging flight distances. If the Interference Hypothesis holds, males with their higher wing-loading should acquire territories more rapidly, occupy areas with the densest patches of flowers, acquire mass more rapidly and either depart sooner or leave fatter than females. Females, if given the opportunity, should also hold feeding territories in dense patches of flowers. Since our study site is midway along the migration route to Mexico, and most birds will have made at least one refattening stopover by the time they reach us, we would expect females to lag behind males if females refatten more slowly.

On the other hand, if the Exploitation Hypothesis holds, females, with their lower wing-loading, should gain mass at comparable rates to males, even when defending poorer territories. In this case, males and females should show little difference in rates and

amounts of mass gain and length of time required to fatten for the next migratory flight.

METHODS

Our study site was a 2 ha meadow at the base of the east slope of the Sierra Nevada, 27 km NW of Bishop, California. This meadow contains the hummingbird-visited Indian paintbrush, *Castilleja linariaefolia* (Scrophulariaceae), which flowers from mid-July to late August or early September.

In most years, Rufous Hummingbirds arrived between late July and early August. At any one time, up to 50 exclusive territories were established in the 2 ha of flowers. We mist-netted the birds, weighed them, identified their sex and age class (Stiles 1972, Johnsgard 1983), and colour-marked them with narrow strips of coloured surveyors' flagging tape glued to the skin of the back. These strips did not add detectably to their mass or bother them.

In 1979, 1985 and 1986, we halved the number of flowers experimentally on several territories and measured the response of the owners. Each manipulated bird was paired with a control bird. For one to two days before and after flower reduction, we collected data on territory area, number of included flowers, and body masses in some cases (methods in Hixon et al. 1983, Carpenter et al. 1983). These birds were then studied until they resumed migration, which was often behaviourally conspicuous. In addition to experimental flower reduction, unusually hot temperatures during 1980, 1985 and 1986 caused flowers to decline naturally, in some areas quite rapidly.

We counted flowers along two permanent 2-m wide transects (one 36 m long; one 50 m long), one to four times each summer. In seven years from 1980 to 1986, we mapped all territories in the meadow and identified the age and sex class of the owners.

RESULTS

We caught and tagged 200-400 individuals over each summer; 5-35% of these established territories, and up to 80% of the territory owners were marked at any one time. About 85% of our netted Rufous Hummingbirds were immatures and 15% adult females.

Under which resource conditions did different sex and age classes establish territories?

The El Niño years of 1982-1983 were anomalous in that this normally aggressive species defended few territories (Carpenter 1987, 1989). In all other years, most flowers were intensely defended (Carpenter 1978, 1987, Carpenter et al. 1983, Hixon & Carpenter 1983, 1988, Paton & Carpenter 1984). In these years, the numbers of non-territorial birds caught in the meadow always exceeded the numbers of territorial birds, suggesting that the numbers of flowers generally were limiting. Nonetheless, members of all sex and age classes held territories.

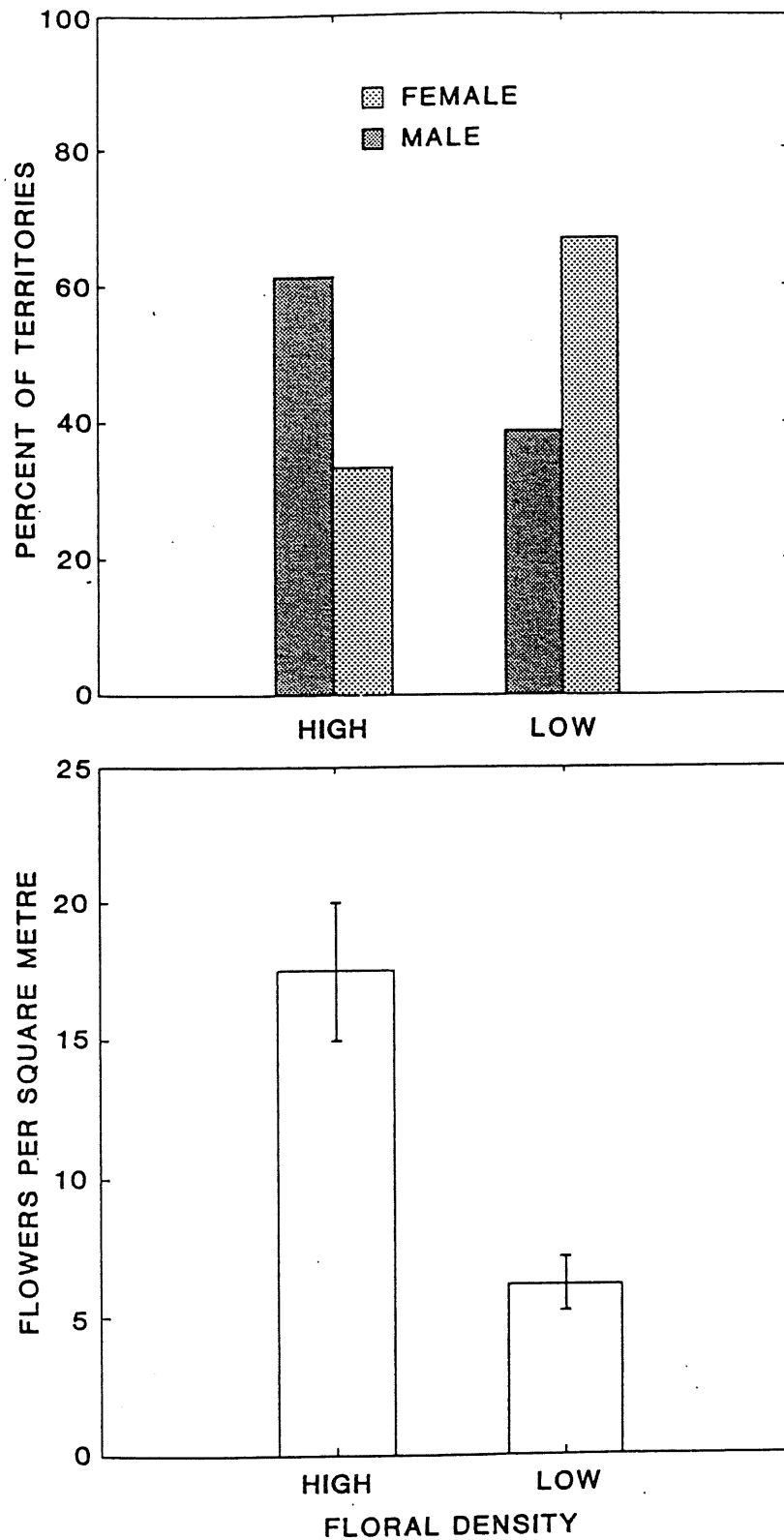


FIGURE 1 – Flower densities occupied by males and females 1980-1986. Top: percent of territories defended by males and females in the vicinity of the high and low flower-density transects; bottom: flower densities (mean flowers.m⁻² ± 1 S.E., data not transformed) were measured along permanent transects in two sites, one ("high") with higher flower density than the other ("low").

The probability of establishing a territory depended on age and sex class. Combined data from 1980-1986 indicated that 58 of 250 marked adult females (23%), 123 of 816 immature males (15%), and 82 of 751 immature females (11%) established territories ($G = 21.9$, $N = 1817$, $df = 2$, $P < 0.001$). Thus, relative to their proportions in the netted population, more males and adult females secured territories than immature females.

One measure of ability to obtain a territory is when one bird displaces another from its territory. Of seven takeovers observed involving birds of known age and sex, five displaced birds were immature females. Immature males were never displaced by females, and did five of the seven displacements. Hence, immature males may be better at obtaining territories than females.

We compared territory quality between sexes by assessing their distributions in two parts of the meadow that consistently differed in flower density in 1980-1986 (paired t-test on log-transformed data, $t = 7.06$, $df = 6$, $P < 0.001$; Figure 1, bottom). Combined data from all years indicated that immature males tended to defend territories in areas of higher rather than lower flower density, whereas the reverse was true for females (Figure 1, top; $G = 11.4$, $N = 146$, $df = 1$, $P = 0.001$).

What were the relative abilities of different sex and age classes in maintaining territories when flower density declined?

Following reductions in flowers, immature males often were capable of aggressively expanding their territories and females were not (Table 1). Whenever females did expand their territories, expansion was passive into undefended areas that had been abandoned recently.

Were there costs of lower territorial ability to females or did they compensate exploitatively?

Our netting data indicated that the relative proportions of sex and age classes changed over the summer in our area. In five of the six years for which we had adequate data, the proportion of netted immature males and adult females peaked early in the season and declined thereafter. In contrast, that of immature females increased, peaking late in the season (Figure 2). These observations suggest that immature females may have been delayed in migration, possibly due to subordinate status and inferior abilities in territory acquisition relative to other sex/age classes.

If immature females were delayed, we would expect them to require more time to secure territories and to gain body mass and/or to resume migration at lower body masses than immature males. We recorded the best, most continuous meadow maps in two years, 1980 and 1981. These two years combined showed that most males required one day or less to establish a territory, whereas significantly more females required two days or more ($G = 6.30$, $N = 73$, $df = 1$, $P = 0.01$). When we included the less accurate data from 1982-1986, which had time gaps in the records, the same trend occurred, but the difference was not significant ($G = 2.57$, $N = 155$, $df = 1$, $P = 0.11$).

Longer pre-territorial periods in females may have delayed gains in body mass. Once birds obtained territories, they gained about 0.2 g.day^{-1} (Carpenter et al. 1983), but birds without territories did not gain mass (mean = $0.0 \text{ g.day}^{-1} \pm 0.2 \text{ g.day}^{-1}$ SD, $N = 19$). These two factors alone could explain the migratory lag in immature females.

TABLE 1 – Responses of different sex/age classes to changes in flower abundance. "Aggressive" expansion involves expropriation of defended flowers; "passive" expansion involves annexation of undefended flowers. Data include experiments and natural flower declines in 1979, 1985, and 1986, and natural flower decline in 1980.

Treatment	Response of birds		
	Aggressively expanded territory boundaries	Passively expanded territory boundaries	Did not successfully expand boundaries
Flowers decreased experimentally	2 immature males	2 immature males	0
		1 adult female	
		3 immature females	
Flowers decreased naturally	3 immature males	10 immature males	2 immature males
		4 immature females	4 immature females
			2 adult females

We monitored the masses of all 1985 and 1986 experimental birds until they resumed migration. Among individuals whose flowers were experimentally halved, the one immature male continued to gain mass at high rates, whereas the one adult female and two of three immature females experienced severe reductions in mass gain or even mass loss.

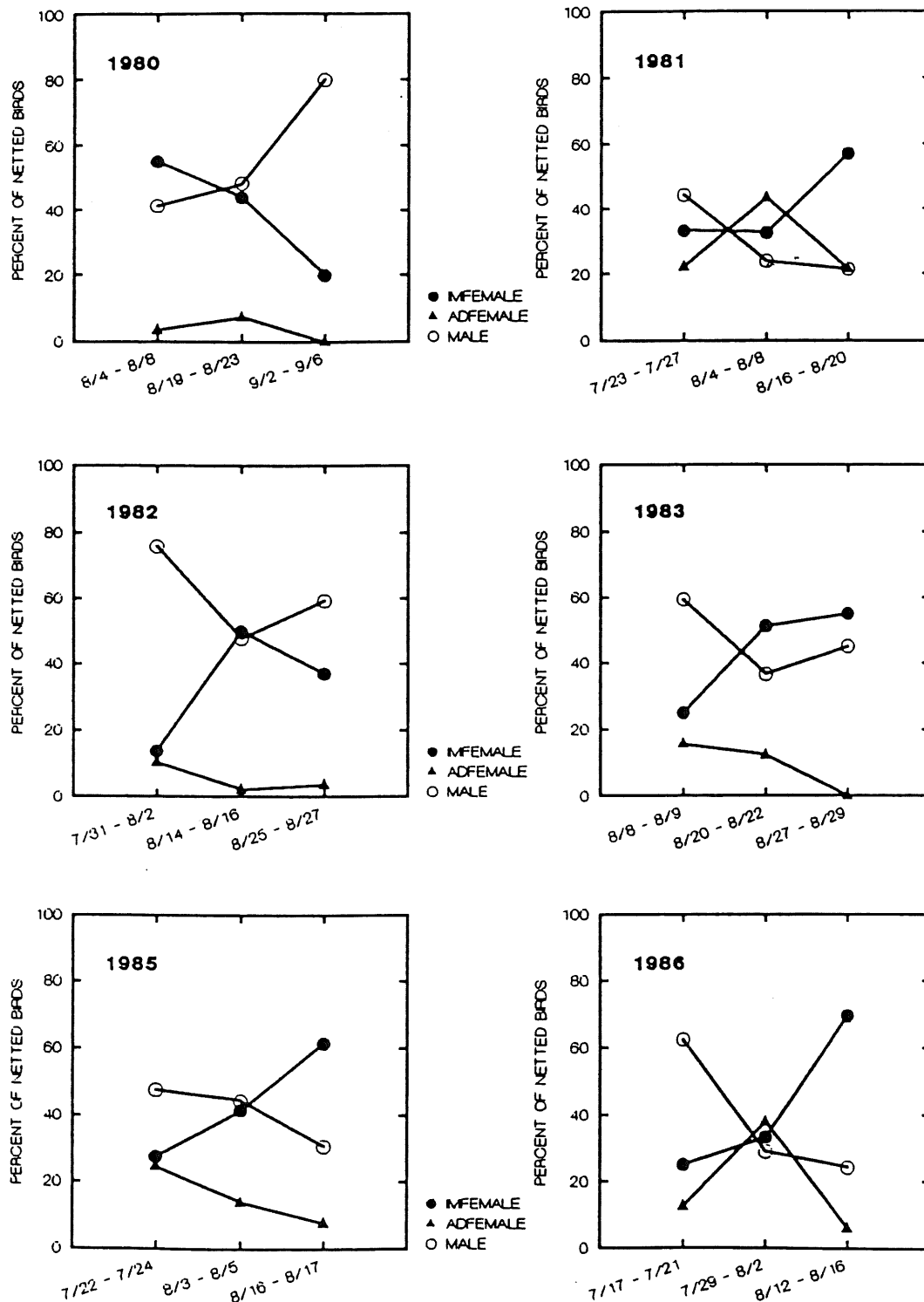


FIGURE 2 – Changes in the relative proportions of different sex-age classes over the season. Data from 1984 are not included because we missed both the beginning and end of the season that year.

However, when we combined all data, age/sex classes did not differ either in total stopover time (one-way ANOVA, $F_{2,223} = 1.25$, $P = 0.29$) or in final body mass the evening before migration (one-way ANOVA, $F_{2,53} = 1.13$, $P = 0.33$). Therefore, our data do not unequivocally show that females suffered a cost in terms of delayed refattening.

In 1980 and 1981, we recorded the identities of persistent intruders that robbed from other birds' territories. Of 19 such birds, 15 were female (10 immatures, 4 adults, 1 undetermined).

DISCUSSION

Our data suggest that Rufous Hummingbird females, primarily immatures, have lower territorial ability relative to immature males. Immature females obtain and defend territories, but relative to males they: 1) require longer to obtain a territory, 2) secure proportionately fewer territories, and 3) are displaced from their territories more often.

This lower territorial ability is associated with defence of territories with sparser flowers on average, and with lower ability to maintain territory size and mass gain in the face of declining flowers. These factors may cause immature females to lag behind immature males along the migratory route. However, our data on whether the territorial disadvantage of immature females translates into an overall migratory disadvantage were contradictory. We cannot discount the possibility that the energetic advantage of lower wing-loading could compensate them exploitatively on stopovers, for example, by permitting successful robbing, and that they merely leave the breeding grounds later than any other age/sex class. This alternative should be explored.

Our data suggest that adult females are intermediate in territorial ability between immature males and immature females. Relatively more adult females secure territories than the other two age/sex classes, yet our few experimental data suggested that they are less able than immature males to expand territories when necessary. Their low wing-loading should confer a disadvantage in "fighting" ability relative to immature males, but their greater experience and colouration could confer advantages over immature females. Immature male and adult female Rufous Hummingbirds both have a patch of iridescent red feathers on the throat and considerable rufous colouration at the base of the tail (Stiles 1972). In contrast, immature female birds are much less brightly coloured. Ewald & Rohwer (1980) demonstrated that drab individuals of another colour-polymorphic species have to chase intruders more frequently and longer to maintain their territories than do brightly-coloured individuals.

Thus, immature males may have a double advantage, bright colour and short wings, whereas immature females are doubly disadvantaged in territorial encounters. Adult females could help distinguish whether colour or wing-loading is more important in aggressive ability, since they are as brightly coloured as immature males, but have wing-loading as low as immature females. If colour is more important, their aggressive abilities should approach those of immature males. If wing-loading is more important, their abilities should approach those of immature females; and if both factors are important, their abilities should fall in between. This hypothesis awaits a rigorous test.

The patterns in our data are thus consistent with the hypothesis that interference is the primary factor causing differences between the sexes in resource use during southward migration. Whether females compensate by higher exploitative efficiency remains an open question.

ACKNOWLEDGMENTS

This work was supported by National Science Foundation grants DEB 77-25124 (FLC), DEB 80-22575 (FLC), and BSR 84-00669 (FLC & MAH), and by the University of California, Irvine Foundation (FLC). We thank B. Tissot, E. Smith, K. Uphoff, and our many other field assistants over the years. We also thank Ken and Marjorie Kaiser for their unfailing hospitality.

LITERATURE CITED

- CALDER, W.A. III. 1987. Southbound through Colorado: migration of Rufous Hummingbirds. National Geographic Society Research Reports 3: 40-51.
- CARPENTER, F.L. 1978. A spectrum of nectar-eater communities. *American Zoologist* 18: 809-818.
- CARPENTER, F.L. 1987. Food abundance and territoriality: to defend or not to defend? *American Zoologist* 27: 387-399.
- CARPENTER, F.L. 1989. Pollen transfer efficiency compensates for pollinator crashes in a specialized bird-pollinated plant. *Acta XIX Congressus Internationalis Ornithologici*: 536-548.
- CARPENTER, F.L., HIXON, M.A. 1988. A new function for torpor: fat conservation in a wild migrant hummingbird. *Condor* 90: 373-378.
- CARPENTER, F.L., PATON, D.C., HIXON, M.A. 1983. Weight gain and adjustment of feeding territory size in migrant hummingbirds. *Proceedings of National Academy of Science* 80: 7259-7263.
- EWALD, P.W., ROHWER, S. 1980. Age, coloration and dominance in non-breeding hummingbirds: a test of the asymmetry hypothesis. *Behavioural Ecology and Sociobiology* 7: 273-279.
- FEINSINGER, P., CHAPLIN, S.B. 1975. On the relationship between wing disc loading and foraging strategy in hummingbirds. *American Naturalist* 109: 217-224.
- GAUTHREAU, S. A., Jr. 1978. The ecological significance of behavioural dominance. Pp.17-54 in Bateson, P.P.G., Klopfer, P.H. (Eds). *Perspectives in ethology*, Volume 3. New York, Plenum Press.
- HEPP, G. R., HAIR, J.D. 1984. Dominance in wintering waterfowl (Anatini): effects on distribution of the sexes. *Condor* 86: 251-257.
- HIXON, M.A., CARPENTER, F.L. 1988. Distinguishing energy maximizers from time minimizers: a comparative study of two hummingbird species. *American Zoologist* 28: 913-925.
- HIXON, M.A., CARPENTER, F.L., PATON, D.C. 1983. Territory area, flower density, and time budgeting in hummingbirds: an experimental and theoretical analysis. *American Naturalist* 122: 366-391.
- JOHNSGARD, P.A. 1983. *The hummingbirds of North America*. Smithsonian Institution Press, Washington, D.C.
- KARASOV, W.H., DIAMOND, J.M., PHAN, D., CARPENTER, F.L. 1986. Food passage and intestinal nutrient absorption in hummingbirds. *Auk* 103: 453-464.
- KODRIC-BROWN, A., BROWN, J.H. 1978. Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant Rufous Hummingbirds. *Ecology* 59: 285-296.
- KUBAN, J.F., LAWLEY, J., NEILL, R.L. 1983. The partitioning of flowering century plants by Black-chinned and Lucifer Hummingbirds. *Southwestern Naturalist* 28: 143-148.
- LEWIN, R. 1985. Why are male hawks so small? *Science* 228: 1299-1300.
- PATON, D.C., CARPENTER, F.L. 1984. Peripheral foraging by territorial Rufous Hummingbirds: defense by exploitation. *Ecology* 65: 1808-1819.
- PETERS, W.D., GRUBB, T.C., JR. 1983. An experimental analysis of sex-specific foraging in the Downy Woodpecker, *Picoides pubescens*. *Ecology* 64: 1437-1443.
- PHILLIPS, A.R. 1975. The migrations of Allen's and other hummingbirds. *Condor* 77: 196-205.

- SELANDER, R.K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* 68: 113-151.
- STILES, F.G. 1972. Age and sex determination in Rufous and Allen Hummingbirds. *Condor* 74: 25-32.
- TEMELES, E.J. 1985. Sexual size dimorphism of bird-eating hawks: the effect of prey vulnerability. *American Naturalist* 125: 485-499.
- TEMELES, E.J. 1986. Reversed sexual size dimorphism: effect on resource defense and foraging behaviours of nonbreeding Northern Harriers. *Auk* 103: 70-78.
- WOLF, L.L. 1975. Female territoriality in the Purple throated Carib. *Auk* 92: 511-522.