

Exploitative compensation by subordinate age-sex classes of migrant rufous hummingbirds

F. Lynn Carpenter¹, Mark A. Hixon², Ethan J. Temeles³, Robert W. Russell¹,
David C. Paton⁴

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

⁴ Department of Zoology, University of Adelaide, GPO Box 498, Adelaide, SA 5001, Australia

Received March 29, 1992 / Accepted after revision June 20, 1993

Summary. The three age-sex classes of rufous hummingbirds (*Selasphorus rufus*) that directly interact on southward migratory stopovers in our California study system differ in territorial ability and resource use. Immature males are behaviorally dominant to adult and immature females and defend the richest territories. Here, we test the hypothesis that the territorially subordinate age-sex classes compensate exploitatively for their exclusion from rich resources. Our results show that females were able to accumulate energy stores at rates comparable to males despite their subordinate territorial status. Territorial females gained body mass at the same rate and in the same pattern as males, and resumed migration at the same body masses. Moreover, during periods when birds were nonterritorial and used dispersed resources, adult and immature females maintained or gained body mass, whereas immature males lost mass. We suggest that females may be energetically compensated by (1) lower costs of flight incurred during foraging and defense, resulting from their lower wing disc loading, and (2) greater success at robbing nectar from rich male territories, resulting from duller coloration (immature females), experience (adult females), and, possibly, hormonal differences. In the future, experiments will be necessary to distinguish the various hypotheses about the mechanisms involved in compensation.

Key words: Intraspecific dominance – Foraging ecology – Migration – Stopovers – Hummingbirds

Introduction

Sexual and age-related differences in resource use have been documented in many studies of nonbreeding birds (for reviews see Selander 1966; Morse 1980; Grubb and Woodrey 1990; Wunderle 1991). One explanation for these differences is based on sex- and age-related differ-

ences in interference competition (Miller 1967; Gauthreaux 1978; Morse 1980; Peters and Grubb 1983). In the accompanying paper (Carpenter et al. 1993b), we examined whether differences in resource use among age-sex classes of rufous hummingbirds (*Selasphorus rufus*) were associated with differences in interference abilities. For the most part, results were consistent with the interference hypothesis. Relative to immature females, immature males were more likely to acquire territories in at least two nectar-limited years, defended these territories in areas of higher flower density, and defended territories with more flowers and more nectar. Moreover, immature males were occasionally observed to aggressively displace females from their territories.

Two important results, however, were not consistent with predictions from the interference hypothesis. First, adult females surpassed immature males by some measures of territorial ability, suggesting that age-related experience may play a role in territorial dynamics. Second, although there was always a surplus of males without territories, both adult and immature females still acquired and maintained some territories at our study site in all years. Females may have been able to withstand the superior fighting ability of males because of prior residency (*sensu* Davies 1978; Krebs 1982) and familiarity with their territories. Arguing against this explanation are our observations of aggressive displacements of territorial females by immature males (Carpenter et al. 1993b), and aggressive expansions of territories held by immature males into areas defended by females (Carpenter et al. 1991).

In this paper we consider an alternative explanation for why some females held territories in the presence of dominant immature males, based upon sexual differences in ability to exploit resources. The “exploitation hypothesis” [also known as the “specialization hypothesis” (Desrochers 1989)] argues that age-sex classes use different resources because they differ in net energy intake per unit time spent foraging, generally as a result of differences in body size, morphology, and/or experience. Under the exploitation hypothesis, each class prefers

Table 1. Bill length and wing length of rufous hummingbirds measured in the field at our study site in 1984 and 1986 ($\bar{x} \pm SE$)

	Age-sex class				One-way ANOVA	
	Adult male	Immature male	Adult female	Immature female	F	P
Bill length (mm)	—	17.0 ± 0.1 (66)	17.9 ± 0.1 (36)	17.8 ± 0.1 (102)	30.2	<10 ⁻⁹ a
Wing length (mm)	40.7	43.0 ± 0.1 (142)	44.6 ± 0.2 (57)	45.1 ± 0.1 (171)	85.8	<10 ⁻⁹ b

Sample sizes are indicated in parentheses. Mean wing length of adult males is taken from Kodric-Brown and Brown (1978); data on bill length of adult males were not available

^a Multiple comparisons indicated that immature males differed significantly from both adult females ($P=10^{-8}$) and immature females ($P<10^{-9}$), but adult and immature females did not differ

significantly from each other ($P=0.60$)

^b Multiple comparisons indicated that immature males differed significantly from both adult females ($P<10^{-9}$) and immature females ($P<10^{-9}$), and adult females differed significantly from immature females ($P=0.017$)

resources most suited to its specific size, morphology, or foraging capabilities (Selander 1966; Glase 1973; Wunderle 1991).

The exploitation and interference hypotheses are not mutually exclusive, however. In some species, young birds may differ from adults in resource use both as a consequence of their own inefficiency and interference from adults (Draulans and van Vessem 1985; Goss-Custard and Durell 1987). Moreover, field studies (Kodric-Brown and Brown 1978; Temeles 1986; Alatalo and Moreno 1987), as well as theoretical analyses (Persson 1985), suggest that when dominants differ from subordinates morphologically, a balance may exist whereby dominants have an interference advantage and subordinates have an exploitative advantage. Specifically, the superior interference ability of dominant classes in the acquisition of preferred resources may be offset by superior exploitative abilities of the subordinate classes in the use of less preferred resources (Kodric-Brown and Brown 1978; Morse 1980; Lynch et al. 1985; Temeles 1986).

In order to evaluate this "dual asymmetry" hypothesis, we assume that subordinate females are "hopeful potential dominants" (*sensu* West Eberhard 1975, p. 15) and that there is no advantage of subordination in the sense proposed by the shepherds hypothesis (Rohwer and Ewald 1981). That is, we assume that differences in resource use by subordinate and dominant classes arise as a direct consequence of exclusion of subordinates by dominants, and that if compensation by subordinates occurs, it must result from morphological and/or behavioral adaptations that enable them to "make the best of a bad bargain" (Lynch et al. 1985). These assumptions are reasonable in our system because all birds should prefer high-density patches of flowers, since flight costs between flowers are reduced, thereby increasing the net rate of energy gain during foraging. Indeed, when rufous hummingbirds are familiar with artificial feeders, all age-sex classes aggregate at these artificially rich resources; under such circumstances, large numbers of females and immatures can sometimes overwhelm the defense of feeders by adult males (Kodric-Brown and Brown 1978).

Previous studies of hummingbirds have suggested a number of mechanisms by which females could be com-

pensated energetically relative to males. First, age-sex classes of rufous hummingbirds differ in wing length (Table 1; see also Stiles 1972; Kodric-Brown and Brown 1978; Johnsgard 1983), and hence in wing disc loading (the ratio of body mass to area swept out by the wings; hereafter WDL). Among individuals with similar body masses, WDL is highest in adult males, followed by immature males, adult females, and finally, immature females. High WDL is thought to improve agility and acceleration while raising flight costs, whereas low WDL reduces costs of hovering and forward flight at the expense of ability to defend a territory (Epting and Casey 1973; Feinsinger and Chaplin 1975; Pennycuick 1975; Epting 1980). Hence, we expect females to have lower flight costs relative to males with similar masses. When compounded over the duration of a stopover, such differences in energy expenditure may be ecologically significant.

Second, male rufous hummingbirds have shorter bills than either adult or immature females (Table 1; see also Johnsgard 1983; Temeles and Roberts 1993). Longer bills increase the rate and efficiency of nectar intake from flowers with long corollas, because they allow greater maximum extraction depths and shorter handling times (Wolf et al. 1972; Hainsworth 1973; Ewald and Williams 1982; Montgomerie 1984; Temeles and Roberts 1993). In a laboratory experiment, Temeles and Roberts (1993) demonstrated that female rufous hummingbirds can feed more quickly than males at artificial flowers with dimensions similar to the flowers we studied. Hence, the longer bills of females might confer an exploitative advantage in our system by allowing females to feed more quickly at flowers, as well as by increasing the size range of flowers they can use in other habitats, since longer bills allow birds to use longer flowers (Temeles and Roberts 1993).

Third, age-sex classes differ in coloration: adult males are brightest, with rufous backs and an iridescent red throat; immature females are dullest, with green backs and no red on the throat; and immature males and adult females are similar in appearance and intermediate between the two extremes (Stiles 1972; personal observations). Ewald and Rohwer (1980) demonstrated that drab individuals of another color-polymorphic hum-

mingbird were more successful at robbing other territories without being detected. Hence, we might expect female rufous hummingbirds, especially immatures, to be more successful at stealing nectar from rich territories than males.

Here we examine whether age-sex classes of rufous hummingbirds differ in ability to exploit flowers distributed at different densities. If females are able to compensate for their interference disadvantages, we expected that when both sexes are nonterritorial and using sparse resources, females would have a higher foraging efficiency (as expressed by rates of mass gain) relative to males. We also expected that, once territorial, females would gain mass as fast on their flower-sparse territories as males do on their flower-dense territories. Finally, we also examine several possible mechanisms underlying exploitative compensation, including spatial variation in nectar production and intraspecific differences in foraging rate and thieving ability.

Methods

Study system. Rufous hummingbirds migrate during the summer from their breeding grounds in northwestern North America to their wintering grounds in Mexico (Grant and Grant 1967; Phillips 1975; Calder 1987). *En route*, all age-sex classes stop periodically in mountain meadows, establish and vigorously defend territories based on patches of flowers, and require up to 3 weeks to replenish their 1–2 g migratory fat store from flower nectar before resuming their journey (Gass 1979; Carpenter et al. 1983, 1993a; Hixon et al. 1983). Adult male rufous hummingbirds finish breeding and migrate about 3–4 weeks before the females and immatures (Phillips 1975; Calder 1976; personal observations), and rarely overlap with the other age-sex classes at our study site (Carpenter et al. 1993b).

Our study site is a 2-ha meadow located along a spring-fed stream flowing from the base of the east slope of the Sierra Nevada, 27 km northwest of Bishop, California (37° 30' N, 118° 30' W, 1700 m elevation). The surrounding habitat is sagebrush scrub high desert, but associated with the stream are willows and a grassy zone supporting a single species of hummingbird-visited plant, *Castilleja linariaefolia* (Scrophulariaceae). The distance from corolla opening to flower base in this plant ranges from 15 to 20 mm (Carpenter 1988).

Procedures. Most of the data reported here were collected each year from 1980 to 1986, beginning in mid- to late July or early August (when rufous hummingbirds arrived), and finishing during the end of the migration in late August or September. At any one time, up to 50 individuals established territories in the 2 ha of *Castilleja* (Carpenter 1987). We mist-netted, identified, weighed, and color-marked the birds (Carpenter et al. 1993b), and measured their bill length and wing length to the nearest millimeter. Netting, marking, and subsequent daily mapping of marked and unmarked territory owners allowed us to obtain data on mass gain by nonterritorial as well as territorial individuals, and to determine dates when individuals resumed migration. Resumption of migration is behaviorally conspicuous (Carpenter et al. 1983, 1993a).

We selected several territorial individuals to study intensively each summer. Territory area, number of flowers defended, and nectar standing crops were measured daily for these birds (Carpenter et al. 1993b). During five 1-h sessions each day over several days, we recorded the time and duration of all major behaviors of these territory owners, including their flower visitation rates (calculated as the ratio of number of flowers visited during a foraging bout to the total elapsed time, including travel time between flowers) and their reactions to intruding birds attempting to poach nectar.

During the same periods, we monitored the birds' body masses with an electronic perch-balance (Carpenter et al. 1983).

Because accurate sampling of nectar required destruction of the flowers, we measured nectar production rates on territories using the following protocol (Carpenter 1983). We bagged one set of flowers on a territory in the evening at the same time that we measured unbagged flowers for standing crops. We collected the bagged flowers 24 h later and measured their nectar contents. The rate of nectar production was then estimated by subtracting the baseline standing crop values from the night before, and dividing the result by the elapsed time. This 24-h bagging technique may underestimate nectar production rates if nectar production is stimulated by more frequent nectar removal, which occurs in unbagged flowers due to foraging by birds. However, a test of this possibility for this population of *C. linariaefolia* showed that no such stimulation occurs (Carpenter 1983).

Statistical analyses. There were missing cells in our two-way classification (year \times age-sex class) of body mass upon resumption of migration, and also of flower visitation rates, so we initially analyzed these data using means model ANOVAs (Milliken and Johnson 1984). In these tests, the null hypothesis was that the means of all non-empty cells are equal. When means model ANOVAs showed no differences among cell means, we lumped data from all years to improve sample sizes, and then conducted one-way ANOVAs to look for differences among the age-sex classes.

Because of an uncorrectable problem with heteroscedasticity in our sample, and because rate of mass gain is in part dependent on body mass (Carpenter et al. 1993a), we treated mass change in birds without territories as a nominal variable. Nonterritorial birds that were opportunistically recaptured and reweighed were classified according to whether they (1) gained or maintained body mass or (2) lost body mass. After first testing for differences in initial body mass among the age-sex classes in this sample, we analyzed these data using a test for independence between age-sex class and mass change.

Intrusion durations were analyzed using a two-way ANOVA, with data log-transformed because of heterogeneous variances.

Significant *F*-tests in ANOVAs were followed with multiple comparisons using Fisher's least significant difference (LSD) procedure (Milliken and Johnson 1984).

All sample statistics reported in text or shown in figures are based on non-transformed data. Unless stated otherwise, all sample sizes refer to numbers of individuals. When multiple measurements were made on the same individual, the mean of these measurements was used as one replicate in statistical analyses.

Results

Mass gain and resumption of migration when territorial

Despite defending more sparsely flowering territories with fewer total flowers and lower nectar standing crops (Carpenter et al. 1993b), immature females gained mass at the same rate and in the same pattern as the other age-sex classes (Fig. 1). Moreover, females departed at body masses similar to those of males (Fig. 2). Empty cells precluded the use of a full two-way ANOVA with year as a factor, but a means model ANOVA applied to the data on departing masses indicated that there were no differences among non-empty year/age-sex cells ($F_{17,36} = 0.54$, $P = 0.91$). When years were then lumped, improving sample sizes, there were still no detectable differences among the age-sex classes (one-way ANOVA: $F_{2,51} = 0.51$, $P = 0.60$).

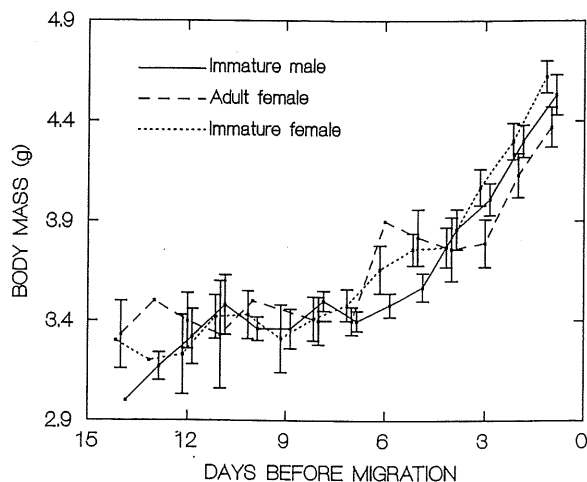


Fig. 1. The time course of body mass change in immature males (solid line), adult females (dashed line), and immature females (dotted line) defending territories during migratory stopovers. Means and SEs of body masses measured in the afternoon or evening are shown for each day from 2 weeks prior to migration. Data depicted represent a total of 396 measurements on 193 hummingbirds during 8 years (1979–1986)

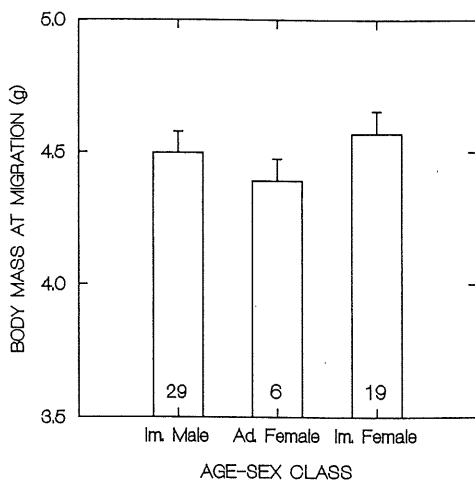


Fig. 2. Body masses (g) measured during the evening before resumption of migration or on the morning when migration was resumed. Bars indicate means and SEs. Sample sizes are shown inside bars

Mass gain when nonterritorial

Some individuals of all age-sex classes spent one day or more without territories (Carpenter et al. 1991). These birds flew long distances between sparsely flowering areas in the meadow and between other birds' territories from which they attempted to poach nectar. By analyzing mass change in these nonterritorial birds, we assessed the relative efficiencies with which the different age-sex classes were able to use sparse resources. We expected that if females are superior at nonaggressive exploitation, then they should be less likely than males to lose mass when nonterritorial. This prediction was upheld: whereas 7 of 11 immature males lost body mass during nonterritorial periods, only 1 of 8 adult females and 2 of 11 immature females lost body mass when nonterritorial ($\chi^2 = 7.24$,

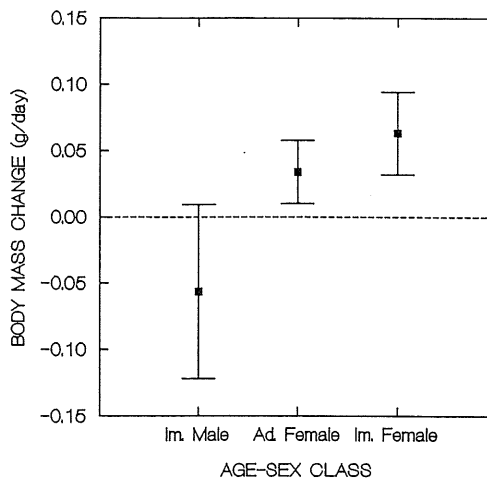


Fig. 3. Rates of body mass change (g/day) in hummingbirds during nonterritorial periods. Means and SEs are shown in figure. Sample sizes are as follows: immature males, 11; adult females, 8; immature females, 11

$df = 2$, $P = 0.027$). Mean rates of mass change were -0.06 g/day in immature males, $+0.03$ g/day in adult females, and $+0.06$ g/day in immature females (Fig. 3). Initial body masses of birds in this sample did not differ among the age-sex classes ($F_{2,27} = 0.82$, $P = 0.45$), and are therefore unlikely to have biased the results on mass change rates.

Nectar production and flower visitation

Spatial variation in nectar production rates is one mechanism that could potentially compensate females for their territorial disadvantages. Specifically, flowers in sparse areas might produce nectar faster than flowers in dense areas. Because nectar production rates differed among years at our study site (Carpenter et al. unpublished data), we tested this possibility using an analysis of covariance (ANCOVA), with nectar production rate on a territory as the dependent variable, year as a categorical variable, and flower density on the territory as the covariate. We restricted this analysis to territories on which nectar production rate and flower density were measured within one day of each other. Because only one relevant data point was available from 1980, this analysis focused on 1981–1986, with a resulting sample size of 36 territories. When we controlled for year effects in this way, we found no relationship between nectar production rate and flower density ($F_{1,30} = 0.63$, $P = 0.43$).

We used flower visitation rate (number of flowers visited per unit time during foraging bouts) as an index of foraging speed and analyzed data from 1981–1986 on birds for which we obtained at least ten foraging bout observations. A means model ANOVA detected no differences among means of non-empty cells in the two-way (year \times age-sex) classification ($F_{11,20} = 1.88$, $P = 0.11$). When we then lumped years, improving sample sizes, the age-sex classes still appeared to have similar flower visitation rates (one-way ANOVA: $F_{2,29} = 0.13$, $P = 0.88$).

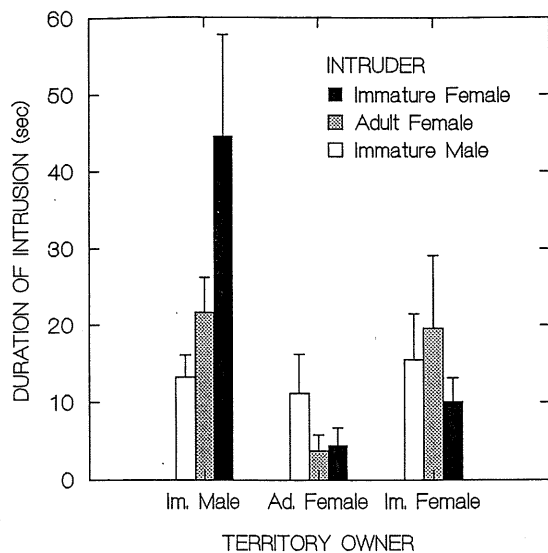


Fig. 4. Durations of intrusions by nectar robbers before being chased by territory owners, in relation to the age-sex classes of both owners and intruders. Intrusions that occurred while a territory owner was temporarily absent are excluded. Intrusion data from 1980 and 1982 are also excluded: data from 1980 were taken in a different way than the other years, and 1982 was an 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. Sample sizes (numbers of intrusions onto territories held by immature males, adult females, and immature females, respectively) are as follows: intruder = immature male (103, 19, 22); intruder = adult female (31, 8, 6); intruder = immature female (22, 30, 49). These sample sizes include data on both marked and unmarked individuals, and reflect total numbers of observations, which exceed the numbers of different individuals involved

Thievery

We assume here that the success of stealing nectar is positively correlated with the length of time an intruding bird is able to remain on its victim's territory before being chased. Intrusion duration depended on the age and sex of both owner and intruder (Fig. 4; two-way ANOVA on log-transformed data, $F_{4,281} = 6.76$, $P < 0.0001$). Separate one-way ANOVAs showed that intrusion durations did not vary among age-sex classes of intruders if the owner was either an adult female ($F_{2,54} = 2.08$, $P = 0.13$) or an immature female ($F_{2,74} = 2.76$, $P = 0.07$). However, on the rich territories defended by immature males, immature male intruders were quickly detected and chased, whereas adult and especially immature females remained much longer (Fig. 4; $F_{2,153} = 11.53$, $P < 0.0001$). Multiple comparisons indicated significant differences between immature males and both adult ($P = 0.006$) and immature ($P < 0.0001$) females, but not between the two age classes of females ($P = 0.10$).

Discussion

Evidence for exploitative compensation

If females were impeded by their territorial disadvantages during migratory stopovers, one would expect rates

of body mass gain and final body masses at migration to be lower than those of males. These predictions were rejected: territorial females gained mass at the same rate and in the same pattern as territorial males, and females and males departed at similar masses. Furthermore, stopover durations did not differ among the age-sex classes (Carpenter et al. 1991; Russell et al. unpublished data). These results suggest that the reason why immature females usually passed through our study site later than the other classes (Carpenter et al. 1991) is not because they are slower to refatten on stopovers, but perhaps because they leave the breeding grounds later. This possibility needs further investigation.

The patterns of mass gain by territorial individuals were identical among the age-sex classes despite the facts that (1) immature females had more sparsely flowered territories than adult females, who in turn had more sparsely flowered territories than immature males; and (2) immature females defended fewer flowers with lower standing crops than immature males, with adult females more similar to males. The lack of any detectable consequences of these disadvantages strongly suggests that females somehow were able to compensate for them exploitatively over the duration of a migratory stopover. Compensatory exploitation is perhaps even more strongly supported by the fact that nonterritorial females gained mass whereas nonterritorial males lost mass during migratory stopovers.

Mechanisms of exploitative compensation

Low flower density is expected to increase the foraging cost per flower by increasing the distance and flight time between flowers. Therefore, all other things being equal, low flower density should reduce the net energy gain per flower visited by birds on sparsely flowered territories (females, especially immatures) relative to birds with densely flowered territories (immature males).

The expected reduction in females' foraging efficiency due to the low flower densities accessible to them could potentially be countered by at least five factors: (1) flowers in sparse areas might produce nectar faster than flowers in dense areas; (2) females might achieve higher rates of energy intake during foraging bouts; (3) females might forage for longer periods of time; (4) females might incur lower flight costs during foraging, as proposed by the WDL hypothesis; and (5) females may be more effective than males at poaching on rich, defended areas.

Our data on nectar production rates clearly ruled out the first hypothesis. The second hypothesis is somewhat more difficult to evaluate, because higher rates of energy intake could result from faster transit flight during foraging and/or faster flower handling. We used flower visitation rate as a measure of foraging speed and were not able to detect any differences among the age-sex classes. However, flower visitation rate is a compound measure that incorporates both flight speed between flowers and flower handling speed, and our data did not allow us to separate the forward flying portion of foraging from flower handling. We have no data on flight speeds, but

flight mechanics theory (Pennycuik 1975) predicts that more heavily wing-loaded individuals have higher optimal flight speeds and should fly faster. We therefore have no reason to expect that females would fly faster than males, but rather the opposite.

If transit flight was actually slower in females, as suggested by flight mechanics theory, then the lack of a detectable difference in flower visitation rates among the age-sex classes, together with the longer distances between flowers on female territories, implies that females handled flowers faster. Faster flower handling in females was predicted on the basis of their longer bills, but could also have been due to the lower nectar standing crops on their territories (see Fig. 3C in Carpenter et al. 1993b), since lower standing crops should reduce the amount of time required to extract the nectar. In any case, we conclude that females were very unlikely to have compensated by way of higher energy intake rates while foraging, because they visited similar numbers of flowers per unit foraging time but obtained less nectar per flower visited than did males.

We have not presented any data with which we can directly evaluate the third hypothesis (females might forage for longer periods of time). However, previous laboratory experiments (Diamond et al. 1986; Karasov et al. 1986) and field studies (Hixon and Carpenter 1988) have strongly suggested that crop-emptying rate constrains the amount of time spent foraging by this species to only c. 20% of each hour. Therefore, extension of foraging bout duration or frequency seems a very unlikely source of compensation for females.

We have no data on flight energetics, but cheaper flight in females would be consistent with flight mechanics theory (Pennycuik 1975), which predicts a positive relationship between cost of flight and WDL. Furthermore, rates of mass gain in nonterritorial birds were inversely related to WDL in a pattern mirroring the theoretical expectations for flight costs (Fig. 3).

Finally, our data on nectar thievery suggest important differences in robbing ability among the age-sex classes. Although most individuals of all age-sex classes were chased eventually when they entered another bird's territory (Carpenter et al. 1993b), the data on intrusion durations (Fig. 4) clearly show that intruding females, especially immatures, were somehow able to remain within the more densely flowered male territories for longer periods than intruding males. Superiority of immature females over immature males as nectar thieves is consistent with the hypothesis that drab-plumaged birds are more difficult to detect visually, but reasons for the superiority of adult females over similarly colored immature males must be sought elsewhere. There are at least two other factors which could influence thievery. First, the age-sex classes also differ in experience. Adult females have performed at least two previous migrations, and their experience might benefit them relative to immatures. Second, sexual differences involve hormonal differences that could be associated with levels of aggression. Females might be more capable than males of invading a male's territory and acting in a submissive way which could forestall chase.

In sum, energetic compensation by females could have resulted from lower flight costs associated with WDL differences, and/or from more effective thievery resulting from coloration differences and other factors, but probably not from the other hypothetical mechanisms. Bill morphology may have conferred some advantage on females in terms of faster flower handling, although none was detected in this study; however, any such advantage was apparently countered by slower flight speeds and/or greater distances between flowers, and therefore not sufficient to account for the compensation we observed.

Multiple causation is common in ecology (Hilborn and Stearns 1982), and it is apparent that no single factor can unambiguously explain our results. Controlled experiments using individuals of known morphology and coloration will be necessary to assess the relative contributions of the different factors to female compensation.

Evolution of sex- and age-related differences

Our observational and correlative approach could not disentangle clearly the relative importance of WDL, color, and bill length in determining exploitative advantages, and it seems likely that they all play some role. A variety of mechanisms based on sexual selection, reproductive role division, and intersexual food competition may have contributed to the evolution of incipient sexual differences in morphology and color of hummingbirds (see Hedrick and Temeles 1989; Shine 1989 for reviews of genetic models of, and empirical evidence for the evolution of sexual dimorphism). Sexually dichromatic features typically are attributed to sexual selection (Darwin 1871; Fisher 1930; Selander 1972), but some authors have suggested that conspicuous coloration may have evolved in hummingbirds in a non-sexual context as an aggressive signal for mediating competitive interactions unrelated to reproduction (Bleiweiss 1985). Kodric-Brown and Brown (1978) hypothesized that the higher WDL, as well as bright coloration, of male hummingbirds reflects sexual selection for increased territory-holding abilities during the breeding season, whereas the lower WDL and duller coloration of females reflect natural selection for increased foraging efficiency during the rearing of young.

Regardless of their evolutionary origin, we suggest that these differences might be magnified through natural selection during migration if they reduce the intensity of intraspecific food competition. Continuing competition between age-sex classes during migration may enforce and augment morphological and plumage differences among them, and future studies should compare and assess the relative importance of different factors in the evolution and maintenance of these differences.

Conclusions

Previous studies of hummingbird communities have found that differences in morphological characteristics are often associated with differences in foraging behavior

and territorial ability (e.g., Feinsinger 1976; Des Granges 1978; Feinsinger and Colwell 1978; Kodric-Brown and Brown 1978; Feinsinger et al. 1979; Snow and Snow 1980). Our results provide direct evidence that, in hummingbirds, territorially inferior individuals can compensate exploitatively for their interference disadvantages.

Behavioral dominance is common in many taxa of animals (reviewed by Gauthreaux 1978), and other forms of compensation are known to occur. Individuals or species with subordinate social status may possess an enhanced capacity for facultative escape behaviors (Alford and Bolen 1977; Bennett and Bolen 1978), or physiological adaptations for energy conservation (MacMillen 1981; Roskaft et al. 1986). We suggest that tradeoffs between interference and exploitation abilities may be widespread yet frequently overlooked strategies in nature.

Acknowledgements. We thank D. Babb (LADWP) for access to our study site and K. & M. Kaiser for their hospitality in the field. We thank our many field assistants – C. Copenhaver, P. Fuller, D. Heinemann, T. Holtsford, C. Huckins, M. Humphries, J. Kohn, R. Lejniaks, C. Lenihan, D. McGrath, P. O'Neil, P. Paton, E. Read, E. Smith, A. Smythe, B. Tissot, and K. Uphoff. We thank P. Ewald, L. Gass, K. E. Linsenmair, J. Thompson, L. Wolf, and an anonymous reviewer for providing valuable comments and suggestions, which helped to substantially clarify and streamline earlier versions of this manuscript. This study was supported by NSF Grants DEB 80-22575 (Carpenter, Paton, and Hixon) and DEB 84-00669 (Carpenter and Hixon).

References

- Alatalo RV, Moreno J (1987) Body size, interspecific interactions, and use of foraging sites in tits (Paridae). *Ecology* 68:1773-1777
- Alford JR III, Bolen EG (1977) Influence of winter temperatures on pintail sex ratios in Texas. *Southwest Nat* 21:554-556
- Bennett JW, Bolen EG (1978) Stress response in wintering green-winged teal. *J Wildl Manage* 42:81-86
- Bleiweiss R (1985) Iridescent polychromatism in a female hummingbird: is it related to feeding strategies? *Auk* 102:701-713
- 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
- 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 (1988) Pollen transfer efficiency compensates for pollinator crashes in a specialized bird-pollinated plant. *Acta Congr Int Ornithol XIX*:537-548
- 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, Russell RW, Paton DC, Temeles EJ (1993b) Interference asymmetries among age-sex classes of rufous hummingbirds during migratory stopovers. *Behav Ecol Sociobiol* 33:297-304
- Darwin C (1871) *The descent of man, and selection in relation to sex*. John Murray, London
- Davies NB (1978) Territorial defence in the speckled wood butterfly (*Pararge aegeria*), the resident always wins. *Anim Behav* 26:138-147
- Des Granges JL (1978) Organization of a tropical nectar feeding bird guild in a variable environment. *Living Bird* 17:199-236
- Desrochers A (1989) Sex, dominance, and microhabitat use in wintering black-capped chickadees: a field experiment. *Ecology* 70:636-645
- Diamond JM, Karasov WH, Phan D, Carpenter FL (1986) Digestive physiology is a determinant of foraging bout frequency in hummingbirds. *Nature* 320:62-63
- Draulans D, van Vessem J (1985) Age-related differences in the use of time and space by radio-tagged grey herons (*Ardea cinerea*) in winter. *J Anim Ecol* 54:771-780
- Epting RJ (1980) Functional dependence of the power for hovering on wing disc loading in hummingbirds. *Physiol Zool* 53:347-357
- Epting RJ, Casey TM (1973) Power output and wing disc loading in hovering hummingbirds. *Am Nat* 107:761-765
- Ewald PW, Rohwer S (1980) Age, coloration and dominance in nonbreeding hummingbirds: a test of the asymmetry hypothesis. *Behav Ecol Sociobiol* 7:273-279
- Ewald PW, Williams WA (1982) Function of the bill and tongue in nectar uptake by hummingbirds. *Auk* 99:573-576
- Feinsinger P (1976) Organization of a tropical guild of nectarivorous birds. *Ecol Monogr* 46:257-291
- 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
- Fisher RA (1930) *The genetical theory of natural selection*. Clarendon Press, Oxford
- 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
- Glase JC (1973) Ecology of social organization in the black-capped chickadee. *Living Bird* 12:235-267
- Goss-Custard JD, Durell SEA (1987) Age-related effects in oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*. I. Foraging efficiency and interference. *J Anim Ecol* 56:521-536
- Grant KA, Grant V (1967) Effects of hummingbird migration on plant speciation in the California flora. *Evolution* 21:457-465
- 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
- Hainsworth FR (1973) On the tongue of the hummingbird: its role in the rate and energetics of feeding. *Comp Biochem Physiol* 46A:65-78
- Hedrick AV, Temeles EJ (1989) The evolution of sexual dimorphism in animals: hypotheses and tests. *Trends Ecol Evol* 4:136-138
- Hilborn R, Stearns SC (1982) On inference in ecology and evolutionary biology: the problem of multiple causes. *Acta Biotheor* 31:145-164
- 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
- Johnsgard PA (1983) *The hummingbirds of North America*. Smithsonian Institution Press, Washington, DC
- Karasov WH, Phan D, Diamond JM, Carpenter FL (1986) Food passage and intestinal nutrient absorption in hummingbirds. *Auk* 103:453-464
- Kodric-Brown A, Brown JH (1978) Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant rufous hummingbirds. *Ecology* 59:285-296
- Krebs JR (1982) Territorial defence in the great tit (*Parus major*): do residents always win? *Behav Ecol Sociobiol* 11:185-194
- Lynch JF, Morton ES, Van der Voort ME (1985) Habitat segregation between the sexes of wintering hooded warblers (*Wilsonia citrina*). *Auk* 102:714-721
- MacMillen RE (1981) Nonconformance of standard metabolic rate with body mass in Hawaiian honeycreepers. *Oecologia* 49:340-343
- 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
- Montgomery RD (1984) Nectar extraction by hummingbirds: response to different floral characters. *Oecologia* 63:229-236
- Morse DH (1980) *Behavioral mechanisms in ecology*. Harvard University Press, Cambridge, MA
- Pennycuik CJ (1975) Mechanics of flight. In: Farner DS, King JR (eds) *Avian biology*, vol 5. Academic Press, New York, pp 1-75
- Persson L (1985) Asymmetrical competition: are larger animals competitively superior? *Am Nat* 126:261-266
- 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
- Rohwer S, Ewald PW (1981) The cost of dominance and advantage of subordination in a badge signaling system. *Evolution* 35:442-454
- Roskoff E, Jarvi T, Bakken M, Bech C, Reinertsen RE (1986) The relationship between social status and resting metabolic rate in great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*). *Anim Behav* 34:838-842
- Selander RK (1966) Sexual dimorphism and differential niche utilization in birds. *Condor* 68:113-151
- Selander RK (1972) Sexual selection and dimorphism in birds. In: Campbell B (ed) *Sexual selection and the descent of man*. Aldine, Chicago, pp 180-230
- Shine R (1989) Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Q Rev Biol* 64:419-461
- Snow DW, Snow BK (1980) Relationships between hummingbirds and flowers in the Andes of Colombia. *Bull Br Mus Nat Hist (Zool)* 38:105-139
- 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
- Temeles EJ, Roberts WM (1993) Effect of sexual dimorphism in bill length on foraging behavior: an experimental analysis of hummingbirds. *Oecologia* 94:87-94
- West Eberhard MJ (1975) The evolution of social behavior by kin selection. *Q Rev Biol* 50:1-33
- Wolf LL, Hainsworth FR, Stiles FG (1972) Energetics of foraging: rate and efficiency of nectar extraction by hummingbirds. *Science* 176:1351-1352
- Wunderle JM Jr (1991) Age-specific foraging proficiency in birds. In: Power DM (ed) *Current ornithology*, vol 8. Plenum, New York, pp 273-324