REVERSED SEXUAL SIZE DIMORPHISM: EFFECT ON RESOURCE DEFENSE AND FORAGING BEHAVIORS OF NONBREEDING NORTHERN HARRIERS

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ABSTRACT.—Sexual differences in resource defense and foraging behaviors during the non-breeding season are detailed for Northern Harriers (*Circus cyaneus*) in California. Female harriers hunted more frequently in high (>0.5 m) vegetation than males. In addition, females hunted at slower speeds and used different hunting behaviors than males. Females in high vegetation showed a significantly greater response (i.e. attack) rate to approaching harriers than males, and females won nearly all (28/29) aggressive interactions with males. These results suggest that sexual differences in harrier foraging behavior during the nonbreeding season result from females excluding males from preferred foraging areas and males adopting alternative foraging strategies. Foraging strategies of harrier sexes are compared with foraging strategies of sexes of birds in which males are larger than females to examine the role of body size in determining sexual foraging strategies. *Received 7 March 1985, accepted 2 July 1985.*

IN many bird species (e.g. ducks, humming-birds, woodpeckers), sexes differ in geographic distribution, habitat use, or foraging behavior during the nonbreeding season (Ligon 1968, Feinsinger and Colwell 1978, Hogstad 1978, Stiles and Wolf 1979, Kilham 1983, Hepp and Hair 1984). Social dominance is one mechanism that may influence nonbreeding sexual foraging differences (Gauthreaux 1978). Usually, social dominance confers priority of access to resources (e.g. food) and is attained by those individuals that are most successful in aggressive interactions (e.g. fights, chases) with others (Morse 1980).

Social dominance during the nonbreeding period affects access to preferred resources and leads to sexual foraging differences in many avian species (see above references). In general, larger males supplant smaller females and forage in areas of highest resource density; these sexual differences in foraging area often are accompanied by sexual differences in foraging behavior when foraging behaviors vary with habitat type. Alternatively, smaller females may adopt different foraging behaviors to exploit the same resources as dominant males. Both patterns of sex-specific foraging during the nonbreeding season are well illustrated in many hummingbird species: larger (heavier), socially dominant males defend high-quality food territories, whereas smaller (lighter), socially sub-ordinate females trapline-forage among dispersed resources, defend poorer-quality territories, or "rob" male territories (Stiles 1973, Wolf et al. 1976, Feinsinger and Colwell 1978, Kodric-Brown and Brown 1978, Stiles and Wolf 1979, Kuban and Neill 1980, Kuban et al. 1983).

I examined the consequences of sexual size reversal on social dominance and sex-specific foraging behavior in the Northern Harrier (*Circus cyaneus*). Females are considerably larger than males in this species, as in virtually all species of predatory birds (Falconiformes, Strigiformes, Stercorariidae). Sexual differences in distribution, habitat use, or foraging behavior during the nonbreeding season have been recorded for harriers (Schipper et al. 1975, Bildstein 1978, Bildstein et al. 1984) as well as for other raptors (Mills 1976, Stinson et al. 1981, Marquiss and Newton 1982) and for nonraptorial species in which females are larger than males (e.g. Puttick 1981). However, female social dominance as the mechanism responsible for these differences has only been hypothesized or inferred (Mills 1976, Mueller et al. 1977, Evans 1980, Boxall and Lein 1982) or deduced from experimental introduction of a captive bird into the territory of a resident bird (e.g. Cade 1955).

I present data on harriers that show that sexual differences in foraging area and behavior during the nonbreeding season are due to fe-

males aggressively excluding males from preferred foraging areas. I then examine the influence of body size on sex-specific foraging strategies by comparing the foraging behaviors of harrier sexes to foraging behaviors of sexes of birds in which males are larger than females.

<center>STUDY AREA AND METHODS</center>

The 25-km² study area was located 3 km northeast of Davis, Yolo Co., California. This area is primarily agricultural cropland composed of the following vegetation types: corn stubble, rice stubble, winter wheat, winter-wheat stubble, plowed field, and fallow field. The observations reported here were part of a long-term study of harrier foraging behavior and cover the period 29 November 1983 to 31 January 1984. These dates were not arbitrarily chosen: harriers began to defend areas in late November and ceased to defend areas in early February (observations in the winter of 1984–1985 corroborate this). I made 20 days of observations involving 8 h of field time per day.

When a foraging harrier was sighted, I recorded the date and time of each observation, the sex and age of the bird, the vegetation type and height, hunting speed (where possible), and hunting behavior (where possible). Adult harriers were easily and unambiguously sexed: adult males are gray dorsally and adult females are brown. Juvenile *C. c. hudsonius* could be distinguished from adult females by their rufous, unstreaked underbelly (Cramp and Simmons 1980). Extreme sexual size dimorphism also facilitated sexing harriers of all ages, especially on occasions when a bird was seen flying with a member of the opposite sex. Because the number of juveniles (= rufous-breasted birds) seen on the study area was extremely low (9 juveniles compared with 153 adults, or 6%), and because studies indicate that foraging of juvenile birds differs from adults (e.g. Marr and McWhirter 1982), I excluded juveniles from the data analyses.

Vegetation types were classified into two categories on the basis of height. Vegetation was described as "high" in fallow fields where all vegetation was >0.5 m high and as "low" in corn, rice, and winter-wheat stubble, winter-wheat fields, and plowed fields where all vegetation was <0.5 m high ($n = 500$ measurements of vegetation height, measured from ground surface to top of plant). Although vegetation type and height were the variables of primary interest for statistical analyses, differences in vegetation type and height also were associated with differences in vegetation density: vegetation in high, fallow fields was much denser than vegetation in low, stubble fields, where rows were separated by 7–10 cm of open space ($n = 500$ measurements of vegetation density, i.e. distances between adjacent plants).

Hunting speeds of harriers were recorded on an automobile speedometer. To insure reliability and consistency of measurement with this technique, I recorded hunting speeds of harriers only when driving parallel to them for a period of >30 s. These measurements were possible owing to the number of roads crossing the study area and the harriers' acceptance of moving automobiles. Because I found that harriers altered their hunting behavior during periods of high winds, I excluded from my analyses those observations of harriers made when wind speeds exceeded 16 km/h. I recognized three categories of hunting speeds: (1) ≤8 km/h, (2) 16–24 km/h, and (3) ≥32 km/h. Following Schipper et al. (1975) and Bildstein (1978), I classified a harrier's hunting behavior in one of three categories: (1) straight flight [less than 5 sharp (>30°) turns/min] through a field, (2) quartering (more than 5 sharp turns/min) back and forth over a field, and (3) border (edge) following (e.g. hunting along ditches, fence rows, road shoulders). I did not record subsequent observations of a particular sex at a site on the same day unless two or more birds of the same sex were observed simultaneously.

In addition to the general observations described above, I made detailed observations of a smaller number of harriers to obtain a better understanding of their foraging behaviors. In this set of observations, each individual harrier was watched for a 30-min focal period (Altmann 1974). During each 30-min period, I recorded the number of prey capture attempts, the number of successful captures, the type of prey, the time spent in foraging, perching, eating, or in aggressive interactions, the total area foraged in, the number of approaches by male/female conspecifics, and the number of interactions with male/female conspecifics and outcome.

I defined a capture attempt as an effort by a harrier to catch a specific prey item; repeated strikes during the pursuit of a single prey item were considered to represent a single capture attempt. Capture success was defined as the percentage of all capture attempts that ended in prey capture (see Temeles 1985). Several features of my study area and the behaviors of harriers allowed me to accurately identify the types of prey (birds, rodents) attacked. First, birds "flush" out of vegetation when attacked by harriers, whereas rodents do not, and because the vegetation on my study site (even in the high areas) never exceeded 1.2 m and most observations were made at distances of less than 100 m, it was possible to see avian prey as they escaped harriers' attacks. Second, on many occasions harriers picked up vole "nests" while executing unsuccessful capture attempts. Third, harriers often utilize different attack strategies for birds and rodents [e.g. they "pounce" at birds in more rapid motions; Schipper et al. (1975), Bildstein (1978); pers. obs.].

All time observations were recorded on a stopwatch or measured from tape-recorder playbacks. By

TABLE 1. Morphology of 10 male and 10 female adult Northern Harriers in the Louisiana State University Museum of Zoology collection. Data are means ± SD.

Measurement	Male	Female	P
Wing chord (mm)	346.4 ± 9.02	383.9 ± 7.68	<0.001
Bill chord (mm)	16.4 ± 0.70	19.3 ± 0.42	<0.001
Middle toe length (mm)	34.9 ± 1.45	41.2 ± 1.03	<0.001
Hallux claw arc (mm)	22.5 ± 0.67	27.6 ± 1.37	<0.001

using different number combinations and colors of surveyor's tape tied on many markers (e.g. fence wires) at regular intervals on flat land, I estimated foraging areas hunted in by harriers. Distances between markers were measured using a 100-m field tape measure or, in cases where the layout of roads permitted, an automobile odometer. Odometer measurements were checked for accuracy against tape measurements and revealed no differences. Foraging areas were measured after each focal period.

I defined an approach as any harrier (male or female) coming within 100 m of the focal bird. I recognized four different harrier aggressive behaviors, which I placed into two categories on the basis of presence or absence of physical contact. Noncontact behaviors were (1) Chase, in which the focal bird flew at the approaching bird and then flew after the approaching bird as it fled, from behind and on level with it; and (2) Escort, in which the focal bird flew at the approaching bird and then flew after the approaching bird as it fled, from behind and below it, both birds flying far out of the focal bird's foraging area (see Bildstein and Collopy 1985). Chase and escort behaviors differed at a quantitative as well as a qualitative level; escorts were considerably longer than chases (P < 0.001, t-test; mean ± SD escort = 35.3 ± 14.2 s, n = 30; mean ± SD chase = 18.3 ± 8.9 s, n = 21; no sex differences). Contact behaviors were (1) Short contact, in which the focal bird flew at and then hit or talon-grappled with the approaching bird; and (2) Long contact, in which the focal bird flew at and then repeatedly hit and grappled with the approaching bird, both birds falling to the ground several times. Long and short contact behaviors also differed considerably in length (P < 0.001, t-test; mean ± SD long = 65.0 ± 17.5 s, n = 8; mean ± SD short = 19.2 ± 9.2 s, n = 6; females only). I defined a winner of an aggressive encounter as a bird that succeeded in driving the other bird (= loser) out of the foraging area within 2 min after initiation of the encounter. In addition, I recorded other aggressive interactions observed (outside of focal samples).

For purposes of statistical independence of data, I attempted to minimize repeat observations of the same individual in two ways. First, I tried to identify as many individuals as possible by noting plumage characteristics (e.g. missing or damaged feathers) and favorite perch sites. Second, my observations of harriers that could be positively identified indicated that

they generally did not utilize the same area for more than 14 days. Consequently, I never made a focal observation of a harrier if a previous focal observation had been made of a harrier of the same sex in the same area within 14 days, unless the new individual differed noticeably in plumage from the old individual. Nonparametric statistical procedures follow Daniel (1978) and Siegel (1956); parametric statistical procedures follow Snedecor and Cochran (1967). Significance levels were determined from tables in Hald (1952).

RESULTS

Morphology.—Size differences between sexes of the North American race *C. c. hudsonius* are highly significant (Table 1; P < 0.001). Cramp and Simmons (1980) presented morphological measurements for the European subspecies *C. c. cyaneus* and verified that all sexual size differences are significant. Smaller body weights and winglengths of males corresponded to smaller wing loading and a large difference in the estimated metabolic cost of flight (Table 2).

Habitat use and hunting speeds.—Sexes differed with respect to vegetation height, where the distributions were 83 females and 21 males in high (>0.5 m) vegetation, and 25 females and 24 males in low (<0.5 m) vegetation (x^2 = 13.3, df = 1, P < 0.0005). Females were observed to hunt more often at slow (≤8 km/h) speeds, whereas males were observed to hunt more often at higher (≥16 km/h) speeds (x^2 = 42.2, df = 2, P < 0.0005; number of observations of each sex at given speeds, ≤8 km/h: 34 females, 1 male; 16–24 km/h: 6 females, 15 males; ≥32 km/h: 1 female, 11 males). The sexual differences in hunting speeds were associated with vegetation heights. In high vegetation, 31/32 females observed were hunting at speeds ≤8 km/h, whereas 16/16 males observed were hunting at speeds ≥16 km/h (x^2 = 43.8, df = 1, P < 0.0005). In contrast, there were no significant differences between the sexes for hunting speeds in low vegetation. Moreover, sexes of

TABLE 2. Measurements of winglength, body weight, and wing loading and calculated minimum power required to fly, P_{min} (W, 1 W = 1 J/s) for sexes of Northern Harriers.

Sex	Winglength[a] (m)	Body wt[a] (kg)	Wing loading[b] (g/cm²)	P_{min}[c]
Male	0.344 (20)[d]	0.350 (90)	0.270 (2)	3.02
Female	0.385 (20)	0.531 (97)	0.315 (2)	5.12

[a] Data from Snyder and Wiley (1976).

[b] Average wing loading from data in Poole (1938) and Brown and Amadon (1968).

[c] P_{min} calculated from Pennycuick's (1972) equations. Wing span, *b*, was estimated from Greenewalt (1962), where $b = 2(\text{winglength})/0.62$. Air density at sea level was used (1.22 kg/m³).

[d] Sample sizes are given in parentheses.

TABLE 3. Hunting areas (km²) determined during 30-min focal observations of Northern Harriers by sex and vegetation height class. *n* = sample size.

Sex	Vegetation height class	Hunting area Median	Hunting area Mean ± SD	*n*
Female	High	0.149	0.185 ± 0.147	16
	Low	0.932	1.018 ± 0.245	3
Male	High	1.126	0.977 ± 0.340	4
	Low	1.087	0.964 ± 0.405	4

harriers showed opposite results in the relation of hunting speed to vegetation height. Hunting speeds of female harriers were negatively associated with vegetation height: 31/34 observations of females hunting at speeds ≤8 km/h were in high vegetation, whereas 6/7 observations of females hunting at speeds ≥16 km/h were in low vegetation ($\chi^2 = 15.8$, df = 1, $P < 0.0005$). Hunting speeds of male harriers were positively associated with vegetation height: 10/16 observations of males hunting at speeds ≤24 km/h were in low vegetation, whereas 10/11 observations of males hunting at speeds ≥32 km/h were in high vegetation (Fisher exact test, two-tailed, $0.01 < P < 0.02$).

Hunting behavior and habitat.—Females were observed to hunt most often by quartering. Males hunted by straight-flying or border-following ($\chi^2 = 42.7$, df = 2, $P < 0.0005$; number of observations of each sex using given behaviors, quarter: 40 females, 2 males; straight flight: 5 females, 26 males; border-following: 16 females, 10 males). The relation among sex, hunting behavior, and vegetation height paralleled the relation among sex, hunting speed, and vegetation height. Sexual differences in hunting behaviors also were associated with high vegetation. In high vegetation, 40/44 females were observed to hunt by quartering, whereas 20/22 males were observed to hunt by straight-flying and border-following ($\chi^2 = 42.4$, df = 1, $P < 0.0005$). No significant differences between the sexes were observed for distributions of hunting behaviors in low vegetation. Quartering by female harriers was associated with vegetation height: 40/44 females observed in high vegetation hunted by quarter-

ing, whereas 17/17 females observed in low vegetation hunted by straight-flying and border-following ($\chi^2 = 44.9$, df = 1, $P < 0.0005$).

Hunting areas.—Hunting areas (as determined during each 30-min focal observation) are presented for harrier sexes with respect to vegetation height in Table 3. A Kruskal-Wallis ANOVA of the medians of these hunting areas, with sex and vegetation height classes (e.g. females observed in high vegetation) as factor levels, was highly significant ($H = 18.0$, $P < 0.005$; $n = 27$ different individuals). Two-tailed nonparametric multiple comparisons indicated that the median of the hunting areas of female harriers in high vegetation was significantly smaller than the median of the hunting areas of male harriers in high or low vegetation, or female harriers in low vegetation ($P < 0.05$ overall).

Capture attempts.—Capture rates varied between harrier sexes with respect to vegetation height (Table 4). A Kruskal-Wallis ANOVA of median capture rates, with sex and vegetation height classes as factor levels, was highly significant ($H = 12.6$, $0.005 < P < 0.01$; $n = 32$ different individuals). Female harriers that hunted in high vegetation had significantly more capture attempts per minute than female harriers hunting in low vegetation ($0.01 < P < 0.05$ overall; two-tailed nonparametric multiple comparisons) and tended to have more capture attempts per minute than male harriers hunting in high or low vegetation (Table 4).

Capture success.—Capture successes for different prey types are presented for harrier sexes with respect to vegetation height in Table 5. No significant differences in harriers' capture successes were observed between sexes within vegetation height classes, between sexes, between vegetation height classes, or between prey types (i.e. birds, rodents), but capture suc-

TABLE 4. Number of prey capture attempts per minute of hunting by Northern Harriers with respect to sex and vegetation height class. n = sample size.

Sex	Vegetation height class	No. of attempts per min hunt		n
		Median	Mean ± SD	
Female	High	0.50	0.53 ± 0.34	16
	Low	0.00	0.15 ± 0.37	7
Male	High	0.04	0.05 ± 0.05	4
	Low	0.00	0.05 ± 0.06	5

TABLE 5. Capture successes of Northern Harriers with respect to sex and vegetation height class for different prey types. Numerators are number of successful attempts, denominators are total number of attempts.

Sex	Vegetation height class	Prey type		
		Rodents	Pheasants	Small birds
Female	High	7/111	0/11	0/2
	Low	0/3	—	0/2
Male	High	1/14	—	0/1
	Low	—	—	0/4

cesses were extremely low [overall capture success, rodents: 8/128 (6.25%), birds: 0/20 (0%)]. When hunting attempts by harrier sexes within each vegetation height class were combined, a significant difference in the distribution of attempts at prey types was observed between vegetation height classes. The distributions were 125 and 3 attacks at rodents in high and low vegetation, respectively, and 14 and 6 attacks at birds in high and low vegetation, respectively (χ^2 = 18.6, df = 1, P < 0.0005).

Aggressive interactions.—Physical contact occurred more frequently in female-female aggressive interactions than in female-male aggressive interactions; 14/40 female-female interactions involved contact, whereas only 2/29 female-male interactions involved contact (Table 6; χ^2 = 7.5, df = 1, P < 0.01). The difference between harrier sexes was also significant in the outcomes of aggressive interactions: in female-female interactions, a female that drove her opponent out of the foraging area within 2 min from the start of the interaction was identified in 19/40 interactions, whereas in female-male interactions, females won 28/29 interactions (χ^2 = 18.6, df = 1, P < 0.0005). Too few male-male interactions (n = 3) were observed for statistical analyses (see Table 6).

From the above data (especially the paucity of male-male interactions), I tentatively concluded that typically only females defended foraging areas. However, the low frequency of male interactions could have been the result of differences between the sexes in approach frequencies. To clarify this issue, I examined approach and attack frequencies for focal birds with respect to sex and vegetation height (i.e. foraging area). No significant differences were found in approach frequencies (number of approaches/30 min) with respect to sex and vegetation height (Table 7; Kruskal-Wallis ANOVA

corrected for ties, H_c = 1.8, P > 0.1; n = 36 different individuals). Responses *to* approaching harriers did differ significantly among sex–vegetation height factor levels (Table 8; Kruskal-Wallis ANOVA, H = 13.8, 0.001 < P < 0.005; n = 27 different individuals). The median response rate (number of attacks/30 min) of females in high vegetation (median = 2) was significantly higher (P < 0.05 overall; two-tailed nonparametric multiple comparisons) than median response rates of males in high (median = 0) or in low vegetation (median = 0). To summarize, females won virtually all aggressive interactions with males, and although both sexes were approached by conspecifics at the same rate, only females usually responded to approaches by conspecifics.

DISCUSSION

Frequency of aggression in wintering raptors.—Harrier sexes differ in degree of resource defense, with females typically defending, and males typically not defending, foraging areas. The aggressive interactions I observed may be attributed to high harrier densities and high, concentrated prey densities. Harriers were extremely abundant in the study area. Densities of 8 harriers/km² and 15 raptors/km² were common, especially in high-vegetation areas. These high raptor densities may have resulted in more frequent aggressive interactions. A similar situation was reported for Snowy Owls (*Nyctea scandiaca*; Evans 1980). Probably, these high raptor densities occurred in response to either high or nonuniform (or both) prey densities within the study area (Snyder and Snyder 1970, Newton 1979). However, under most circumstances prey densities may not be high

TABLE 6. Number of observations of inter- and intrasexual aggressive interactions of nonbreeding Northern Harriers. Male-male interactions (2 escorts, 1 chase) are not included. Also not included are 2 avoidance movements by males at the approach of females.

Sexes	Chase	Escort	Short contact	Long contact
Female-female	13	13	6	8
Female-male	8	17	1	1

TABLE 7. Number of approaches by conspecifics to individual Northern Harriers per 30-min focal observation by sex and vegetation height class. n = sample size.

Sex	Vegetation height class	No. of approaches Median	No. of approaches Mean ± SD	n
Female	High	1.50	1.72 ± 1.32	18
	Low	1.00	1.22 ± 1.09	9
Male	High	1.00	1.00 ± 1.00	5
	Low	1.50	1.25 ± 0.50	4

enough for raptors to be concentrated in one area, and hence aggressive interactions between individuals may occur so infrequently as to be rarely or never recorded. In addition, degree of aggression has been shown to vary with resource quantity or quality (Ewald and Carpenter 1978, Frost and Frost 1980). Consequently, interactions between raptors may be much less overt than in this study and may take the form of avoidance (rather than aggressive) behaviors, which are more difficult to discern. These are important points to consider in understanding sexual differences in wintering distributions of birds, because failure to observe overt, aggressive interactions may not necessarily indicate an absence of social dominance.

Sexual differences in foraging areas.—These results support the view that niche differences between nonbreeding harrier sexes arise from female dominance. I suggest that female dominance conferred priority of access to preferred resources (i.e. the high-vegetation areas) and that as a result of female attacks, male harriers and subordinate females shifted from preferred to less-preferred foraging areas in low vegetation. Some evidence supports the conclusions that the high-vegetation areas defended by females were preferred and that subordinates were forced to forage elsewhere. For example, females in high vegetation hunted over much smaller foraging areas than either females in low vegetation or males in high and low vegetation, which is expected from the numerous studies that show inverse correlations between size and quality of foraging areas (see Hixon 1980). In addition, females in high vegetation showed a much greater attack response to approaching harriers than males, and females won virtually all aggressive interactions with male harriers. Finally, it is unlikely that subordinate harriers preferred to hunt in low-

vegetation areas because capture success was higher there, since I found no differences in capture success between high- and low-vegetation areas.

Sexual differences in foraging behaviors.—Sexual differences in flight speeds and foraging behaviors were observed only in high-vegetation areas, where female harriers hunted by slow quartering whereas male harriers hunted by fast, straight flight. The highest hunting speeds recorded were for male harriers hunting in high vegetation, which contradicts all previous studies on the relationship between harrier hunting speeds and vegetation type (Brown and Amadon 1968, Schipper et al. 1975, Bildstein 1978). I propose that fast foraging flight was an alternative male strategy that allowed male harriers to forage in areas defended by females while minimizing detection. Ideally, this hypothesized shift should be tested by experiments in which male foraging behavior and hunting speed are examined in the absence of females (Morse 1974, Peters and Grubb 1982). However, my observations suggest that fast male flight was a behavioral shift from the slow-quartering hunting behavior usually associated with high vegetation. First, one male that entered a high-vegetation area in the absence of a defending female hunted at slow speeds (≤8 km/h) by quartering flight and made as many capture attempts per minute as females hunting that area. (He eventually was chased away by a female.) Second, at the beginning of the 1984 breeding season, male harriers began to attack females by chasing or hitting them (although they were unable to drive females from their foraging areas and hence "win" the interaction). Such attacks by breeding males have been observed in other avian species (Armstrong 1955, McLaren 1975). At this time, both

TABLE 8. Number of responses (e.g. attacks) to conspecifics by individual Northern Harriers per 30-min focal observation with respect to sex and vegetation height class (approached individuals only). n = sample size.

Sex	Vegetation height class	No. of responses		n
		Median	Mean ± SD	
Female	High	2	2.00 ± 1.15	13
	Low	1	0.86 ± 0.69	7
Male	High	0	0.00 ± 0.00	3
	Low	0	0.00 ± 0.00	4

male and female harriers hunted in high vegetation at slow speeds by quartering. Finally, no differences were observed between sexes of harriers that foraged in areas of low vegetation (see Results), yet female (but not male) hunting speeds and foraging behaviors changed in high vegetation in the manner (i.e. slow, quarter) predicted by previous studies (Brown and Amadon 1968, Schipper et al. 1975, Bildstein 1978).

Comparisons with large male–small female species.—The foraging strategies used by sexes of Northern Harriers during the nonbreeding season show striking resemblances to those of other birds, especially hummingbirds. Given that both harriers and hummingbirds are distinguished by the fact that they forage primarily on the wing, perhaps this is not surprising. Resource defense by hummingbirds is associated with differences in body weight and winglength (i.e. wing disc loading; Feinsinger and Chaplin 1975, Kodric-Brown and Brown 1978, Feinsinger et al. 1979). Heavy weight and proportionally shorter wings result in greater maneuverability, which presumably is an advantage in territorial defense by large species and the larger sex (usually males in hummingbird species weighing more than 4 g; Lasiewski and Lasiewski 1967, Carpenter 1976). The lighter weight and longer wings of smaller species and female hummingbirds result in more energetically efficient flight and hence a better ability to exploit resources, which may be important in marginal habitats or when a bird is restricted to foraging around a nest area (Kodric-Brown and Brown 1978).

In harriers, heavy weight also may be advantageous in territorial defense, but in a somewhat different way. Because terminal speed in a dive (and presumably the force of a raptor's strike) increases with increasing body mass (Andersson and Norberg 1981), weight (and overall size) may be the decisive factor in aggressive interactions between harriers, especially between males and females, where females have a size advantage (Tables 1, 2). [On this point, Marquiss and Newton (1982) commented that female Eurasian Sparrowhawks (*Accipiter nisus*) often kill and eat smaller male sparrowhawks during the nonbreeding season.] Flight costs for male harriers are much less than for female harriers, however, owing to their smaller size and lighter wing loading (Table 2). Hence, males may be better able to survive in and to exploit marginal environments.

Similarities between harriers and hummingbirds are apparent in the types of aggressive interactions between the sexes. In this study, female harriers engaged in prolonged interactions marked by much hitting, talon-clasping, and tumbling to the ground. Often an intruding female returned to a resident female's area and repeatedly harrassed her. Male harriers, on the other hand, were wary and inconspicuous. They entered a female's area quickly by flying low to the ground and fled immediately when discovered and chased by a resident female. Rapid flight is especially important if a male captures prey in a female's area: one male I observed fleeing a female's area with prey was struck by the female and had the prey snatched from him. These observations of harrier strategies correspond well to the "challenger" male (large, conspicuous, aggressive) and "robber" female (small, submissive, inconspicuous) hummingbirds discussed by Kodric-Brown and Brown (1978).

The above comparisons between harriers and hummingbirds illustrate the significance of body size in determining both the outcome of aggressive interactions and the foraging strategies of sexes of nonbreeding birds. Dominance by the larger sex may reduce food competition and may insure priority of access to preferred resources (Gauthreaux 1978, Morse 1980). However, the lower energy demands of individuals of the smaller sex may allow them to survive where larger individuals cannot (Morse 1980).

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