

## PROXIMATE DETERMINANTS OF FORAGING EFFORT IN BREEDING MALE MERLINS

NAVJOT S. SODHI<sup>1</sup>

**ABSTRACT.**—I studied foraging effort of male Merlins (*Falco columbarius*) during the breeding season. Males significantly increased percentage of time flying (when presumably foraging) as the breeding season progressed. Number of foraging trips made by males per hour increased from the incubation to nestling period and then declined during the fledging period. Females then started hunting and providing food for the fledglings. Duration of the foraging trips of males declined with an increase in the number of foraging trips per unit of time. In the incubation period males with high prey abundance in their ranges spent less time flying than males with low prey abundance in their ranges, and males with larger hunting ranges spent more time flying and made foraging trips of longer duration. During the nestling period males flew more in longer foraging trips, males with larger broods spent more time flying than those with smaller broods, and males made fewer foraging trips in areas where the number of active Merlin nests within 1-km radius of the nest was greater. Received 18 Dec. 1991, accepted 10 May 1992.

In this study, I examine the effect of phase of the breeding cycle, clutch/brood size, prey abundance, intruder density, body mass, hunting range size, and time allocated to incubation on foraging efforts of breeding male Merlins (*Falco columbarius*). Male Merlins are appropriate subjects for this study because they provide most of the food for the family at nests during the entire breeding season (Sodhi et al. 1992) and feed mainly on House Sparrows (*Passer domesticus*); consequently, prey size is expected to have little influence on their foraging effort, and can be monitored by radio-tracking with minimum apparent effect on their behavior (Sodhi et al. 1991a).

I examined three components of the foraging effort (1) percentage of time flying when males were presumably foraging, (2) number of feeding trips made per hour, and (3) mean duration of foraging trips (i.e., sum of prey search, capture, and transport time). I determined variation in the foraging effort among males in relation to the aforementioned variables, as well as variation in the foraging effort within individual males in relation to the phase of the breeding cycle.

### METHODS

The research was conducted in Saskatoon (52°07'N, 106°38'W), Saskatchewan, Canada, from May to July 1988–1990. The study area is described by Sodhi et al. (1992). Merlins

<sup>1</sup> Dept. of Biology, Univ. of Saskatchewan, Saskatoon, Saskatchewan S7N 0W0, Canada (Present address: Dept. of Zoology, Univ. of Alberta, Edmonton, Alberta T6G 2E9, Canada).

first nested in the city in 1963, since then their population has been increasing steadily (Sodhi et al. 1992). During the study years, the nesting density of Merlins was higher than anywhere else recorded (Sodhi et al. 1992).

Males were captured near the nests using either mist or dho-gaza nets (Clark 1981), using tethered House Sparrows or a tethered Great Horned Owl (*Bubo virginianus*) as lures. Radio transmitters (model SS-1; Biotrack, Dorset, U.K.), weighing about 2% of the body mass, were attached dorsally to two tail feathers using a method described by Kenward (1978). The birds were not followed during the first day of radio-attachment, but were monitored continuously thereafter during the first and last four daylight hours (i.e., periods of maximum foraging activity, unpubl. data) on fair weather days.

Five different males were radio-tracked in 1988 and 1989, and six in 1990. As each male was not followed during the entire breeding cycle, this resulted in 12, 13, and 5 males being monitored during the incubation, nestling, and fledging periods, respectively. Each male was followed for a total of 24 h during the incubation and 16 h each during the nestling and fledging periods. Overall, 576 hours of radio-monitoring were performed during the study. During the nestling and fledging periods, I adjusted my observations days, so that all monitored males were followed when they had chicks of equivalent age ( $\pm 7$  days). Merlin nestlings were aged using an aging method developed from wild Merlin nestlings (Sodhi, unpubl. data).

Because measuring only the number of feeding trips per unit time gives an incomplete picture of overall foraging effort (Royama 1966), I recorded three dependent variables of the foraging effort. (1) Number of feeding trips per hour for a male during a breeding period was calculated as the number of foraging trips observed divided by the duration of total observation period. (2) Percentage of time flying for each male during a breeding period was calculated as the proportion of time flying in all the foraging trips observed. Merlins attack prey both when in flight and from perches (Sodhi et al. 1991b). However, when sitting, it was not apparent whether Merlins were resting or hunting; therefore, for this variable, I used only flight activity as an index of foraging. The changes in signal amplitude of the radio-transmitter revealed whether a male was sitting or flying. (3) The duration of foraging trips refers to mean duration of all foraging trips made by a male during a breeding period. This and variable one included both flying and sitting time of a foraging male.

Hunting ranges were estimated by using the minimum convex polygon method (Mohr 1947). Minimum convex polygons were calculated for each Merlin by using all radio-locations taken on that bird. Prey abundance in the hunting ranges of males was estimated by making bird counts on 1 km randomly selected transects. I counted all birds (seen or heard) within 90 m on each side of a transect. The transects were surveyed once during each breeding period. For males that were observed for more than one breeding period in the same hunting range, I repeated the transect counts. The bird surveys were made within the first four daylight hours during fair weather ( $< 10\%$  cloud cover,  $< 15$  km/h wind speed). In Saskatoon, Merlins feed almost exclusively on birds weighing less than 100 g (Oliphant and McTaggart 1977, Sodhi et al. 1990). Thus, I only considered birds in this weight class as potential prey species. As predators may adjust their foraging effort based only on the abundance of their main prey (Temeles 1987), I did preliminary analyses comparing Merlin foraging effort variables with the abundance of the House Sparrow (principal prey, which made up about 65% of the kills made during the breeding season; Oliphant and McTaggart 1977, Sodhi et al. 1990). I failed to find any significant correlations and, therefore, did not subdivide the potential prey category for further analysis.

To minimize the chances of nest desertions (Oliphant 1974), the clutch and brood sizes were determined by climbing each nest tree during the early nestling period. The clutch size was taken as the number of hatched young plus unhatched eggs found. As I did not have

any information on the number of eggs and chicks before the nest trees were climbed, my clutch and brood size estimates are minimums. The clutch and brood sizes of the studied males ranged from two to five and one to five, respectively.

Intruder pressure can be derived from two sources, neighbors and non-neighbors (Myers et al. 1979). As Merlins in the study area were not individually color marked, it was not possible to determine if agonistic encounters observed between hunting Merlins involved neighbors or non-neighbors. To compute an index of intruder density, I counted the number of active Merlin nests within 1-km radius of a nest (observed range 0–4), thus restricting my analyses primarily to neighbors. I used active Merlin nests within 1 km of a nest to compute intruder density because hunting ranges among Merlins nesting more than 1 km from each other rarely overlap (Sodhi and Oliphant 1992).

If a male was monitored for more than one breeding period, it was captured and weighed again during the subsequent breeding period (two males were excluded from the nestling period body mass versus foraging effort analyses).

Data from different years were combined because I found no significant difference in the foraging activities (percentage of time flying, number of foraging trips made per hour, and mean duration of foraging trips) of the males during each breeding period among different years (Kruskal-Wallis ANOVA,  $df = 2$ ,  $P > 0.05$ ). Foraging effort variables and proximate factors could not be compared during the fledging period due to lack of adequate sample sizes for correlation analyses.

## RESULTS

During the incubation period, the duration of foraging trips of males declined with an increase in the number of foraging trips per unit time (Kendall rank-order correlation;  $T = -0.55$ ,  $N = 12$ ,  $P = 0.012$ ). In the nestling period, foraging trips were similar ( $T = -0.67$ ,  $N = 13$ ,  $P = 0.014$ ), and, in addition, males flew more in longer foraging trips ( $T = 0.54$ ,  $N = 13$ ,  $P = 0.008$ ).

The mean percentage of time spent flying by males increased from the incubation to fledging periods (Kruskal-Wallis ANOVA,  $KW = 21.72$ ,  $df = 2$ ,  $P = 0.002$ ; Fig. 1A). Of 11 males tracked both during the incubation and nestling periods, all increased the percentage of time flying in the nestling period (Fig. 2A). Of four birds that were followed during both the nestling and fledging periods, three increased and one decreased flying time (Fig. 2A).

The mean number of feeding trips per hour peaked in the nestling period and then declined ( $KW = 12.31$ ,  $df = 2$ ,  $P < 0.01$ ; Fig. 1B). The number of feeding trips increased from the incubation to nestling period for all 11 males (Fig. 2B). All males tracked both during the nestling and fledging periods decreased the number of foraging trips in the fledging period (Fig. 2B). The mean duration of the foraging trips did not differ significantly among the three breeding periods ( $KW = 4.76$ ,  $df = 2$ ,  $P > 0.20$ , Fig. 1C). This foraging variable increased for seven males but decreased for the other four from the incubation to nestling period (Fig. 2C). Two males increased while two decreased the mean duration of their foraging trips from the nestling to fledging period.

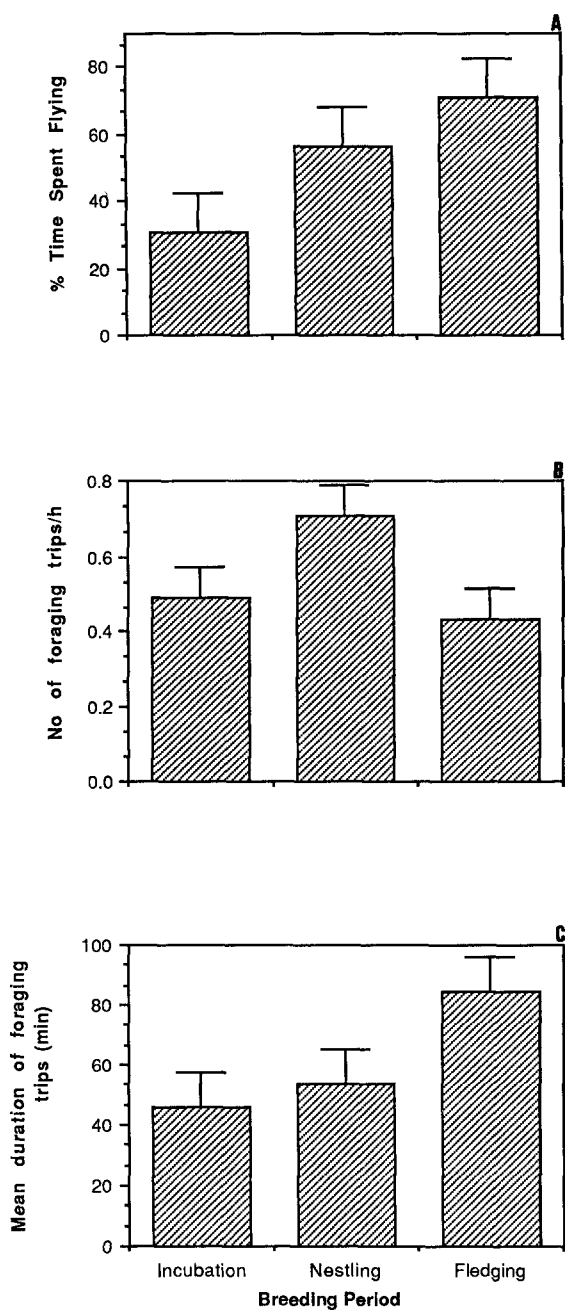


FIG. 1. Foraging effort of male Merlins with the progress of the breeding season. Each bar represents the mean for all males observed during that period (for sample sizes, see Fig. 2). The lines on the bars represent SE.

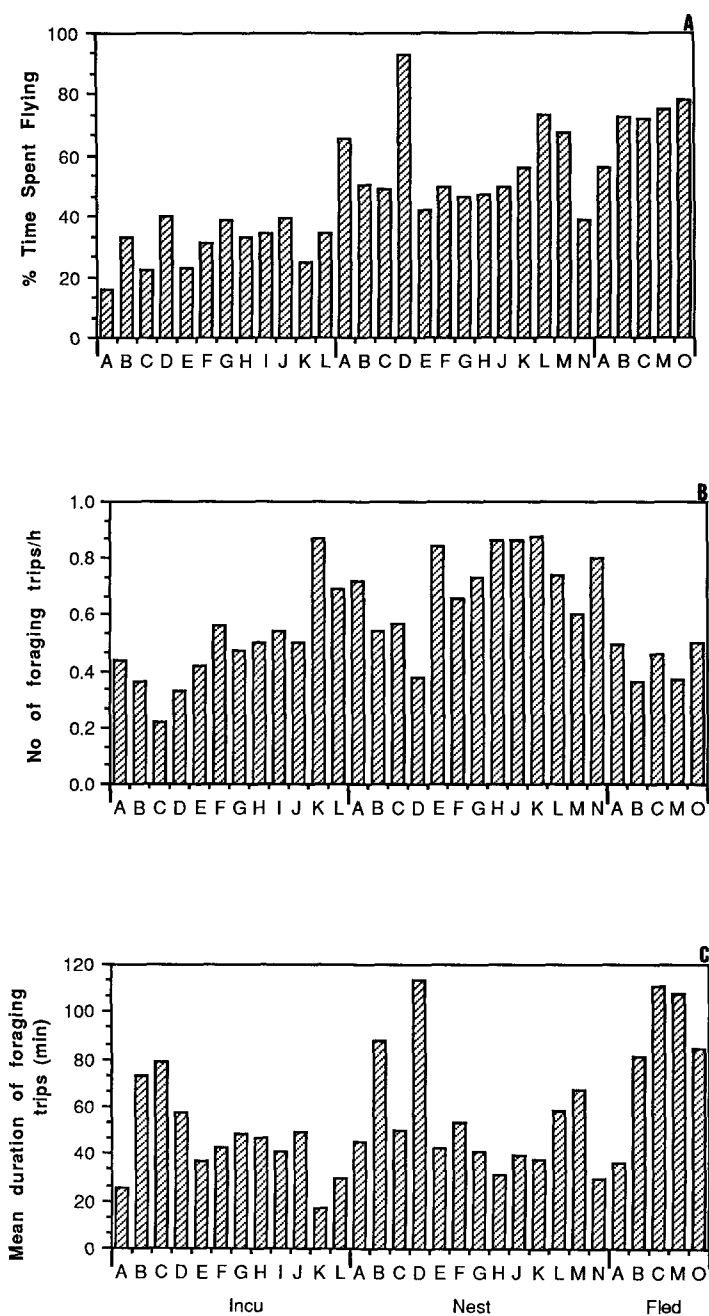


FIG. 2. Foraging effort of individual breeding male Merlins with the progress of the breeding season. Letters represent individual males.

TABLE 1

KENDALL'S PARTIAL RANK ORDER CORRELATION ANALYSES TO DETERMINE THE RELATIVE EFFECT OF DIFFERENT VARIABLES ON FORAGING EFFORT OF MALE MERLINS DURING THE INCUBATION PERIOD<sup>a</sup>

Controlled variable	PTF vs PA (-0.45)		PTF vs RS (0.44)		DFT vs RS (0.54)	
	<i>T</i>	<i>P</i>	<i>T</i>	<i>P</i>	<i>T</i>	<i>P</i>
Clutch size	-0.46	<0.05	0.47	<0.05	0.56	<0.02
No. active nests	-0.40	0.05	0.47	<0.05	0.58	<0.02
Body mass	-0.46	<0.05	0.40	0.05	0.51	<0.02
Time spent incubating	-0.48	<0.05	0.51	<0.05	0.55	<0.02

<sup>a</sup> DFT = duration of foraging trips, PA = prey abundance, PTF = percentage of time spent flying, and RS = hunting range size.

During the incubation period (1) with higher potential prey abundance, the percentage of time flying declined ( $T = -0.45$ ,  $N = 12$ ,  $P = 0.02$ ), (2) with increase in range size the percentage of time flying increased ( $T = 0.44$ ,  $P = 0.04$ ), and (3) with increase in range size the duration of foraging trips increased ( $T = 0.54$ ,  $P = 0.016$ ). I performed Kendall's partial correlation analyses (Siegel and Castellan 1988:254-262) to determine the relative effects of different proximate variables (i.e., clutch size, prey abundance, body mass, intruder density, hunting range size, and time allocated to incubation) on foraging effort of males. If total prey abundance and range size had an independent effect on foraging effort of males, I expected the above correlations to remain significant when other studied variables were controlled statistically. The partial correlation analyses showed that prey abundance and range size significantly correlated with the foraging effort independently of other studied variables (Table 1).

During the nestling period, with the increase in brood size the percentage of time flying increased ( $T = 0.44$ ,  $N = 13$ ,  $P = 0.04$ ), and with the increase in the number of active nests within a 1-km radius (intruder density) the number of feeding trips declined ( $T = -0.43$ ,  $N = 13$ ,  $P = 0.04$ ). These correlations remained significant when other variables were controlled statistically (Table 2).

#### DISCUSSION

Considerable literature exists on the foraging effort of raptors during the breeding season (e.g., Green 1976, Picozzi 1978, Stinson et al. 1987, Holthuijzen 1990). Many of these studies show an increase in foraging effort (largely determined by prey delivery rates) with the progress of the breeding cycle. Male Merlins significantly increased percentage of time

TABLE 2

KENDALL'S PARTIAL RANK-ORDER CORRELATION ANALYSES TO DETERMINE THE RELATIVE EFFECT OF DIFFERENT VARIABLES ON FORAGING EFFORT OF MALE MERLINS DURING THE NESTLING PERIOD<sup>a</sup>

Controlled variable	PTF vs BS (0.44)		NFT vs AN (-0.43)	
	<i>T</i>	<i>P</i>	<i>T</i>	<i>P</i>
Brood size	—		-0.43	<0.05
No. of active nests	0.47	<0.02	—	
Prey abundance	0.49	<0.02	-0.51	<0.02
Body mass	0.42	<0.05	-0.46	<0.05
Range size	0.45	<0.02	-0.44	<0.02

<sup>a</sup> AN = number of active Merlin nests, BS = brood size, NFT = number of feeding trips made per hour, and PTF = percentage of time spent flying.

flying while presumably foraging with the progress of the breeding season. Eurasian Kestrels (*F. tinnunculus*), however, did not increase their hunting flight activity with the progress of the breeding season (Masman et al. 1988).

Geer (1981) documents that male Eurasian Sparrowhawks (*Accipiter nisus*) decrease prey delivery rates at the nest as females increase such deliveries during the nestling period. Male Merlins increased the number of foraging trips per hour from the incubation to nestling period and decreased such trips when females started supplementing food at nests.

An increase in the foraging effort with increasing brood size (e.g., Collopy 1984, Poole 1988, Holthuijzen 1990) or no such increase (e.g., Snyder and Snyder 1973, Simmons 1986, Stinson et al. 1987) are reported. I found that male Merlins with large broods spent proportionally more time flying than males with small broods, suggesting that male Merlins adjust their flying time in response to the nestling number. During the nestling period, males also tended to make fewer foraging trips if the number of other active Merlin nests near the vicinity of their nests was high. Perhaps during this period, higher intruder density suppresses the number of foraging trips a male can make or high food abundance in such areas causes this trend.

Male Bobolinks (*Dolichonyx oryzivorus*) increase nestling feeding rates when food is scarce (Wittenberger 1982). On the contrary, breeding House Martins (*Delichon urbica*) forage more intensively when food is more abundant (Bryant and Westerterp 1983). Male Merlins with high prey abundance on their ranges spent less time flying than males with low prey abundance on their ranges.

My data also showed individual differences in the foraging effort among

males (Fig. 2). This indicates individual differences in hunting efficiency (e.g., McKean 1990), current reproductive effort, or variation in prey abundance in ranges. During the fledging period, these differences may result from differences in foraging effort of their mates. Smith et al. (1989) show that male Pied Flycatchers (*Ficedula hypoleuca*) reduce incubation feeding of the females that are supplemented with food. Therefore, male Merlins could probably adjust their foraging effort depending upon the rate of feeding to the fledglings by their mates.

I found no significant influence of body mass, clutch size, or time allocated to incubation on foraging effort of male Merlins. Bryant and Westerterp (1983) reports that House Martins reduce the nestling feeding rate with a deterioration in body mass.

In summary, foraging of breeding male Merlins is affected by the phase of the breeding cycle, prey abundance, hunting range size, brood size, and intruder density. However, I found seasonal differences in the effect of these factors on foraging of male Merlins. For example, prey abundance influenced the foraging effort in the incubation period but not during the nestling period. This suggests that variables affecting foraging effort of male Merlins are not fixed over the breeding season.

#### ACKNOWLEDGMENTS

I thank F. Messier, R. G. Clark, R. J. F. Smith, L. W. Oliphant, B. R. Neal, D. A. Boag, C. R. Blem, and three anonymous reviewers for commenting on the manuscript. I am also grateful to G. Peat, J. Freeland, and C. Sodhi for field assistance. This study was supported by a Natural Sciences and Engineering Research Council of Canada grant to L. W. Oliphant and a Univ. of Saskatchewan graduate scholarship to the author.

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