

FORAGING ECOLOGY OF URBAN-BREEDING

MERLINS (FALCO COLUMBARIUS)

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ABSTRACT

I studied the foraging ecology of breeding Merlins (Falco columbarius) in Saskatoon (Canada) from May to July, 1987-90. I identified 1332 prey items belonging to 36 vertebrate species from prey remains collected near 65 Merlin nests. The principal prey of breeding Merlins was the House Sparrow (Passer domesticus), which along with the Horned Lark (Eremophila alpestris) were usually taken more frequently than expected from their relative abundance in the environment. Other potential prey species were usually taken in proportion to, or less than expected.

The proportion of adult House Sparrows in the diet decreased while that of juveniles increased significantly as the Merlin breeding season progressed. During the incubation and nestling periods, the relative abundance of male and female House Sparrows did not differ significantly from rates at which they were consumed. In the fledging period, based on relative abundances, adult House Sparrows were taken less often than expected while juveniles were eaten more often than expected by Merlins.

Twenty-seven Merlins were radio-tracked. Mean hunting range sizes of resident (hatched in the city) and immigrant (presumed to have hatched outside the city) males were 6.3 ± 1.3 (SE) km^2 and 33.7 ± 12.1 km^2 , respectively. Mean hunting range sizes of resident and immigrant females were 6.6 ± 3.4 km^2 and 8.6 ± 1.6 km^2 , respectively. Merlins

that hunted exclusively in the city used all habitats in proportion to availability. Merlins that hunted both in and outside the city usually avoided hunting in agricultural areas, which were relatively low in prey abundance.

During the incubation and nestling periods, males with more prey birds in their ranges had significantly smaller hunting ranges. Male Merlins with more prey birds in their ranges spent relatively less time hunting and males with larger broods spent more time hunting compared to those with smaller broods. For female Merlins, hunting range sizes were inversely correlated with both body mass and House Sparrow abundance.

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1. GENERAL INTRODUCTION

Animals should evolve strategies that maximize their life-time reproductive success. Foraging models have been developed (Emlen 1966, MacArthur and Pianka 1966, Pulliam 1974) to predict how animals should feed in order to maximize survival and life-time reproductive success. An organism that makes optimal foraging choices (the most effective or efficient compared to alternatives), is assumed to maximize its fitness (Schoener 1987a).

Field studies of foraging are particularly valuable because animals have evolved in complex environments which may be difficult to replicate in the laboratory (Zach and Smith 1981). To understand properly the foraging ecology of a species, however, comprehensive data are needed. Lack of studies to produce such data will limit identification of pivotal foraging variables (Kamil and Sargent 1981, Tinbergen 1981), thus making foraging models poor mimics of nature.

I made a comprehensive study of the foraging ecology of free-ranging breeding Merlins (Falco columbarius) in an urban environment. I studied their diet, prey selection, habitat requirements, hunting ranges, and factors affecting foraging and range sizes. I tested hypotheses of foraging theory, where possible, and anticipated that the study would generate hypotheses for future foraging studies.

Merlins were suitable for this study because: 1) their diet can be estimated without sacrificing or disturbing individuals (e.g., Newton et al. 1984), 2) they feed mainly on birds making the assessment of their prey abundance relatively easy compared to other birds (Zach and Smith 1981), and 3) they can be radio-tagged (Becker and Sieg 1987, Warkentin and Oliphant 1990), which facilitates the assessment of their hunting ranges and habitat requirements.

Previously, Becker (1984) reported the diet, hunting range sizes, and habitat selection of rural-breeding Merlins from Montana. There are many reports of the breeding season diet of this species from various regions of the World (Sperber and Sperber 1963, Bengston 1975, Oliphant and McTaggart 1977, Hodson 1978, Newton et al. 1978, 1984, Watson 1979, Laing 1985, Bibby 1987, James and Smith 1987, Meek 1988, Ellis and Okill 1990). Baker and Bibby (1987) compared the relative abundance of prey birds in habitats frequented by breeding Merlins with the relative prey consumption of breeding Merlins. They concluded that Merlins took bird species in the order of their relative abundances, i.e., they are non-selective bird predators. A few other workers have studied the hunting behaviour of this species during the breeding season (Armitage 1932, Craighead and Craighead 1940, Lawrence 1949, Roberts 1962, Kermott 1981, Sodhi et al. 1991).

In summary, prior to my study we knew that breeding Merlins feed mainly on small birds and prey species likely are taken from the prey population based on their relative abundances. Usually Merlins attack prey from perches or while flying. Merlins have overlapping hunting ranges in a rural habitat where some hunting habitats are used preferentially.

I report data on prey use and selection in Chapter 2. The objective of this research was to determine the diet and to evaluate hypotheses regarding prey selection. In Chapter 3, I document hunting range characteristics (sizes and overlaps), and patterns of habitat use and selection by Merlins. I attempt to determine factors which may influence hunting range size of breeding Merlins in Chapter 4. To determine the foraging strategy of breeding Merlins, I examine the factors which may effect their foraging effort in Chapter 5. To conclude (Chapter 6), I discuss the research study as a whole.

As most of my data were collected by radio-tagging Merlins, I also evaluate the possible influences of this technique on Merlins (Appendix B).

2. PREY USE AND SELECTION BY URBAN BREEDING MERLINS

2.1 Introduction

Studies of prey selection in carnivorous predators have concluded either that predators take prey according to their relative abundances (e.g., Jaksic et al. 1981, Nilsson 1981, Turner 1982, Village 1982a), or that predators take prey based presumably on relative profitabilities rather than relative abundances (e.g., Korpimaki 1985, Hunter et al. 1988, Steenhof and Kochert 1988, Canova 1989, Derting and Cranford 1989, Bochencki 1990, Brigham 1990). Predators following the former strategy are referred to as opportunistic feeders while those following the latter are known as selective feeders (Jaksic 1989). Studies that examined the species-level of prey selectivity usually considered only one prey characteristic, i.e. prey abundance. Further, few data are available on sex, age, and size selectivity by carnivorous predators.

The Merlin (Falco columbarius) is one of the smallest Holarctic falcons. There are many reports of the diet of breeding Merlins from North America, both from urban and rural habitats (Oliphant and McTaggart 1977, Hodson 1978, Becker 1985, Knapton and Sanderson 1985, Laing 1985, James and Smith 1987). These studies, however, all suffered from either a small sample of Merlin nests or a sporadic collection schedule. More detailed documentation of the

diet of breeding Merlins comes from Britain (Newton et al. 1984, Bibby 1987). The only study of prey selection in this species has been by Baker and Bibby (1987), who compared the relative abundance of bird species in habitats frequented by Merlins (based on questionnaires sent to ornithologists) with the relative consumption of those species. They concluded that breeding Merlins took birds in the order of their relative abundance. However, as Baker and Bibby (1987) did not make actual bird counts, there is a possibility of errors in their analysis.

My objectives were to: 1) describe quantitatively the diet of urban-breeding Merlins based on systematic collection of prey remains; 2) examine whether Merlins show prey selectivity according to sex and age of their primary prey, i.e. House Sparrow (scientific names of prey species in Table 2.1); and 3) test the null hypothesis that Merlins would take prey species according to the relative abundance of each prey species in nature. The alternative hypothesis relates to a classical optimal foraging model, which states that a predator should take prey species in relation to their relative profitabilities (i.e., to maximize net energy intake) rather than their relative abundance in the environment (Emlen 1966, Pulliam 1974). According to this hypothesis, I predict that Merlins would not take prey species in accordance to their relative abundance.

In addition, I attempt to determine whether the

relative numbers of different species outside cover influence their relative vulnerability to predation. Tinbergen (1946) postulated, and later Newton (1986) reiterated, that the association of different prey species with cover may be critical in determining their relative vulnerabilities to predation. In other words, relative species vulnerabilities depend upon the relative number of individuals of different species outside cover. I also test whether Merlins select prey based only on exposure (number outside cover), independent of relative prey abundance and prey weight.

Finally, I examine two qualitative predictions of the prey model (sensu optimal diet model) of foraging theory, tested in previous studies of other animals (e.g., Schluter 1981, Steenhof and Kochert 1988; other references in Stephens and Krebs 1986). This model predicts that when prey abundance is high, a predator should feed only on more profitable prey species, but when prey abundance declines, it should include a wider variety of prey species in its diet. Put simply, a predator feeds more selectively when encounters with profitable prey species are frequent (Stephens and Krebs 1986). Second, consumption of different prey species should not be dependent upon their abundance, but on absolute abundance of the most profitable prey. According to this prediction, I should observe an inverse relationship between absolute abundance of the most

profitable prey species and diet diversity.

2.2 Methods

2.2.1 Study Area

The study was conducted in Saskatoon, Saskatchewan, Canada (52° 07'N, 106° 38'W). Saskatoon, a city of about 122 km² with human population of approximately 185,000, is situated at 500 m above sea level. The city is bisected by the South Saskatchewan River; the uninhabited river banks have retained native shrubs and trees, viz. chokecherry (Prunus virginianus), pincherry (P. pennsylvanicus), Saskatoon berry (Amelanchier alnifolia), silverberry (Elaeagnus commutata), white birch (Betula papyrifera), and trembling aspen (Populus tremuloides). With urban development, many introduced species were planted in neighbourhoods. The trees in Merlin nesting areas include: white elm (Ulmus americana), Manitoba maple (Acer negundo), balsam poplar (Populus balsamifera), weeping birch (B. pendula), green ash (Fraxinus pennsylvanicus), mountain ash (Sorbus sp.), white spruce (Picea glauca), and blue spruce (P. pungens). The average temperature during the Merlin breeding season (April-July) in Saskatoon usually ranges from 5.5 °C in April to 18.8 °C in July. The total monthly precipitation usually ranges from 20.4 mm in April to a maximum of 53.1 mm in June.

2.2.2 Methods

Prey remains consisting of feathers, feet, mandibles, and heads were collected near 65 Merlin nests between May and July, 1987-1990. Fourteen, 18, 16, and 17 nests were surveyed once a week during 1987, 1988, 1989, and 1990, respectively. Prey remains were identified by comparison with a museum skin collection in the Department of Biology, University of Saskatchewan. Less than 1% of bird remains could not be identified and were discarded in this analysis. House Sparrow heads were identified by sex and age following Robbins et al. (1983) and Nero (1951).

The minimum number of individuals of each species was determined by counting the most frequently occurring body part in each collection. Biomass of each prey species was computed by using average weights reported by Dunning (1984) or those obtained from the museum-skin collection. When average weights of a species differed between sexes, calculations were made using the mean of sex-specific averages. Following Newton and Marquiss (1982), juvenile weights were arbitrarily assumed to be two-thirds of the adult weight.

I present three analyses of the food data: relative frequency of prey species (in percentage number or numerical analysis), biomass of prey by species, and the mean percentage of a species observed at individual nests. The relative frequencies of prey species give equal weight to

each prey species consumed while the mean percentage of occurrence of a species gives equal weight to each nest investigated (Swanson et al. 1974).

To assess prey abundance, bird counts were made on 12 randomly selected 1-km transects once a month, from May to July, 1988-1990. Because Merlins feed both in and outside the city (Chapter 3), six transects were in each of these feeding areas. Rural transects were selected from areas visited by radio-tagged Merlins during the breeding season. Birds encountered (seen or heard) within 90 m on both sides of the transects were recorded. On average, city transects were completed in 12.5 ± 1.6 (SD) and rural transects in 12.7 ± 2.1 minutes. All censuses were made in fair weather (<10% cloud cover; <15 km/h wind speed) and within the first 4 hours of daylight. To maintain consistency, each year, bird counts were made in the last 10 days of each month.

I weighted the data on prey abundance by the time spent by hunting Merlins in and outside the city. The time spent by Merlins in each habitat was determined from radio-tracked birds during that year (for sample sizes, see Chapter 3). Dietary analyses showed that Merlins rarely took bird species weighing more than 100 g. Therefore, to calculate potential prey abundance, I only considered bird species with a body mass of less than 100 g (Appendix A).

To test for diet selectivity, relative prey abundance and consumption were compared using Bonferroni's Z-tests if

a significant difference between the two was found using the chi-square test (Neu et al. 1974, Byers et al. 1984). When the expected proportion of prey use was outside of the confidence interval computed by the Bonferroni Z-test, the difference between the expected and observed was considered significant. Throughout the text, I refer to a species being avoided when eaten less often than expected (based on bird counts) and selected when eaten more often than expected at a probability level of 0.05.

Reliability of these transect counts was determined by comparing my bird censuses with those made by two independent observers. Both these observers initiated bird counts during the first 4 hours of daylight in fair weather, 10 minutes after me. Observer A and I made transect counts in July 1989 on 12 1-km transects in the city. On average, it took me and observer A, 11.5 ± 0.9 (SD) and 12.3 ± 0.9 minutes, respectively, to complete a transect. Of 10 potential prey species (<100 g) recorded by both of us, no significant difference in the relative abundance was observed ($\chi^2 = 5.7$, $df = 9$, $P > 0.70$). At low frequency, I recorded two more potential prey species than observer A. Observer B and I made transect counts on six 1-km urban transects in July 1990. On average, it took me and observer B, 10.8 ± 0.7 and 11.5 ± 1.0 minutes, respectively, to complete a survey on a transect. Of eight common potential prey species recorded by both of us, the relative abundances

did not differ significantly ($\chi^2 = 12.4$, $df = 7$, $P > 0.10$). At low frequency, each of us registered one prey species different from the other.

To determine the relative vulnerability of different potential prey species, surveys were made on 12 1-km transects (six urban, six rural; 30 m on both sides were surveyed on each transect) once each month, May-July 1988. Birds were recorded as being in cover (in trees, shrubs, and under low vegetation) or outside cover (on pole, shrub, fence, and roof tops, periphery of trees and shrubs, flying, and perched outside cover). Like bird abundance transects, all surveys were made in fair weather and within the first 4 hours of daylight. Surveys on each transect took 40 minutes (this time was determined by surveying 6 such preliminary transects in April 1988). I assumed that individual birds outside cover were more vulnerable to predation (Pulliam and Mills 1977, Lima 1990, Watts 1990, Sodhi 1991a). This assumption was supported by radio-tracking data which showed that, of 73 observed Merlin hunting attempts, only two were on birds in cover ($\chi^2 = 20.1$, $df = 1$, $P < 0.001$; expected frequencies for this test were obtained using exposure count data).

The relative abundance of different species out of cover was compared with that in the diet using Kendall's rank-order correlation coefficient (Siegel and Castellan 1988:245-254). For this analysis, I collected sufficient

data from exposure transect counts (>10 individuals/ breeding period) for nine bird species (House Sparrow, American Robin, Clay-colored Sparrow, Chipping Sparrow, Yellow Warbler, Western Meadowlark, Horned Lark, Savannah Sparrow, and Brewer's Blackbird). To assess whether Merlins select prey based on the relative prey exposure, independent of relative abundance and prey weight, I used Kendall's partial rank-order correlation analysis (Siegel and Castellan 1988:254-262).

In 1990 (May-July), once every 15 days, six 1-km urban transects were surveyed to determine the age and sex structure of the House Sparrow population. Twenty-five minutes (determined by preliminary surveys of two transects in May 1990) were spent surveying 30 m on both sides of each transect during the first 4 hours of daylight in fair weather. Individual House Sparrows were identified as males, females, or juveniles, and whether in or outside cover. The juvenile category was identified as having yellowish hinges on their beaks, yellowish legs and plumage (Summers-Smith 1963). The juveniles exhibit these characters up to 4-6 weeks after fledging, after which they are difficult to distinguish from the adult females (Summers-Smith 1963). In Saskatoon, House Sparrows start fledging from mid-May, but fledging peaks in early-June and then in late-July (P.C. James, pers. comm.). This suggests that the proportion of females in the House Sparrow

population recorded during the nestling and fledging period of the Merlin may be slightly inflated because some older juveniles may have been misidentified as females.

All birds encountered on the bird abundance transects were categorized into 11 weight classes and the relative abundance and consumption of these species were compared using the Bonferroni Z-tests to determine prey size selection.

Diet diversity was calculated using the formula (Levins 1968): $1 / \sum p_i^2$ where p_i is the proportion of prey i in the diet. Values of this index range from $\frac{1}{n}$ to 1 ($\frac{1}{n}$ for equally used resources; see Levins 1968:43). As recommended by Greene and Jaksic (1983), I used species-level of prey identification to compute this index.

I arrange most data as a function of the three breeding periods : incubation, nestling, and fledging. For each Merlin nest, these breeding periods were determined by subjectively aging the chicks and assuming: an egg-laying interval of two days (Palmer 1988); incubation starting one day prior to laying of the last egg (Ruttledge 1985); synchronous hatching (Cramp and Simmons 1980, Ruttledge 1985, Palmer 1988); and young fledging at 29 days of age (Becker and Sieg 1985, Oliphant and Tessaro 1985). During the fledging period, young are out of the nest, but they remain near the nest and are fed by both parents.

2.3 Results

2.3.1 Diet

Overall, 1332 prey items of 36 vertebrate species were identified (Table 2.1). Over 99% of prey were birds and the remainder were mammals. The House Sparrow was the principal prey, accounting for about 64% of kills and 55% of ingested biomass. I encountered House Sparrow remains at all the studied nests, the percentage ranging from 10 to 93% of total prey remains. The second most important prey species was the Horned Lark, which made up about 9% of the diet both by number and biomass. About 68% of the sampled nests had at least one individual of the Horned Lark and the percentage of this species at these nests ranged from 3 to 69%. These two birds species consistently represented the most important prey both within and among years, although their proportions differed. There were three periods when Horned Lark was not the second most important prey species (1987-fledging, 1988-incubation, and 1990- nestling).

The numbers of the three most common prey species (House Sparrow, Horned Lark, and American Robin) did not differ significantly within the three periods of the breeding season in 1989 ($\chi^2 = 4.8$, $df = 4$, $P > 0.30$), but did so in 1987 ($\chi^2 = 32.2$, $df = 4$, $P < 0.001$), 1988 ($\chi^2 = 14.6$, $df = 4$, $P < 0.01$), and 1990 ($\chi^2 = 19.9$, $df = 4$, $P < 0.001$) (Table 2.2).

Table 2.1. Diet of breeding Merlins in Saskatoon, 1987-1990. Data were based on identification of prey remains collected near 65 nests. % No = relative frequency of prey species, % mean no = mean percentage of a species observed at individual nests, and % Biomass = percent biomass by species.

Prey species	No. of individuals				% No	% Mean	% Biomass
	87	88	89	90			
House Sparrow							
(<u>Passer domesticus</u>)	254	268	164	174	64.5	60.2	55.5
Horned Lark							
(<u>Eremophila alpestris</u>)	33	23	38	27	9.1	11.4	8.8
American Robin							
(<u>Turdus migratorius</u>)	18	12	13	15	4.3	4.2	10.5
Swainson's Thrush							
(<u>Catharus ustulatus</u>)	9	14	13	14	3.7	4.4	3.6
Cedar Waxwing							
(<u>Bombycilla cedrorum</u>)	12	2	6	15	2.6	2.7	2.6
Chipping Sparrow							
(<u>Spizella passerina</u>)	6	4	8	11	2.2	2.3	0.9

Yellow Warbler

(<u>Dendroica petechia</u>)	6	4	9	7	1.9	1.9	0.6
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Snow Bunting

(<u>Plectrophenax nivalis</u>)	3	10	5	1	1.4	1.6	1.9
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Brewer's Blackbird

(<u>Euphagus cyanocephalus</u>)	5	8	3	3	1.4	1.1	2.8
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Bohemian Waxwing

(<u>B. garrulus</u>)	5	5	5	3	1.3	1.3	2.4
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Clay-colored Sparrow

(<u>S. pallida</u>)	5	2	1	4	0.9	0.9	0.2
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White-throated Sparrow

(<u>Zonotrichia albicollis</u>)	1	2	3	3	0.7	0.7	0.5
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Hermit Thrush

(<u>C. guttatus</u>)	2	3	1	3	0.6	0.6	0.6
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Little Brown Bat

(<u>Myotis lucifugus</u>)	0	0	0	7	0.5	0.4	0.2
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Others*

	19	13	12	16	4.9	-	8.9
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* Less than 0.5% of the total including 5 Savannah Sparrows (Passerculus sandwichensis), 5 Dark-eyed Juncos (Junco hyemalis), 5 Black-capped Chickadees (Parus atricapillus), 4 Least Flycatchers (Empidonax minimus), 4 Rock Dove juveniles (Columbia livia), 4 Lapland Longspurs (Calcarius lapponicus), 4 Mountain Bluebirds (Sialia currucoides), 3 Song Sparrows (Melospiza melodia), 3 Western Kingbirds (Tyrannus verticalis), 3 Hairy Woodpeckers (Picoides

villosus), 3 Richardson's Ground Squirrels (Spermophilus
tricolor), 2 Barn Swallows (Hirundo rustica), 2 House Wrens
(Troglodytes aedon), 2 Killdeers (Charadrius vociferus), 2
Yellow-rumped Warblers (D. coronata), 2 Blue Jays
(Cyanocitta cristata), 2 White-crowned Sparrows (Z.
leucophrys), 1 Common Starling (Sturnus vulgaris), 1 Yellow-
bellied Sapsucker (Sphyrapicus varius), 1 Red-necked
Phalarope (Phalaropus lobatus), 1 Pine Siskin (Carduelis
pinus), and 1 Western Meadowlark (Sturnella neglecta).

Table 2.2. Number of individuals of the three most important prey species eaten by Merlins in different years and breeding periods. I = incubation, N = nestling, and F = fledging period. Each year, four collection trips per nest were made during the incubation and nestling periods, whereas only three such trips were made during the fledging period. Therefore, to adjust for this, I increased the number of individuals of a species by 33% during the fledging period.

	87			88			89			90		
Species	I	N	F	I	N	F	I	N	F	I	N	F
House Sparrow	77	115	82	86	119	84	45	72	62	31	67	101
Horned Lark	20	12	1	11	5	9	16	12	13	15	5	9
American Robin	14	2	3	9	2	1	6	4	4	3	5	9

2.3.2 Sex and Age Selection

More male than female House Sparrows were taken by Merlins ($\chi^2 = 14.8$, $df = 1$, $P < 0.001$; Table 2.3). I could also separate sexes based on plumage colour or pattern for two other prey species, and found that Merlins took more male Brewer's Blackbirds ($\chi^2 = 10.2$, $df = 1$, $P < 0.01$; males = 17, females = 2), but more female Yellow Warblers ($\chi^2 = 9.0$, $df = 1$, $P < 0.01$; males = 2, females = 16) than expected were eaten (assuming in each case that males and females were equally abundant in the environment).

The proportion of male and female House Sparrows in the diet decreased while that of juveniles increased with the progress of the Merlin breeding season ($\chi^2 = 77.6$, $df = 4$, $P < 0.001$; Table 2.3). The relative number of exposed adults in the House Sparrow population decreased while that of juveniles increased with the advancement of the breeding season (Fig. 2.1). The relative abundance and consumption of different House Sparrow categories (male, female, and juvenile) did not differ significantly during the incubation ($\chi^2 = 0.02$, $df = 1$, $P > 0.80$) and nestling periods ($\chi^2 = 5.6$, $df = 2$, $0.05 < P < 0.10$), but did differ during the fledging period ($\chi^2 = 9.4$, $df = 2$, $P < 0.01$). By performing Bonferroni's Z-tests on the latter data, I found that both males and females were avoided, but juveniles were selected (Fig. 2.2).

Table 2.3. Different age and sex categories of House Sparrows eaten by Merlins during different breeding periods (1987-1990)^a. Numbers of male, female, and juvenile House Sparrows were adjusted for the fledging period (see Table 2.2).

Breeding period	Males	Females	Juveniles
Incubation	57	29	12
Nestling	62	43	74
Fledging	29	16	102

^aSame trend was observed in different years, therefore data were lumped.

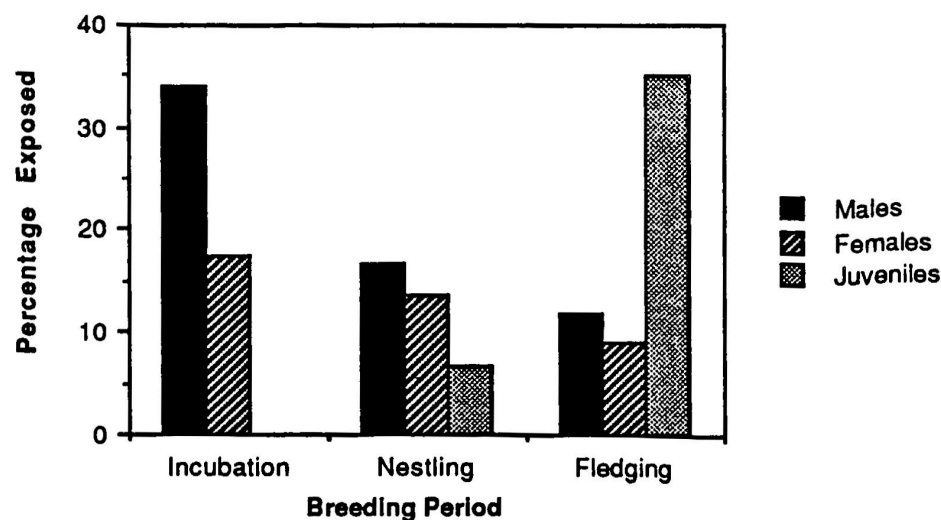


Figure 2.1. Relative abundance (%) of male, female, and juvenile House Sparrows out of cover (exposed) during different breeding periods of Merlins in Saskatoon during 1990. Sample sizes: incubation (Total: males = 153, females = 85; Exposed: males = 81, females = 42), nestling (Total: males = 97, females = 59, juveniles = 56; Exposed: males = 36, females = 29, juveniles = 14), and fledging (Total: males = 61, females = 45, juveniles = 189; Exposed: males = 35, females = 27, juveniles = 104).

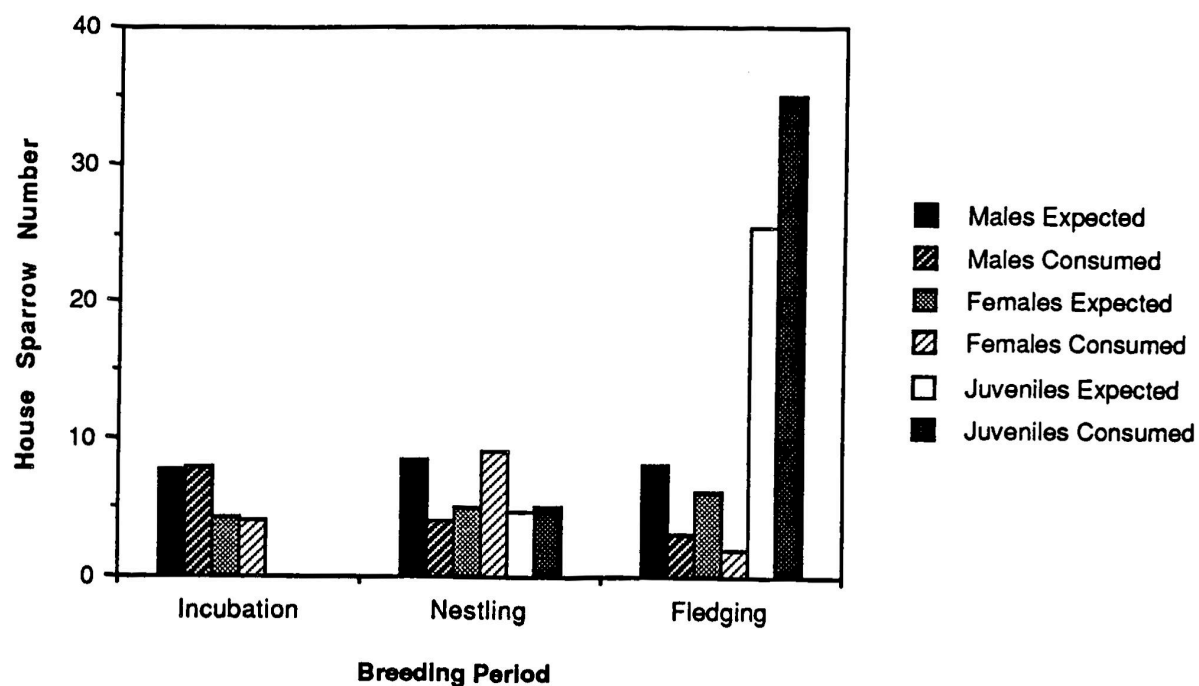


Figure 2.2. Comparison between expected and consumed number of male, female, and juvenile House Sparrows during different breeding periods of Merlin in Saskatoon during 1990. Comparison was made using chi-square tests, which was only significant during the fledging period. During this period, Bonferroni Z-tests revealed that males and females were significantly avoided while juveniles were selected ($P < 0.05$).

2.3.3. Prey Abundance and Selection

The relative abundance and consumption of prey species differed significantly in all three breeding periods of all years (Chi-square tests, $df = 1$ to 4 , $P < 0.05$ to < 0.01). Numerically, only three species were selected, Horned Lark 7 times, House Sparrow 4, and Cedar Waxwing 1 time out of 9 (three years x three breeding periods) (Table 2.4).

For testing qualitative predictions of the prey model, I performed correlations between the total prey abundance, and absolute abundance(s) of all selected prey (Table 2.4) during a particular breeding period with diet diversity. The only significant correlation showed an inverse relationship between the absolute abundance (s) of selected (most profitable) prey species and diet diversity ($r_s = -0.63$, $n = 9$, $P = 0.04$; one-tailed).

2.3.4. Prey Size Selection

Merlins usually selected prey that weighed between 21-40 g (Table 2.5). The species in this category that occur in Saskatoon and surrounding areas include: House Sparrow, Horned Lark, Vesper Sparrow, Swainson's Thrush, Red crossbill, and Northern Oriole.

2.3.5. Prey Exposure and Selection

I found a significant positive correlation between the relative prey exposure and consumption during the incubation

Table 2.4. Prey selection (by number killed) by breeding Merlins in Saskatoon. When a species was encountered in the diet as well as in bird counts, data were analysed using Bonferroni Z-test. S = selected, A = avoided, E = eaten in proportion to abundance, NE = encountered on the transects but not eaten, NA = not encountered on the transects, and NAE = not encountered on the transects but eaten. When S or A, $P < 0.05$. I = incubation, N = nestling, and F = fledging. *These data were not analysed statistically because of expected frequencies of < 5 in $> 20\%$ of cells.

Prey species	88			89			90		
	I	N	F	I	N	F	I	N	F
House Sparrow	E	S	S	A	E	E	A	S	S
Chipping Sparrow	A	A	A	E*	A	A	A	A	A
American Robin	E	A	A*	A	E	E	A	E	E
Cedar Waxwing	NA	E*	NE	NAE	A	NE	S*	E	NE
Yellow Warbler	A	A	E*	NAE	E*	A*	A*	E	NE
Red-winged Blackbird ¹	NA	NA	NA	NA	NA	NE	NE	NE	NE
Black-capped Chickadee	NE	E*	E*	NE	NAE	NE	NAE	NA	NE
White-throated Sparrow	E	NA	NA	NAE	NAE	NA	E*	NA	NE
House Wren	NE	NE	NA	NE	NE	A*	NE	NE	NE
Western Meadowlark	NE	NE	NE	NE	NE	NE	A*	NE	NE
Savannah Sparrow	E	NE	NE	NE	NE	NE	E*	NE	NE

Horned Lark	S	E*	S*	S*	S*	S*	S*	E	S
Vesper Sparrow ²	NE	NE	NE	NA	NA	NA	NE	NA	NE
Brewer's Blackbird	E	E*	E*	NE	NE	E*	NE	E	A
Clay-colored Sparrow	A	NE	NE	NE	A*	NE	E*	NE	E
Red-eyed Vireo ³	NE	NA	NA	NA	NA	NA	NA	NE	NA
Swainson's Thrush	NAE	NAE	NA	NAE	E	NA	NAE	E	NA
Killdeer	NA	NA	NA	NA	NAE	NA	NA	NE	NA
Red Crossbill ⁴	NA	NA	NA	NA	NA	NA	NE	NA	NA
American Goldfinch ⁵	NA	NA	NA	NA	NE	NA	NA	NA	NA
Hairy Woodpecker	NA	NA	NA	NAE	NE	NA	NA	NA	NA
Tree Swallow ⁶	NE	NE	NA	NA	NA	NA	NA	NA	NA
Brown Thrasher ⁷	NA	NE	NA	NA	NA	NA	NA	NA	NA
Red-breasted Nuthatch ⁸	NE	NA	NA	NA	NA	NA	NA	NA	NA
Northern Oriole ⁹	NE	NA	NA	NA	NA	NA	NA	NA	NA
Barn Swallow	NE	NA	NA	NA	NAE	NAE	NAE	NA	NAE

No of prey

consumed	159	136	75	107	108	67	110	97	96
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¹Agelaius phoeniceus, ²Pooecetes gramineus, ³Vireo

olivaceus, ⁴Loxia curvirostra, ⁵Carduelis tristis,

⁶Tachycineta bicolor, ⁷Toxostoma rufum, ⁸Sitta canadensis,

and ⁹Icterus galbula.

Table 2.6. Kendall's partial rank-order coefficients between the relative prey exposure and relative consumption (simple correlation), and controlling either the relative abundance of prey in the environment or prey weight. Simple correlations are based on one-tailed and partial correlations on two-tailed tests.

Period	<u>n</u>	Simple Correlation	Controlling for rel. abu	Controlling for weight
Incubation	7	0.72, <u>P</u> = 0.01	0.39, <u>P</u> > 0.20	0.69, <u>P</u> < 0.05
Nestling	6	0.83, <u>P</u> = 0.01	0.43, <u>P</u> > 0.20	0.85, <u>P</u> < 0.02

and nestling periods (Table 2.6), but not during the fledging period ($T = 0.43$, $n = 6$, $p = 0.11$; one-tailed). Further, to evaluate whether Merlins select prey based only on the relative prey exposure independent of the relative abundance and prey weight, I performed Kendall's partial rank-order correlation analyses (Table 2.6). If Merlins selected prey only based on the relative prey exposure, I expected the correlation between the relative prey exposure and consumption to remain significant after the relative prey abundance or prey weight was controlled statistically. I found that during both the incubation and nestling periods, Merlins appeared to select prey based on the relative prey exposure independent of prey weight, but not independent of the relative prey abundance (Table 2.6).

2.4 Discussion

2.4.1 Diet

Most dietary studies report that breeding Merlins feed mainly on one or two locally abundant bird species. Some studies have documented a small proportion of mammals, insects, and reptiles in the diet (Newton et al. 1984, Becker 1985, Bibby 1987). Three characteristics of the principal prey species seem evident: a) it is the most abundant species, b) it leaves cover frequently and therefore is vulnerable, and c) it weighs between 21-40 g.

For example, in urban habitats of North America, the major prey of Merlins is the House Sparrow (Oliphant and McTaggart 1977, James and Smith 1987, present study), whereas in rural areas it is the Horned Lark (Hodson 1978, Becker 1985). Similarly, in Europe the chief prey of breeding Merlins is the Meadow Pipit (Anthus pratensis), which has all three characteristics noted above (Sperber and Sperber 1963, Bengston 1975, Newton et al. 1978, 1984, Watson 1979, Bibby 1987, Meek 1988). In the majority of the diet studies, the main prey formed >50% of the diet in terms of number of prey killed.

Newton et al. (1984) acknowledged two biases in food studies based on prey remains collected near the nests. First, pluckings of a certain colour or size may be more conspicuous than others. This potential bias can be minimized by a thorough and systematic search of the nesting area, which I did. Second, small prey species may be under-represented in Merlin diets because: 1) Merlins may eat small-sized prey away from the nests (as predicted by the central place foraging theory; Orians and Pearson 1979), or 2) Merlins may wholly consume such prey near the nests, thus leaving no remains. My radio-tracking of breeding Merlins revealed, however, that out of 73 prey individuals captured by foraging Merlins, only 3 (4%) House Sparrows were eaten wholly near the kill sites while the rest were all transported to the nests (Sodhi 1992). Moreover, near the

nests, I encountered remains of small birds like Yellow Warblers and Black-capped Chickadees. This suggests that total consumption of a prey near the nest may depend upon factors such as hunger rather than prey size.

2.4.2 Prey Selection

Sex-biased predation by Merlins and other raptors has been documented previously (Korpimäki 1985, James and Smith 1987, Donazar and Ceballos 1989, Moller 1989, Struhsaker and Leakey 1990). I found evidence of sex-biased predation on the House Sparrow, Yellow Warbler, and Brewer's Blackbird by Merlins. Sexual differences in vulnerability of prey to predation may depend on differences in activity (Geer 1982, Donazar and Ceballos 1989), plumage conspicuousness (Baker and Bibby 1987), size, or body condition (Moller 1989). I noted that male and female House Sparrows were not taken significantly differently from their encounter rates in nature during the incubation and nestling periods. This suggests that sexual difference in encounter rates is an important factor influencing sex-biased predation (see Struhsaker and Leakey 1990 for a similar conclusion).

Merlins fed increasingly on juvenile House Sparrows as the breeding season progressed. Other workers who studied Merlin diets have also reported increased predation on juveniles as the breeding season progressed (Newton et al. 1984, Bibby 1987). The proportion of juveniles in the House

Sparrow population increased with the progress of the Merlin breeding season. Juvenile House Sparrows were most abundant when Merlin chicks were fledging and, in addition, juvenile House Sparrows were more likely than adults to be found out of cover (Fig. 2.1). Merlins preyed selectively on juvenile House Sparrows, the most abundant and vulnerable category during the fledging period. Similarly, Kus et al. (1984) recorded that a wintering female Merlin took proportionally more juvenile Dunlins (Calidris alpina) than were available.

Some birds taken by Merlins were not encountered on the bird count transects. Each year the proportion of these birds declined as the breeding season progressed (averages: incubation = 27%, nestling = 3%, and fledging = 1%). Most of these birds were migrants, e.g. Bohemian Waxwing, Snow Bunting, and Dark-eyed Junco, eaten by Merlins early in the breeding season.

The Merlin appears to be a selective predator and presumably captures prey according to their relative vulnerabilities rather than relative abundances. The two species that were more frequently taken than expected from their abundance levels (both by number and biomass) were the Horned Lark and House Sparrow. About 70-85% of the individuals of these species were recorded outside of cover during different breeding periods. Therefore, both these species may be easier to catch by Merlins. The escape tactic of the Horned Lark may work to its disadvantage.

When attacked by a Merlin, it does not normally duck into cover, but tries to outfly the predator (Sodhi et al. 1991), which may make it more susceptible to predation. Increased use of cities by Merlins has been a recent phenomenon in North America (Houston and Schmidt 1981, Oliphant and Haug 1985, James et al. 1987). Therefore Merlins evolved in a habitat (rural) where Horned Larks were their principal prey. This ultimate predator-prey interaction may have favoured specialization in preying on larks by urban Merlins.

Characteristics of the species that were usually avoided or taken in proportion to relative abundance included having 45% or more of their individuals in cover (e.g., Chipping Sparrow and Clay-colored Sparrow), low frequency of occurrence (e.g., Vesper Sparrow), larger size (e.g., Western Meadowlark), inconspicuous plumage (e.g., House Wren), or some combination of these characteristics.

I also found that Merlins primarily selected medium-sized birds (21-40 g). Larger or smaller birds were generally avoiding or taken in proportion to abundance. Previous studies on prey size selection have concluded that a predator either selects prey size according to abundance or profitability of capture (see Griffiths 1975).

I did not find evidence that Merlins select prey based on the relative prey exposure independent of the relative prey abundance. I found that more abundant species also had

more of its individuals out of cover. Therefore, my study failed to show that the relative exposure of different prey species is an important independent variable affecting prey selection of Merlins.

My data do not support the prediction of increased prey selectivity at higher prey abundances. My data do support another prediction of the prey model, that absolute abundance of the preferred prey is negatively correlated with overall diet diversity, i.e. the degree of prey selectivity increased with an increase in the absolute abundance(s) of the preferred prey.

3. HUNTING RANGES AND HABITAT USE AND SELECTION OF URBAN-BREEDING MERLINS

3.1 Introduction

Merlins have been increasingly colonizing North American cities (Oliphant and Haug 1985, James et al. 1987, James 1988). No study has examined ranges, habitat requirements, and spacing patterns of urban-breeding Merlins. Becker and Sieg (1987), studied hunting range sizes and habitat selection of three rural-breeding Merlins in Montana. Dickson (1988), based on sightings of wintering Merlins in different habitats, reported habitat use of Merlins in West Galloway (Scotland). Warkentin and Oliphant (1990) documented hunting range sizes, habitat use, and foraging behaviour of wintering urban Merlins in Saskatoon (Saskatchewan). These studies show that in general, hunting ranges of Merlins vary in size and that Merlins use some hunting habitats preferentially.

My objectives were to study hunting range characteristics (sizes and overlaps) of breeding Merlins in an urban population and to examine habitat use and selection by these Merlins. I also compare hunting habitats and hunting ranges of resident and immigrant Merlins. Little data are available on foraging differences between resident and immigrant birds in a population (but see, Heredia et al. 1991). I predicted that resident and immigrant Merlins

would differ in hunting habitats and hunting ranges because of prior experience with different habitats.

3.2 Methods

The research was conducted in Saskatoon, Canada from May to July, 1987 through 1990. The study area has been described in Chapter 2. Merlins first nested in the city in 1963 and have increased steadily since 1971 (Houston and Schmidt 1981, Oliphant and Haug 1985). During my study, the density of nesting Merlins was higher (19.7-24.6 pairs/100 km²) than recorded anywhere else.

For this study, Merlins were radio-tagged because they range over large areas and focal individuals could not be followed otherwise. Radio-tagging appeared to have minimal effect on long-term behaviour, reproductive success, and survival of Merlins (Appendix B).

Merlins were captured near their nests using either mist or dho-gaza nets (Clark 1981). Two tethered House Sparrows (Passer domesticus) or a tethered Great Horned Owl (Bubo virginianus) were used as lures. Radio transmitters (model SM-1, AVM Electronics, Livermore, Calif., U.S.A; or model SS-1, Biotrack, Dorset, U.K.), weighing approximately 2% of male and female body mass, were attached dorsally to two tail feathers ($n = 26$) by a method described by Kenward (1978), or were mounted to legs ($n = 4$) by modification of the method described by Grier (1970). The birds were not

followed during the first day of radio-tagging, but periodically monitored thereafter during the first and last 4 daylight hours (i.e., periods of maximum foraging activity; unpubl. data) on fair weather days.

Thirty birds were radio-tagged (1987: 2 males, 1 female; 1988: 5 males, 1 female; 1989: 5 males, 6 females; and 1990: 6 males, 4 females). Because of premature transmitter failure, data from two males (1987) and one female (1990) lacked completeness and were, therefore, excluded from the analyses. As each male was not followed during the entire breeding cycle, this resulted in 12, 14, and 5 males being monitored during the incubation, nestling, and fledging periods, respectively. All females were followed only during the fledging period, when they began hunting and providing food for the young. Each bird was tracked for a total of 24 hours during the incubation period and 16 hours during the nestling and fledging periods. Overall, 768 hours of radio-tracking were logged during the study. I adjusted observation days during the nestling and fledging periods so that all monitored birds of the same sex were followed when they had chicks of similar age (± 7 days). Range size data from different years were lumped because I did not find a significant difference among years in the range sizes of males during the incubation and nestling periods (Kruskal-Wallis ANOVA, $df = 2$, $P > 0.20$ and 0.10 , two-tailed). Similarly, hunting range sizes among

females during the fledging period did not differ significantly between years (1989 and 1990 compared; Mann-Whitney $U = 14$, $df = 3,6$, $P > 0.20$, two-tailed).

When being followed, each bird was located every 3-min and changes in location were plotted on a 1:50,000 map. As locations near the nest could bias my results (Haug and Oliphant 1990), I plotted locations of birds near their nests only when they made hunting attempts. After releasing a radio-tagged bird, two persons checked location error of attached radio-tag, one remained near the radio-tagged bird, and the other located it from various distances. From 1 km, my radio-location error averaged about 50 m. I visually located Merlins about 25% of the time. The remaining locations included in this chapter were obtained when Merlins were ≤ 1 km away from me. At each radio-location, I also recorded time, whether the bird was perched or flying, and habitat being used when possible.

I calculated hunting range sizes by using the minimum convex polygon method (Mohr 1947). This method has been used widely to calculate hunting range sizes of birds (e.g., Vander Haegen et al. 1989, Widen 1989, Warkentin and Oliphant 1990). All plotted radio-locations of a bird were used to calculate its minimum convex polygon.

To study habitat use and selection of breeding Merlins, I used locations of birds taken at 30-min intervals to reduce data dependency. I used a 30-min span between two

consecutive locations because during this time, a Merlin could travel about 25 km, assuming an average flight speed of 50 km/h (Warkentin and Oliphant 1990). This distance would cover all potential habitats in my study area (see Kenward 1987, Widen 1989).

I delineated four habitats in each hunting range: 1) urban- human habitation in and outside the city except parks and cemeteries, 2) parks- parks and cemeteries both in and outside the city, 3) agricultural- cultivated areas, and 4) grasslands- areas with tame pastures and native grasses. Each year (1987-90), a vehicular survey of the study area was made in July. These data, supplemented with aerial photographs taken in 1986, were used to develop a yearly habitat map of the study area. This habitat map was used to calculate the areas of different habitat types in individual hunting ranges.

I compared habitat availability with use (based on number of radio-locations in each habitat) to assess habitat selection. To determine habitat selection, I used Bonferroni's Z-tests if a significant difference between habitat availability and use was found using chi-square tests (Neu et al. 1974, Byers et al. 1984; see Chapter 2 for details of this test). I refer to a habitat being selected when used more often than expected and avoided when used less often than expected at a probability level of 0.05.

To determine whether Merlins frequent habitats with

higher prey densities (e.g., Preston 1990), bird abundance (total number of all potential prey species) in each habitat was estimated. Bird counts at five randomly selected points within each habitat type were made in 1989. At each station, birds seen or heard within 25 m for 4 min were recorded. Birds were counted for 4 min because preliminary counts (two 10-min counts/habitat) revealed that bird abundance tends to reach an asymptote in 4 min in each habitat. Bird counts were made once a month (May-July) within the first 4 hours of daylight in fair weather (<10% cloud cover, <15 km/h wind speed). Different random points were used each month. I calculated the mean number of birds for each habitat following Hutto et al. (1986). Because breeding Merlins in Saskatoon feed almost exclusively on birds <100 g in weight (Oliphant and McTaggart 1977, Sodhi et al. 1990, Chapter 2), I only considered birds in this weight class as potential prey species. As I did not find that bird abundance recorded in each habitat to be significantly different among survey months (Chi-square tests, $df = 2$, $P > 0.05$ to $P > 0.20$), I lumped data from the different months.

I refer to unbanded breeding birds as immigrants and breeding birds banded as nestlings in the city as residents (Newton 1988). A long-term nestling and adult banding program has been in operation in Saskatoon since 1971 (Warkentin et al. 1990). However, every year approximately

4-10% of the nests were missed. Thus, there is a possibility that a bird I classified as an immigrant may have originated from this population. Locations of the nests of immigrant and resident radio-tracked Merlins are presented in Fig. 3.1.

I analysed data on immigrant and resident Merlins separately. Further, I analysed habitat data separately for birds that hunted exclusively in Saskatoon and those that hunted both in and outside the city. When >1 bird was radio-tracked in each of the above categories, I used the aggregate method (Swanson et al. 1974; see also Chapter 2) to calculate habitat availability and use. I report SE with means.

3.3 Results

3.3.1 Hunting Range Descriptions

Mean hunting range sizes of resident and immigrant males were $6.3 \pm 1.3 \text{ km}^2$ (2.2-13.7 km^2 , range) and $33.7 \pm 12.1 \text{ km}^2$ (12.5-64.3 km^2), respectively ($U = 46$, $df = 4, 12$, $P < 0.005$; one-tailed test). All immigrant males spent some time out of the city hunting. Eight of 12 (66.7%) resident males were only observed to hunt in the city.

In 1988, two neighbouring males (one resident and one immigrant; inter-nest distance, 0.8 km) were radio-tracked from the incubation to fledging period. The resident and

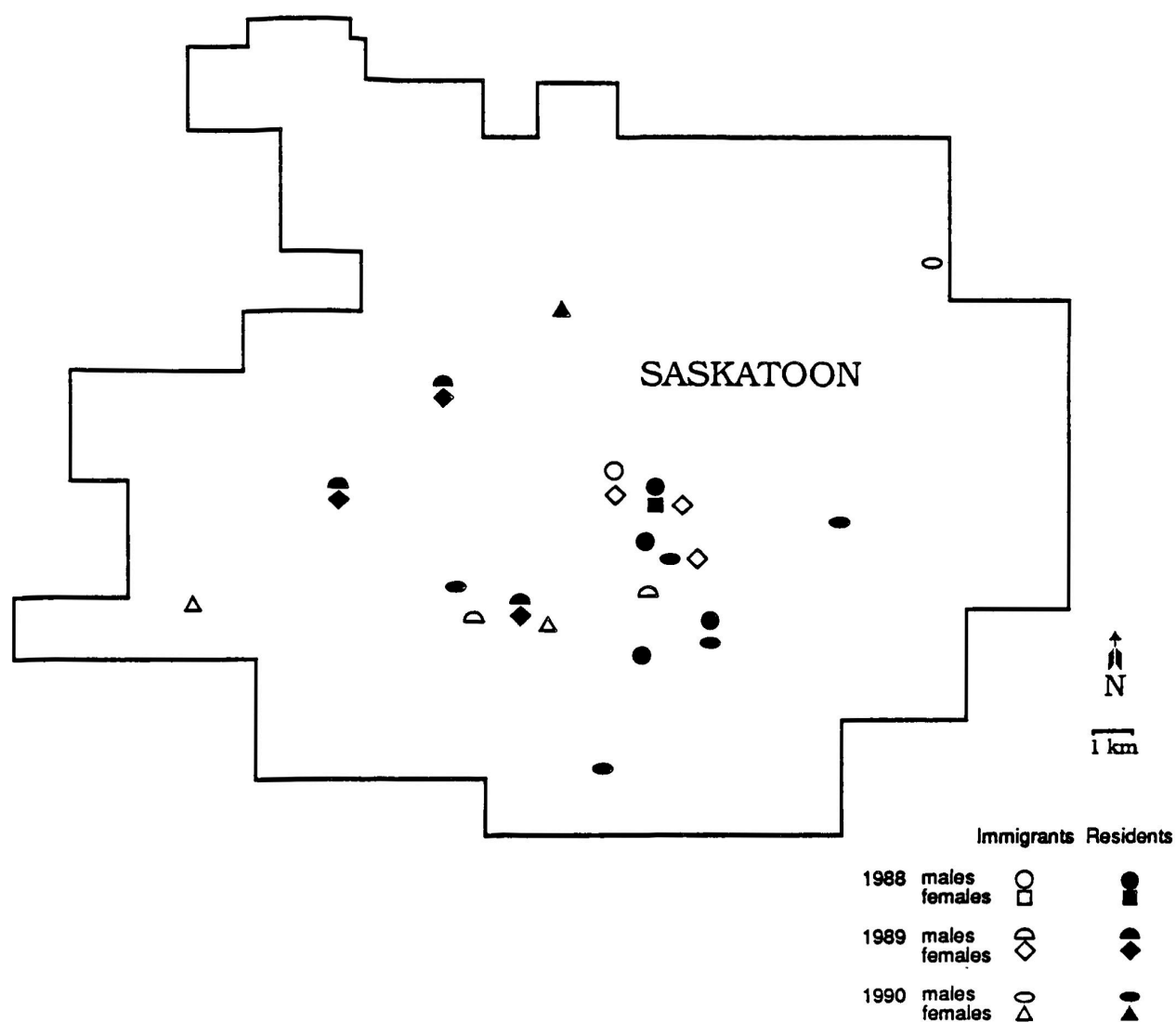


Figure 3.1. Nest locations of radio-tracked resident and immigrant Merlins.

immigrant males spent 34.4% and 50.8% of their foraging time (>100 m from the nest) outside of the city, respectively. Similarly, in 1989, neighbouring males were radio-tracked (one resident, one immigrant; inter-nest distance, 0.8 km) during the incubation and nestling periods. The resident and immigrant males spent 0% and 33.3 % of the foraging time outside the city, respectively. In 1990, I radio-tracked two males, one resident and one immigrant, nesting in the city at 1.3 and 0.5 km from the city limits, respectively. The resident male spent 37.5% of its time hunting outside the city compared to 99% for the immigrant male.

Mean hunting range sizes of resident and immigrant females were $6.6 \pm 3.4 \text{ km}^2$ (2.5-13.4 km^2) and $8.6 \pm 1.6 \text{ km}^2$ (0.6-17.5 km^2), respectively ($U = 14$, $df = 3,8$, $P > 0.20$, 1-tailed). Seven of eight (87.5%) immigrant females went out of the city to hunt compared to only one (33.3%) of three resident females. No neighbouring resident and immigrant females in a year were radio-tracked, therefore hunting time spent outside the city is not compared between the two categories.

3.3.2 Hunting Range Overlaps

Preliminary analyses revealed that birds nesting >2 km from each other had no spatial overlap in hunting ranges. Therefore, for the following analyses, I calculated spatial overlaps among radio-tracked birds nesting within 2 km of

each other.

For males the mean spatial overlap in hunting ranges was $11.8 \pm 6.3\%$ (0-77.3%; number of overlaps calculated $n = 12$), $11.4 \pm 4.3\%$ (0-36.4%; $n = 8$), and $10.6 \pm 4.1\%$ (0-46.4%; $n = 10$) during the incubation, nestling, and fledging period, respectively. Mean spatial overlap in ranges of residents with other resident and (or) immigrant males was $15.7 \pm 8.2\%$ (0-77.3%; $n = 9$), $12.2 \pm 5.3\%$ (0-36.4%; $n = 6$), and $12.2 \pm 4.6\%$ (0-46.4%; $n = 8$) during the incubation, nestling, and fledging period, respectively. Spatial overlap in ranges of immigrant males with other immigrant and (or) resident males was $0.1 \pm 0.1\%$ (0-0.3%; $n = 3$), $9.1 \pm 9.2\%$ (0-18.3%; $n = 2$), and $2.1 \pm 2.1\%$ (0-4.2%; $n = 2$) during the incubation, nestling, and fledging period, respectively. The extent of spatial overlap in ranges did not differ among resident and immigrant males during the incubation period ($U = 19.5$, $df = 3,9$, $P > 0.20$, two-tailed). (Sample sizes were only sufficient to test statistically the extent of differences in spatial overlap during the incubation period between immigrant and resident males).

Mean spatial overlap in hunting ranges for females during the fledging period was $29.6 \pm 4.4\%$ (15.7-45.1%; $n = 6$). Mean spatial overlap by resident females was slightly larger ($32.9 \pm 8.5\%$; 20.8-45.1%; $n = 4$) than by the immigrant females ($27.9 \pm 6.5\%$; 15.7-37.8%; $n = 2$). My

estimates of spatial overlap for both males and females are conservative because, each year, not all neighbouring individuals were radio-tracked (e.g., Fig. 3.2).

To determine whether neighbouring males show temporal partition in ranges, neighbours were simultaneously radio-tracked during the nestling period in 1988. Two neighbours (inter-nest distance, 0.8 km) which had 18.3% and 14.9% spatial overlap in ranges with each other, hunted in the same general area in one 8-hour period. They did not hunt at the same location at the same time. Both these males caught at least one House Sparrow from the same farm during the 8-hour period.

On 10 occasions, I observed agonistic encounters between hunting males away from their nests. Following such encounters, one of the birds left the area. I was sure on only three occasions that agonistic encounters involved neighbouring breeders. As Merlins in the study area were not individually colour-marked, it was not possible on other occasions to determine if observed agonistic encounters were between neighbours or involved floaters.

3.3.3 Habitat Use And Selection

Merlins that hunted exclusively in the city used habitats in relation to their availability (Tables 3.1-3.4). Immigrant Merlins had proportionally less urban habitat available in their ranges than residents, except during the

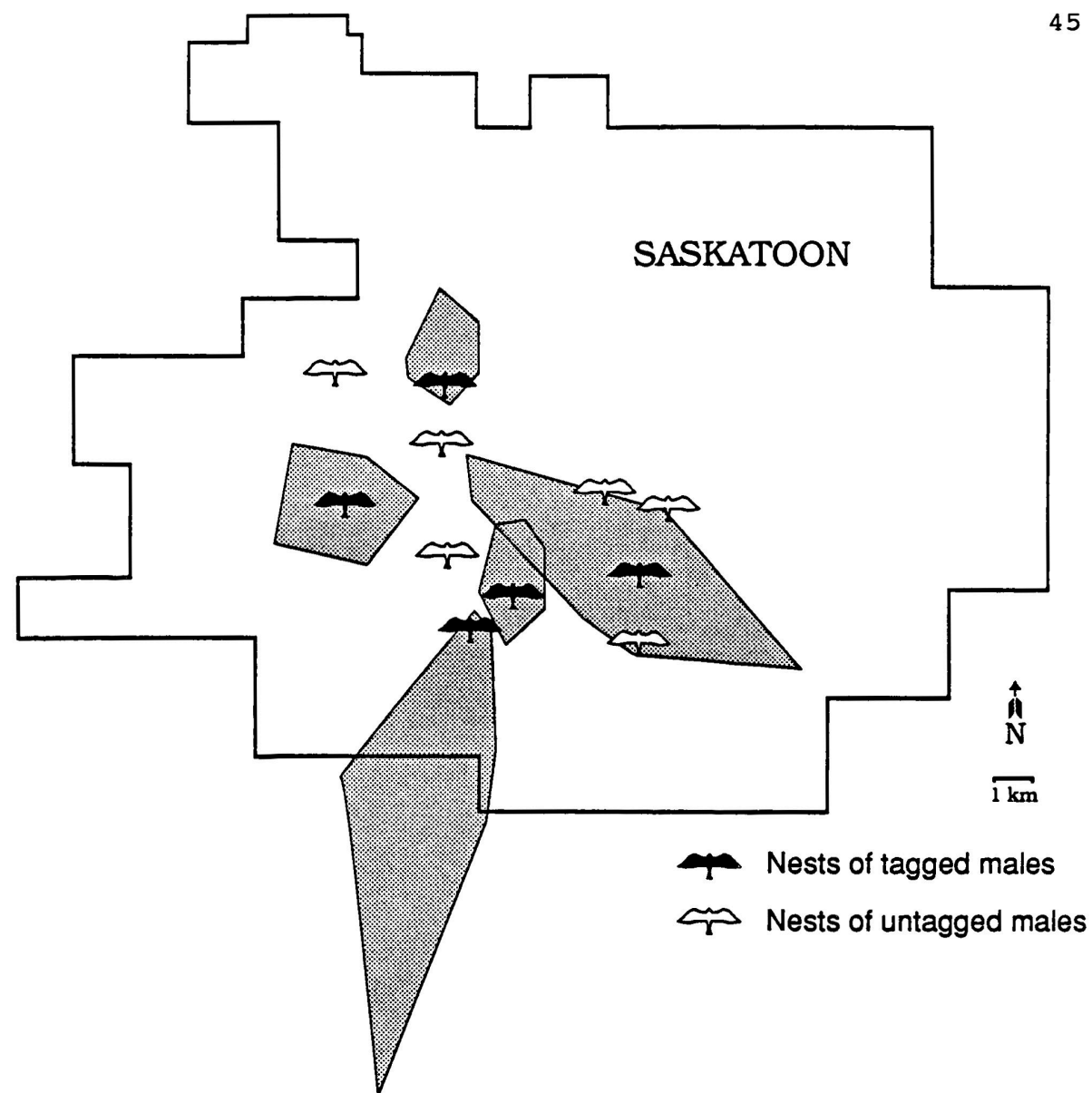


Figure 3.2. Locations of the nests of radio-tagged males and their untagged neighbouring males in 1989. Hunting ranges of tagged males are shown during the nestling period.

Table 3.1. Habitat use and selection by breeding male Merlins in Saskatoon during the incubation period. Values for availability and use for each habitat were obtained using the aggregate method (Swanson et al. 1974). When habitat availability and use differed significantly, I used Bonferroni's Z-tests to determine habitat selection. A = avoided, S = selected, and E = used not significantly differently from availability. A and S at $P < 0.05$.

Habitat	Residents					Immigrants		
	U ¹ (<u>n</u> = 7)		R ² (<u>n</u> = 2)		Hab	(n = 3)		
	Prop	Prop	Prop	Prop		Prop	Prop	Hab
	Avail	Used ³	Avail	Used	Sel	Avail	Used	Sel
Urban	85.7	83.6	58.5	79.1	S	53.7	38.8	A
Parks	14.2	16.3	9.5	6.2	E	7.7	14.5	S
Agricultural-		-	34.0	20.8	A	25.3	11.8	A
Grassland	-	-	16.0	14.7	E	13.1	34.7	S
Total area	12.3		7.0			93.2		
(km ²)								
Total Radio								

Locations	336	96	144
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¹Hunted only in urban habitat and parks.

²Hunted in all 4 habitats.

³Bonferroni's Z-test not applied because $\chi^2 = 1.0$, $df = 1$,
 $\underline{P} > 0.20$.

Table 3.2. Habitat use and selection by breeding male Merlins in Saskatoon during the nestling period. Values for proportion of habitats available and used were obtained using the aggregate method. Habitat selection was determined using Bonferroni's Z-tests when habitat availability and use differed significantly. For abbreviations see Table 1. A and S at $P < 0.05$.

Habitat	Residents					Immigrants		
	<u>U¹ ($\underline{n} = 7$)</u>		<u>R² ($\underline{n} = 3$)</u>			<u>($\underline{n} = 4$)</u>		
	Prop	Prop	Prop	Prop	Hab	Prop	Prop	Hab
	Avail	Used ³	Avail	Used	Sel	Avail	Used	Sel
Urban	84.1	78.7	61.7	56.8	E	48.5	41.5	E
Parks	15.8	21.3	5.2	10.9	E	11.6	11.8	E
Agricultural-	-	-	28.2	17.2	A	42.2	17.7	A
Grassland	-	-	7.1	14.1	S	14.5	44.4	S
Total Area	26.3		26.1			63.4		
(km ²)								
Total Radio								

Locations	224	96	128
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¹Hunted only in urban habitat and parks.

²Hunted in all 4 habitats.

³Bonferroni's Z-test not applied because $\chi^2 = 2.7$, $df = 1$, $P > 0.10$.

Table 3.3. Habitat use by breeding male Merlins in Saskatoon during the fledging period. When >1 bird was radio-tracked in each of the categories, the aggregate method was used to calculate proportion of habitat availability and use.

Habitat	Residents				Immigrants	
	U ¹ (<u>n</u> = 2)		R ² (<u>n</u> = 2)		(<u>n</u> = 1)	
	Prop Avail	Prop Used ³	Prop Avail	Prop Used ⁴	Prop Avail	Prop Used ⁴
Urban	83.7	82.2	77.2	67.2	84.0	78.1
Parks	16.3	17.8	4.9	18.7	0.1	6.2
Agricultural	-	-	8.0	12.5	11.7	6.2
Grassland	-	-	19.8	15.6	4.2	9.5
Total Area (km ²)	8.3		20.9		9.4	
Total Radio Locations		64		64		32

¹Hunted only in urban habitat and parks.

²Hunted in all 4 habitats.

³Bonferroni's Z-test not applied because $\underline{X}^2 = 0.1$, $df = 1$, $\underline{P} > 0.20$.

⁴Chi-square test not attempted because of <5 expected radio locations in >20% of habitats.

Locations	64	32	32	224
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¹Hunted only in urban habitat and parks.

²Hunted in all 4 habitats.

³Bonferroni's Z-test not applied because $\underline{X}^2 = 0.1$, $df = 1$, $\underline{P} > 0.20$.

⁴Chi-square test not attempted because of <5 expected radio locations in >20% of habitats.

⁵Bonferroni's Z-test not applied because $\underline{X}^2 = 0.6$, $df = 1$, $\underline{P} > 0.20$.

fledging period (Tables 3.3-3.4).

Male Merlins that hunted both in and outside the city generally avoided agricultural habitat (Tables 3.1-3.3). This was also true for immigrant females (Table 3.4). However, these birds (both males and females) selected urban habitat, parks, and grasslands during one breeding period or another.

The mean number of potential prey species was 1.5 ± 0.4 , 2.7 ± 0.3 , 3.7 ± 0.6 , and 4.5 ± 0.8 in agricultural, grassland, parks, and urban habitat, respectively (Kruskal-Wallis ANOVA, $KW = 13.8$, $df = 3$, $P < 0.02$, two-tailed). Further analysis by the multiple comparison method of Siegel and Castellan (1988:213-214) revealed that both parks and urban habitat had significantly more birds than in agricultural habitat ($P < 0.05$).

3.4 Discussion

Some males were followed during one breeding period only, and this could have biased my hunting range size analyses. Hunting range sizes of more than 50% of males followed for at least 40 hours reached asymptotes (Odum and Kuenzler 1955) with 16-hours of observations (Fig. 4.1). Moreover, hunting range sizes did not differ among the three

stages of breeding (incubation, nestling, and fledging) both in resident ($KW = 5.6$, $df = 2$, $0.05 < P < 0.10$, one-tailed) and immigrant ($KW = 2.7$, $df = 2$, $P > 0.20$, one-tailed) males. This suggests that my inclusion of males followed for only 16 or 24 hours should have not greatly affected hunting range size estimates.

Becker and Sieg (1987) calculated hunting range sizes of male Merlins during the nestling period in Montana (Merlin nesting density 3.8 pairs/100 km²). They recorded mean range size of three radio-tracked males to be 23.3 ± 4.6 km² (12.6-28.1 km²). In Saskatoon, I found mean range size of 14 radio-tracked males during the nestling period to be 8.2 ± 2.7 km² (1.3-41.5 km²). Range sizes recorded for Merlins by Becker and Sieg were significantly larger than those of Saskatoon Merlins ($U = 38$, $P < 0.04$, two-tailed). It has been suggested that range sizes are inversely correlated with population density (Krebs 1971, Schoener and Schoener 1982). Beside population density, range sizes could be affected by other factors such as prey abundance (Village 1982b).

Warkentin and Oliphant (1990) found mean winter hunting range size of adult (5 females, 1 male) and juvenile (1 female, 2 males) Merlins to be 19.6 ± 5.8 and 17.9 ± 3.4 km², respectively. Mean range sizes of breeding Merlins

(males, females, immigrants, and residents lumped) in Saskatoon was $11.1 \pm 13.4 \text{ km}^2$ ($n = 27$), slightly smaller than that for wintering birds.

The spatial overlap between neighbouring radio-tracked Merlins ranged from 0 to 77.3%. However, as stated earlier, my estimates of spatial overlaps are conservative. Previously, Becker and Sieg (1987) also recorded spatially overlapping ranges for breeding Merlins. Warkentin and Oliphant (1990) did not measure hunting range overlaps among wintering Merlins but suggested that overlaps must exist as different birds were recorded at the same site within a short time (<1 hr).

Several factors may influence whether Merlins have overlapping rather than mutually exclusive hunting ranges in Saskatoon during the breeding season. Nesting density of Merlins in Saskatoon is high, suggesting that defence costs may be high. The prey base for Merlins in Saskatoon is abundant and relatively stable (Chapter 2), thus there are reduced benefits of exclusively defending prey. Further, Merlins feed on mobile prey (i.e., birds), which also show altered behaviour in response to Merlin presence (Sodhi et al. 1990, Sodhi 1991a, b) and, therefore, would be hard to defend. Overlapping ranges offer relatively more foraging area for Merlins. This may be beneficial for Merlins as

they rely mostly on surprise while hunting (Sodhi et al. 1991). These factors make defence of exclusive hunting ranges a sub-optimal choice (Brown 1964, Brown and Orians 1970, Davies 1980, Davies and Houston 1984).

While Cramp and Simmons (1980) stated that there are no records of aggressive encounters between conspecific Merlins during the breeding season, I recorded agonistic encounters between hunting Merlins (see Sodhi 1991c for conspecific agonistic encounters near Merlin nests). These agonistic encounters may reflect food-based territoriality or dominance hierarchy at preferred foraging sites (Hickey and Fenton 1990). As mentioned earlier, I found little evidence of spatially mutually exclusive, food-based territories for Merlins. However, the presence of a dominance hierarchy at preferred foraging sites appears to be operating as two males using the same foraging site did not use it simultaneously. Further, when a male was supplanted by a neighboring male ($n = 3$) from a hunting area, it was observed in the same area subsequently. Other studies also report the existence of dominance hierarchies in animals at higher population densities (Kaufmann 1983).

Immigrant Merlins generally had relatively less urban habitat in their ranges (except during the fledging period; Table 3.3). I also noted that immigrant males spent more

time hunting outside the city than locally hatched residents. It is possible that immigrants have prior experience with out-of-city habitats which influences their use of such habitats during the breeding season (Hilden 1965, Klopfer and Granzhorn 1985; see also Chapter 4).

Generally, Merlins avoided agricultural habitat. This may be because prey counts made in 1989 in different habitats showed that this habitat had lower prey abundance than other habitat types. Similar results have been reported by other workers (Craig et al. 1986, Preston 1990). Beside prey abundance, habitat selection in raptors is also influenced by other factors such as cover availability for prey (Kenward 1982, Janes 1985, Preston 1990).

4. CORRELATES OF HUNTING RANGE SIZE IN BREEDING MERLINS

4.1 Introduction

Various studies have demonstrated that either food abundance, intrusion pressure from conspecifics and (or) heterospecifics, or both, affect hunting range (feeding territory) sizes in different species, e.g., insects (Hart 1987), fishes (Dill et al. 1981, Norman and Jones 1984), lizards (Simon 1975), birds (Village 1982b, Temeles 1987), and mammals (Mares and Lacher 1987). Some studies also have examined the effect of factors such as season, habitat, age, body mass, and energetic requirements on hunting range sizes (Schoener and Schoener 1982, Prescott and Middleton 1988, Cave et al. 1989, Adriaensen and Dhondt 1990, Finck 1990, Grahm 1990, Piper and Wiley 1990, Tidemann 1990). In breeding birds, in addition to prey abundance and intruder pressure, other variables that may affect hunting range sizes include familiarity with the habitat, body mass, clutch and brood size, and phase of the breeding cycle. However, the effect of all these variables on hunting range sizes has not been examined in a study of a breeding bird.

Consequently, I studied the effect of the aforementioned variables on hunting range sizes of breeding Merlins (Falco columbarius). Breeding Merlins were ideal for testing hypotheses concerning hunting range sizes because: their hunting range sizes can be estimated by

radio-tracking (Becker and Sieg 1987, Warkentin and Oliphant 1990), and assessment of the abundance of their prey is easier than for most other birds (see Zach and Smith 1981).

I evaluated six main hypotheses concerning hunting range sizes. Because breeding Merlins appear to be foraging time-minimizers (Chapter 5), I tested all these hypotheses in the context of the time-minimization foraging strategy.

First, some studies (e.g., Marquiss and Newton 1981) have found that hunting ranges fluctuate in size over the course of the breeding season, possibly as a result of changing food demands at the nests. Consequently, I hypothesized that range sizes of male Merlins might vary with food requirements at the nests as young hatch and grow, and predicted that range sizes of males should expand from the incubation to the nestling period and then contract during the fledging period when young leave the nest (Breeding Cycle hypothesis). Male Merlins provide almost all food at their nests during the incubation and nestling periods (Sodhi et al. 1992). Females start hunting and providing food at the nest only during the fledging period (Oliphant 1974; Sodhi et al. 1992). Therefore, I also examined the alternative hypothesis that range sizes of males increase during the fledging period due to competition for food with females.

The second hypothesis I considered was the Prey Abundance hypothesis, which suggests that animals might

assess prey abundance in their hunting ranges and adjust range sizes accordingly (Myers et al. 1979, 1981), leading to an inverse relationship between prey abundance and hunting range size (Hixon 1980, McFarland 1986).

Alternatively, range sizes often increase where there are more competitors (Hixon 1980). Merlins in the study area have overlapping hunting ranges (Chapter 3). Thus, the third hypothesis I evaluated was the Intruder Density hypothesis, which maintains that range sizes depend upon intruder density.

Several studies have noted that body mass is correlated with range sizes (McNab 1963, Schoener 1968, Harestad and Bunnell 1979, Schoener and Schoener 1982). The explanation for these correlations is that heavier individuals have higher energetic demands and thus have to search a greater area to obtain food (Mace et al. 1983). Therefore, the fourth hypothesis I examined was the Energetic Requirement hypothesis, which predicts a positive correlation between body mass and hunting range size.

The fifth hypothesis I considered is based on clutch/brood size (Clutch/brood Size hypothesis). Specifically, a female that lays more eggs may require more food to build up lost body reserves (Martin 1987). This hypothesis posits that range size should be positively correlated with clutch or brood size, owing to the increased food demands of females that lay larger clutches and/or

larger number of chicks to feed in larger broods (Schoener 1968).

Finally, habitat selection in birds is thought to be reinforced by habitat imprinting (Hilden 1965, Gluck 1984, Klopfer and Granzhorn 1985, Grunberger and Leisler 1990). Ecologically distinct populations of the same species may have different habitat preferences (Wecker 1964). Early experience with a certain habitat may improve an individual's ability to exploit it (Alcock 1979, Finck 1990, Morton 1991). One might expect individuals raised in a particular environment to use that habitat more efficiently when they breed in such habitat compared with individuals that were not raised there (Breeding Bird Origin hypothesis). If so, I predicted that breeding birds hatched and raised in the study area (residents) would have smaller hunting ranges than immigrants presumed to have originated outside the study area.

4.2 Methods

The research was conducted in Saskatoon, Canada, from May to July, 1987 through 1990. For this study, Merlins were radio-tagged. Detailed methods are presented in Chapter 3.

I define hunting range as an area used by Merlins to obtain food. I use hunting range as synonymous to feeding territory.

Prey abundance in hunting ranges was estimated by counting birds on 1-km randomly selected transects (except for one female in 1987). I counted all birds, seen or heard, within 90 m on each side of a transect. The transects were sampled once during each breeding period. For males that were observed for more than one breeding period, I repeated the transect counts. The bird surveys were made within the first four daylight hours in fair weather (<10% cloud cover, <15 km/h wind speed). In Saskatoon, Merlins feed almost exclusively on birds <100 g in weight (Oliphant and McTaggart 1977, Sodhi et al. 1990, Chapter 2). I therefore considered only birds in this weight class as potential prey species. Since predators may adjust their hunting range sizes based only on the abundance of the principal prey (Temeles 1987), I performed two analyses, one with the abundance of all birds (<100 g) and another with abundance of House Sparrows (which represented about 65% of the diet by number during the breeding season; Oliphant and McTaggart 1977, Sodhi et al. 1990, Chapter 2).

To minimize the chances of nest desertion (Oliphant 1974), clutch and brood sizes were determined by climbing the nest trees during the early nestling period. The clutch sizes were taken as the number of hatched young plus unhatched eggs found. As I did not have any information on number of eggs and chicks before the nest investigation, my clutch and brood size estimates were minimum values. The

clutch and brood sizes of the studied Merlins ranged from 2 to 5 and 1 to 5, respectively.

When a male was monitored for more than one breeding period, it was captured and weighed again during the subsequent breeding period (except for two males). During the incubation and nestling periods, body masses of males ranged from 158 to 195 g, whereas those of females ranged from 228 to 261 g during the fledging period.

Myers et al. (1979) stated that intruder pressure can be derived from two sources, neighbours and non-neighbours (floaters) (see also Temeles 1987, 1990). As Merlins in the study area were not individually colour-marked, it was not always possible to determine if agonistic encounters observed between hunting Merlins ($n = 10$) were between neighbours or involved floaters (Chapter 3). 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 neighbours. I used active Merlin nests within 1 km of a nest to compute neighbour intruder density because data analyses showed that hunting ranges among Merlins nesting more than one kilometer from each other did not overlap extensively.

As my results were based on directional predictions, I used one-tailed statistical tests. Hunting range sizes and different proximate variables were not correlated for males during the fledging period because of insufficient sample

sizes. To assess the relative importance of different variables in explaining hunting range size variation in Merlins, I used Kendall's partial rank-order correlation analyses (Siegel and Castellan 1988:254-262). Throughout the text, " \pm " refers to SE.

4.3 Results

On average, hunting range size of resident males was the smallest during the incubation period ($2.7 \pm 0.6 \text{ km}^2$, range = $0.9\text{-}5.7 \text{ km}^2$, $n = 9$) and increased in size statistically insignificantly thereafter (nestling = $5.1 \pm 1.4 \text{ km}^2$, $1.3\text{-}12.8 \text{ km}^2$, $n = 10$; fledging = $7.1 \pm 2.2 \text{ km}^2$, $3.1\text{-}13.3 \text{ km}^2$, $n = 4$; Kruskal-Wallis ANOVA, $KW = 5.6$, $df = 2$, $0.05 < P < 0.10$; to ensure comparable tracking effort among breeding periods, for this test I randomly selected 16-hour data for males during the incubation period). Mean hunting range of immigrant males was largest during the incubation period ($31.1 \pm 16.9 \text{ km}^2$, $12.5\text{-}64.3 \text{ km}^2$, $n = 3$), although not statistically different from that in the other two breeding periods (nestling = $15.8 \pm 8.6 \text{ km}^2$, $4.1\text{-}41.5 \text{ km}^2$, $n = 4$; fledging = 9.5 km^2 , $n = 1$; $KW = 2.7$, $df = 2$, $P > 0.20$). The hunting ranges of immigrant males were significantly larger than those of resident males during the incubation period (Mann-Whitney $U = 27$, $P = 0.005$; Fig. 4.1). The respective hunting range sizes of immigrant and resident Merlins did not differ significantly among males

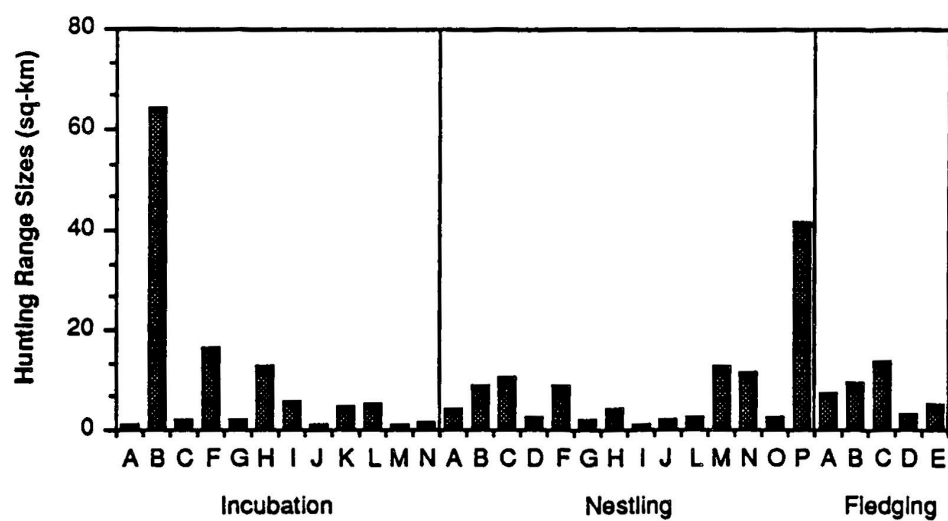


Figure 4.1. Hunting range sizes of male Merlins during different breeding periods. Letters represent individual males. Note that B, F, H, and P are immigrants.

during the nestling period ($U = 30.5$, $0.05 < P < 0.10$) or among females during the fledging period ($U = 13.5$, $P > 0.10$).

During the incubation period, the hunting range sizes of males were negatively correlated with abundance of both House Sparrows ($T = -0.52$, $n = 12$, $P = 0.009$) and all birds ($T = -0.43$, $P = 0.02$). I performed partial correlation analyses to assess the relative importance of other variables (clutch size, number of active nests in 1-km radius, and male body mass) in determining hunting range sizes. If abundance of House Sparrows and all birds had an independent effect on hunting range size of males, I expected these correlations to remain significant when the other variables were controlled statistically. The partial correlation analyses revealed that abundance of both House Sparrows and all birds were significantly correlated with hunting range sizes of males independently of clutch size, density of Merlin nests, and male body mass (Table 4.1).

In the nestling period, hunting range sizes of males were negatively correlated with all bird abundance ($T = -0.47$, $n = 14$, $P = 0.01$), but not with the House Sparrow abundance ($T = -0.25$, $P = 0.11$). All bird abundance significantly correlated with hunting range sizes of males independently of brood size, density of Merlin nests, and male body mass (Table 4.1).

Of 11 males studied both during the incubation and

nestling periods, five decreased their range sizes with a concomitant increase in all bird abundance in their ranges. Four males increased their range sizes from the incubation to nestling period as bird abundance declined in their ranges. While the other two males either increased or decreased range sizes parallel to bird abundance changes in their ranges (see Fig. 4.1 and Table 4.2).

For females during the fledging period, two correlations were significant, both were negative, one between range sizes and the House Sparrow abundance ($T = -0.65$, $n = 11$, $P = 0.003$) and another between range sizes and body mass ($T = -0.59$, $P = 0.006$). The partial correlation analyses revealed that both the House Sparrow abundance and body mass independently correlated with hunting range sizes of females (Tables 4.1 and 4.3).

4.4 Discussion

The mean hunting ranges were largest and smallest, for immigrant and resident males during the incubation period, respectively. Data from resident males provided support for the Breeding Cycle hypothesis. Previously, Haak (1983) found that in male Prairie Falcons (*F. mexicanus*), hunting ranges were larger during incubation than nestling period. He attributed this to males making more exploratory flights during the incubation period. Perhaps immigrant male Merlins make more exploratory flights than residents, which

Table 4.1. Kendall's partial rank-order correlation analyses to assess the relative importance of different variables in determining hunting range sizes of Merlins (both sexes) in different breeding periods. The table based on two-tailed tests (except simple correlations). HRS = hunting range size, HSA = House Sparrow abundance, and ABA = all bird abundance.

Simple correlation	Controlled Variable								
	Clutch/brood size			No. of active nests within 1-km			Body mass (g)		
	<u>T</u>	<u>n</u>	<u>P</u>	<u>T</u>	<u>n</u>	<u>P</u>	<u>T</u>	<u>n</u>	<u>P</u>
<u>Incubation</u>									
HRS vs HSA									
(-0.52)	-0.56	12	<0.01	-0.53	12	<0.02	-0.57	11	<0.01
HRS vs ABA									
(-0.43)	-0.51	12	<0.02	-0.45	12	<0.05	-0.45	11	<0.05
<u>Nestling</u>									
HRS vs ABA									
(-0.47)	-0.45	14	<0.02	-0.53	14	<0.01	-0.51	12	<0.01

Fledging*

HRS vs HSA

(-0.65) -0.78 11 <0.01 -0.66 11 <0.01 -0.63 11 <0.01

*Data from females; there were too few males to conduct a test.

OTHER SIMPLE CORRELATIONS

IncubationHRS vs clutch size $\underline{T} = -0.29$, $\underline{P} = 0.10$ HRS vs active nests $\underline{T} = -0.03$, $\underline{P} = 0.44$ HRS vs body mass $\underline{T} = 0.00$, $\underline{P} = 0.50$ NestlingHRS vs brood size $\underline{T} = 0.26$, $\underline{P} = 0.09$ HRS vs active nests $\underline{T} = 0.11$, $\underline{P} = 0.29$ HRS vs body mass $\underline{T} = -0.20$, $\underline{P} = 0.18$ FledgingHRS vs brood size $\underline{T} = 0.37$, $\underline{P} = 0.06$ HRS vs active nests $\underline{T} = 0.21$, $\underline{P} = 0.18$ HRS vs all birds $\underline{T} = -0.34$, $\underline{P} = 0.08$

Table 4.2. Potential prey abundance (birds <100 g) recorded on 1-km transects in hunting ranges and range sizes of male Merlins tracked during both incubation and nestling periods.

Bird	Incubation		Nestling	
	Birds	Range size	Birds	Range size
		(km ²)		(km ²)
A	58	0.9	23	4.1
B	30	64.3	37	8.7
C	67	2.0	62	10.7
F	14	16.4	23	2.2
G	19	2.3	37	2.2
H	44	12.5	62	4.1
I	32	5.7	39	1.3
J	36	1.0	45	2.3
L	34	5.0	25	2.5
M	54	1.0	21	12.8
N	50	1.5	20	11.5

Table 4.3. Kendall's partial rank-order correlation analysis to determine the relative effect of different variables on hunting range sizes of female Merlins during the fledging period. Partial correlations are based on two-tailed tests. HRS = hunting range size and BM = body mass.

Controlled variable	HRS vs BM		
	(-0.59)		
	<u>T</u>	<u>n</u>	<u>P</u>
Brood size	-0.56	11	<0.02
No. of active nests*	-0.59	11	<0.01
All bird abundance	-0.64	10	<0.01
House sparrow abundance	-0.56	10	<0.02

*Within 1-km of a nest

results in larger hunting ranges for immigrants as predicted by the Breeding Bird Origin hypothesis. Once immigrants survey their breeding habitat, they are perhaps able to decrease their hunting range sizes. Finck (1990) reported that Little Owls (Athene noctua) with no experience breeding in the study area occupied larger hunting ranges than the experienced owls. However, he found that both experienced and inexperienced owls showed similar patterns of seasonal variation in hunting range size.

Finck (1990) also noted that hunting range sizes of male Little Owls decreased as the breeding season progressed. In male Eurasian Sparrowhawks (Accipiter nisus), however, Marquiss and Newton (1981) observed that hunting ranges were smaller during the prelaying and incubation periods and increased in size thereafter. However, my study underscores a need to examine temporal variation in hunting range sizes for immigrants and resident males separately, which the latter study did not. Seasonal variation in male hunting range sizes in different species may also be affected by: 1) changes in prey abundance in the ranges, 2) food contribution by mates, and 3) nest and mate guarding requirements (Moller 1990).

Both male and female Merlins had smaller ranges in rich prey areas. I also found that the majority of males adjusted their range sizes from one breeding period to another in relation to changes in prey abundance (Table

4.2). These results support the Prey Abundance hypothesis. Earlier studies have also documented hunting ranges in birds to be smaller in rich prey areas: e.g., the Ovenbird, Seiurus aurocapillus (Stenger 1958); Golden-winged Sunbird, Nectarinia reichenowi (Gill and Wolf 1975); Eurasian Kestrel, F. tinnunculus (Village 1982b); New Holland Honeyeater, Phylidonyris novaehollandiae (McFarland 1986); Northern Harrier, Circus cyaneus (Temeles 1987); and Fairy Wrens Malurus spp. (Tidemann 1990). However, food abundance did not significantly explain hunting range size variation in the Sanderling, Calidris alba (Myers et al. 1979); Rufous-sided Towhee, Pipilo erythrophthalmus (Franzblau and Collins 1980); and Willow Flycatcher, Empidonax traillii (Prescott and Middleton 1988). This suggests that the importance of food abundance as a determinant of range size varies among different species.

The number of Merlin nests within 1-km radius of a nest did not significantly explain hunting range size variation in Merlins, providing little support for the Intruder Density hypothesis (Table 4.1). This may be because breeding Merlins do not defend hunting ranges for exclusive use (Chapter 3) and therefore neighbours may exert minimum pressure on hunting range sizes (Brown 1964). However, in testing this hypothesis, I did not examine the other factor causing intruder pressure, i.e., density of floaters. My data also failed to support the Clutch/brood size hypothesis

(Table 4.1).

Contrary to the Energetic Requirement hypothesis, I found that heavier females had relatively smaller hunting ranges. Smaller ranges may benefit females in three ways: 1) by permitting a bird to become familiar with and remember food locations (Zach and Falls 1976), 2) by saving energy by searching a smaller area for food (Andersson 1978), and 3) by helping in guarding the fledglings more efficiently. Alternatively, heavier females may have had mates with higher quality ranges providing relatively more food for the young, and thus the females may have required smaller areas to obtain food.

5. PROXIMATE DETERMINANTS OF FORAGING EFFORT IN BREEDING MALE MERLINS

5.1 Introduction

Many previous studies have examined whether a parent is maximizing its foraging effort to feed its young (e.g., Royama 1966, Drent and Daan 1980, Weathers and Sullivan 1989). However, few studies have attempted to determine 1) what balance is reached by a parent between foraging time and energy needs, and 2) how it behaves in accordance to that balance. Depending upon their biology, animals have developed two alternate foraging strategies to balance time and energy needs, i.e., foraging time minimization and food energy maximization (Schoener 1971). Time minimizers maximize fitness by minimizing foraging time to that required to satisfy current energy demands, and using remaining time for nonforaging activities (e.g., nest guarding). Energy maximizers are those animals whose fitness is maximized by gaining maximum energy, thus spending most their time foraging (sensu foraging time maximizers; Hixon 1982).

I determined the foraging strategy of breeding male Merlins (Falco columbarius). Male Merlins were appropriate subjects for this study because: 1) they provide most of the food at nests during the entire breeding season (Sodhi et al. 1992); 2) they feed mainly on House Sparrows (Passer

domesticus) and, consequently, prey size has minimal influence on their foraging effort (Royama 1966, Schaffner 1990); and 3) they can be monitored by radio-tracking with minimum apparent bias on their behaviour (Appendix B). Because measuring only the number of feeding trips per unit time gives an incomplete picture of overall foraging effort (Royama 1966), I examined three variables to estimate foraging effort: 1) the percentage of time flying when males were not at their nests (i.e., an index of time spent foraging), 2) number of feeding trips made per hour, and 3) mean duration of foraging bouts (i.e., sum of prey search, capture, and transport time).

If an animal is a time minimizer and merely meets its current food demands, it should increase its foraging effort as energy demands increase (Barclay 1989). Thus, I expected that males that are foraging time minimizers would increase their foraging effort from the incubation to nestling periods as food demands at the nests increase. The females start supplementing food at their nests during the fledging period (ca 65% of prey deliveries by males, 35% by females); therefore, I predicted a decline in male foraging effort during this period. However, I also made an alternative prediction for this period: because more birds (both male and female Merlins) hunt in the study area, males may have

to search more to meet foraging demands, thereby increasing foraging effort during the fledging period than the nestling period. Further, for time minimizer males, I predicted an increase in foraging effort with increase in clutch or brood size, low prey abundance, increasing body mass, more competitors (as determined by number of active Merlin nests within 1-km radius), or a decrease in the time allocated to incubation (Norberg 1977, Hixon 1980, Zach and Smith 1981, Mace et al. 1983, Schoener 1983). The latter two predictions examined the effect of other time budget constraints on foraging (e.g., Ydenberg 1984). A converse prediction was proposed by Ydenberg and Krebs (1987) concerning the influence of number of competitors on males; males may stay near the nests more and, thus, decrease the foraging effort when exposed to more competitors.

Males that are energy maximizers should store some energy when food demands are low and use those energy reserves when the energy demands are high. If male Merlins are energy maximizers, I would predict no significant increase or decrease in foraging effort as the breeding season progresses (Barclay 1989). If foraging is the only activity maximized by males, I would also predict no significant effect on their foraging effort of clutch or brood size, prey abundance, body mass, number of

competitors, or time allocated to incubation (Zach and Smith 1981, Hoffman 1983, Schoener 1987b, Barclay 1989).

5.2 Methods

The research was conducted in Saskatoon from May to July, 1988-1990. Males for this study were radio-tagged. Methods are detailed in Chapters 3 and 4.

Five different males per year 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 (data from a yearling male were excluded). Each male was followed for a total of 24 hours during the incubation and 16 hours 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 so that all monitored males were followed when they had chicks of equivalent age (± 7 days). Data from different years were pooled because I found no significant difference in the foraging activities of the males during each breeding period among different years (Kruskal-Wallis ANOVA, $df = 2$, $P > 0.05$ - $P > 0.50$). Foraging effort variables and proximate factors could not be compared during

the fledging period because sample sizes were too low to perform correlation analyses.

The 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. 1991). However, when sitting, it was not apparent whether Merlins were resting or hunting, therefore, I used only flight activity as an index of foraging time. The changes in signal amplitude of the radio-transmitter revealed whether a male being observed was sitting or flying. The number of feeding trips per hour for a male during a breeding period was determined as the number of foraging trips observed divided by the duration of total observation period. The duration of foraging bouts refers to mean duration of all foraging trips made by a male during a breeding period.

Prey abundance in the hunting ranges of males was estimated by making bird counts on 1-km randomly selected transects. Transect count methods are detailed in Chapter 4. As predators may adjust their foraging effort based only on the abundance of their main prey (Temeles 1987, Chapter 4), 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, Chapter 2). I failed to find any significant correlations and therefore did not subdivide the potential prey category for further analysis.

As my results were based on directional predictions, I used one-tailed statistical tests.

5.3 Results

Among the three variables of foraging effort studied (Fig. 5.1), there was a significant inverse relationship between mean duration of foraging bouts and number of feeding trips during the incubation period (Kendall rank-order correlation; $T = -0.55$, $n = 12$, $P = 0.006$). In the nestling period, a similar relationship was found ($T = -0.67$, $n = 13$, $P = 0.0007$), as well a correlation between mean duration of foraging bouts and percentage of time flying was also significant ($T = 0.54$, $n = 13$, $P = 0.004$).

The mean percentage of time spent flying by males increased from the incubation to fledging periods (Kruskal-Wallis ANOVA, $KW = 21.72$, $df = 2$, $P = 0.001$; Fig. 5.1A). Of 11 males tracked both during the incubation and nestling periods, all increased their proportion of time flying in

the nestling period, although the degree of the increase varied (Fig 5.2A). Of four birds that were followed during both the nestling and fledging periods, three increased and one decreased flying time (Fig. 5.2A).

The mean number of feeding trips peaked in the nestling period and then declined ($KW = 12.31$, $df = 2$, $P < 0.01$; Fig. 5.1B). The number of feeding trips increased from the incubation to nestling period for all 11 males (Fig. 5.2B). All males tracked both during the nestling and fledging periods decreased the number of foraging trips in the fledging period (Fig. 5.2B). The mean duration of the foraging bouts did not differ significantly among the three breeding periods ($KW = 4.76$, $df = 2$, $0.05 < P < 0.10$). This foraging variable increased for seven males but decreased for four from the incubation to nestling period (Fig 5.2C). Two males increased while two decreased the mean duration of their foraging bouts from the nestling to fledging period.

Among the different proximate factors (i.e, clutch size, prey abundance, body mass, number of competitors, and time allocated to incubation) and three variables of foraging effort, only the correlation between total potential prey abundance and percentage of time flying was significant for the incubation period ($T = -0.45$, $n = 12$, $P = 0.02$). The partial correlation analyses showed that prey

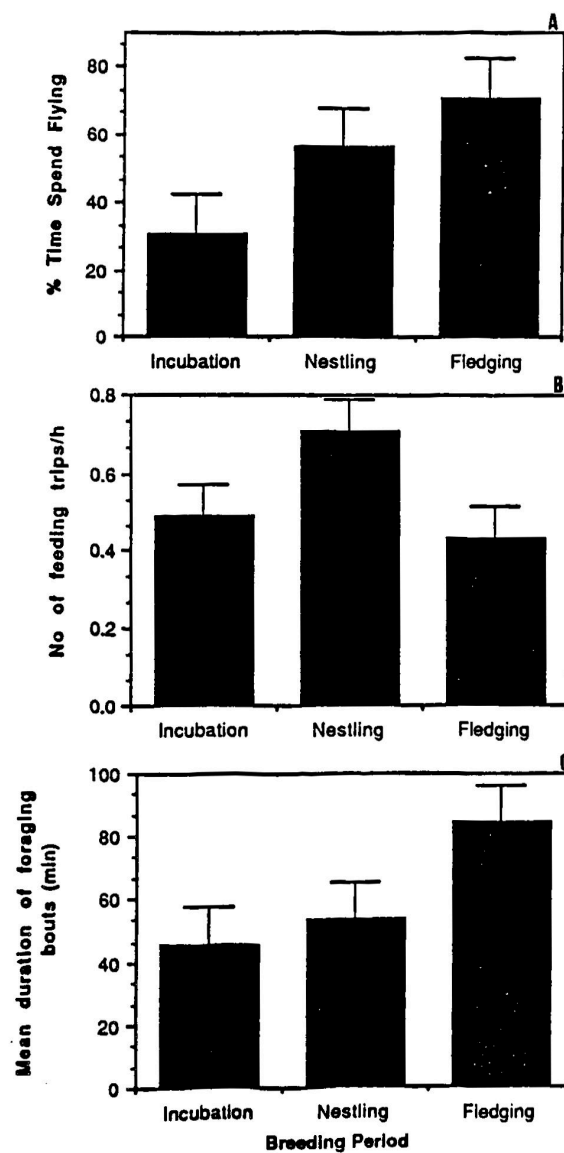


Figure 5.1. Foraging effort of male Merlins during the breeding season. Each bar represents the mean for all males observed during that period (for sample sizes see Fig. 5.2). The lines on top of the bars represent SE.

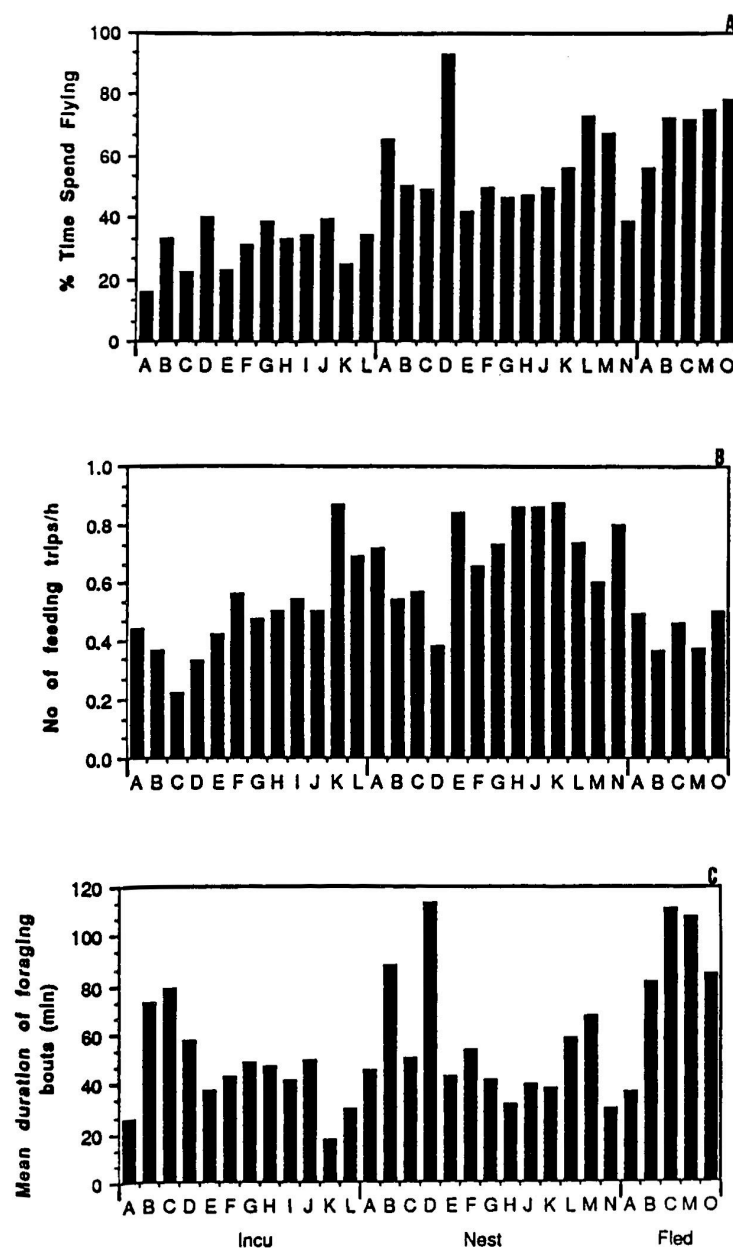


Figure 5.2. Foraging effort of breeding male Merlins with progress of the breeding season. Letters represent individual males.

abundance is independently correlated with the percentage of time spent flying by males (Table 5.1).

For the nestling period, two correlations were significant: brood size and percentage of time flying ($\bar{r} = 0.44$, $n = 13$, $P = 0.02$), and number of active nests within 1 km and number of feeding trips ($\bar{r} = -0.43$, $n = 13$, $P = 0.02$). These correlations remained significant when other studied variables were controlled statistically (Table 5.2).

5.4 Discussion

Males increased significantly time spent foraging with the progress of the breeding season. Males increased the number of foraging trips per unit time from the incubation to nestling period and decreased such trips when females started supplementing food at the nests. Consistent with the foraging time minimization strategy, both these foraging variables increased in all studied males from the incubation to nestling periods despite of individual differences in prey abundance changes in their ranges (see Table 4.3). Previously, Geer (1981) documented that male Eurasian Sparrowhawks (Accipiter nisus) decreased prey delivery rates at the nest as females increased such deliveries during the nestling period.

Table 5.1. Kendall's partial rank order correlation analyses to determine the relative effect of different variables on foraging effort of males Merlins during the incubation period. Partial correlations are based on two-tailed tests. PA = prey abundance and PTF = percentage of time spent flying.

Controlled variable	PTF vs PA	
	(-0.45)	
	<u>T</u>	<u>P</u>
Clutch size	-0.46	<0.05
No. active nests	-0.40	0.05
Body mass	-0.46	<0.05
Time allocated to incubation	-0.48	<0.05

Table 5.2. 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. Partial correlations are based on two-tailed tests. AN = number of active Merlin nests, BS = brood size, NFT = number of feeding trips made per hour, and PTF = percentage of time spent flying.

Controlled variable	PTF vs BS		NFT vs AN	
	(0.44)		(-0.43)	
	<u>T</u>	<u>P</u>	<u>T</u>	<u>P</u>
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

Male Merlins showed a decrease in foraging time in rich prey areas during the incubation period, and with decreasing brood size during the nestling period. Both these results are consistent with the foraging time minimization strategy. However, I found no significant influence of body mass, clutch size, and, somewhat surprisingly, time allocated to incubation on the foraging effort. These results are in accordance with the energy maximization strategy.

The more feeding trips per unit time male Merlins made, the shorter the trips were, both in the incubation and nestling periods. This indicates that males adjust their foraging trip durations in a fixed foraging time during a breeding period. Males flew more often in longer foraging trips in the nestling period, showing that indeed males did increase foraging effort during this period not only foraging time. Both these results are in accordance with the time-minimization strategy.

Considerable literature exists on the foraging effort of raptors during the nestling period (e.g., Newton 1978), but few studies have examined their foraging effort over the whole breeding season (e.g., Green 1976, Masman et al. 1988, Holthuijzen 1990). Most of the latter studies showed an increase in foraging effort (largely determined by prey delivery rates) with the progress of the breeding cycle.

With respect to the influence of brood size on foraging effort, both an increase with increasing brood size (e.g., Holthuijzen 1990) and no increase (e.g., Simmons 1986) have been reported. Although not implied by the authors, these different results may reflect different foraging strategies of the parents.

A recent study of the Eurasian Kestrel (*F. tinnunculus*) indicated that they acted as energy maximizers during the breeding season as they did not increase their hunting flight activity with the progress of the breeding season and with experimental manipulation of the hunger level of the young (Masman et al. 1988).

Most of my results suggest that male Merlins are foraging time minimizers. In future, energy-budget data should be collected to confirm the results of present time-budget study of male Merlins. There are two main reasons why time minimization might be an optimal strategy for male Merlins. First, energy maximization would have increased fat deposits, which increases body mass but may decrease maneuverability (Andersson and Norberg 1981). As Merlins are aerial predators, this could decrease foraging efficiency. Second, due to the high density of the nesting Merlins in Saskatoon, nonforaging time can be used to prevent extra-pair copulations (Sodhi 1991c), intraspecific

brood parasitism (Sodhi 1991c), and nest predation (Wiklund 1990). Over the whole breeding season, about 60% of the attacks against potential nest predators (corvids) were by males (Sodhi et al. 1992). On average, males spent $65.1 \pm 2.6\%$ (SE; range: 47.8-80.4%), $42.2 \pm 4.0\%$ (12.5-60.0%), and $9.2 \pm 2.0\%$ (5.3-15.1%) percent of their time near their nests (within 100 m), during the incubation, nestling, and fledging periods, respectively. Therefore, it is likely that males enhance their fitness by staying near their nests and adopting a time minimizing foraging strategy.

During the nestling period, males 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 of high food demand, increased nesting density suppresses the number of foraging trips a male can make.

My data also show individual differences in the foraging effort among males (Fig. 5.2), perhaps a reflection of differences in current reproductive efforts or variations in prey abundance in individual ranges (Table 4.3). During the fledging period, these differences may result from differences in foraging effort of their mates. Smith et al. (1989) showed that male Pied Flycatchers (Ficedula hypoleuca) reduced incubation feeding of the females that were supplemented with food. Therefore, male Merlins could

probably adjust their foraging effort depending upon the rate of feeding to the fledglings by their mates.

6. GENERAL DISCUSSION

Food is considered to be a major factor affecting reproduction and abundance of birds (Lack 1954, 1966, Fretwell 1972, Drent and Daan 1980, Newton 1980). It does so by varying seasonally (Fretwell 1972, Newton 1980), stochastically (Wiens 1977), in a density dependent manner (Lack 1954, 1966), or by affecting spacing behaviour (Patterson 1980).

In some birds, food supplementation has increased population density (Hogstedt 1981), clutch size (Reese and Kadlec 1984, Hochachka and Boag 1987, Arcese and Smith 1988, Knight 1988), nestling mass gain (Dhindsa and Boag 1990), fledgling success (Hogstedt 1981, Hochachka and Boag 1987, Dhindsa and Boag 1990), and (or) advanced the time of breeding (e.g., Davies and Lundberg 1985, Arcese and Smith 1988, Korpimäki 1989, Dhindsa and Boag 1990). However, the results of food supplementation have not been consistent or replicated in all populations studied (e.g., Smith et al. 1980).

Observational studies also documented the indirect or direct impact of food supply on bird reproduction and numbers (e.g., Jespersen 1929, Kluyver 1951, Lack 1966, Galushin 1974, Goss-Custard et al. 1977, Korpimäki 1988). Recently, Korpimäki and Norrdahl (1991) demonstrated that food supply affects bird populations by regulating

immigration and emigration. Studies that have specifically compared foraging ecology of birds with food density, have found that birds at presumed, or measured, higher food densities show an increase in feeding rates (Goss-Custard 1977, Monaghan et al. 1989), but a decrease in feeding time (Gibb 1954, 1960, Feare 1972) intraspecific aggression (Gibb 1954, 1960, Goss-Custard 1977) and feeding territory (hunting range) size (Stenger 1958, Gill and Wolf 1975, Village 1982b, McFarland 1986, Temeles 1987, Collopy and Edwards 1989, Tidemann 1990). My study revealed an inverse effect of food density on hunting range size (Chapter 4) and foraging time (males- incubation period; Chapter 5) of breeding Merlins. For a future study, I suggest that supplemental food be provided to breeding adult or nestling Merlins to test precisely the effect of food abundance and nestling hunger on foraging effort and hunting range sizes of breeding Merlins.

The Merlin nesting population in Saskatoon has increased from one pair in 1971 to 30 pairs in 1990 (Oliphant and Haug 1985, Sodhi et al. 1992). The availability of safe nesting sites and abundant food are two main factors that could produce this population expansion (Sodhi et al. 1992). Rapid urbanization has also been recorded for many other avian species. For example, the Mistle Thrush (Turdus viscivorus), which originally nested in continuous conifer forests of Germany, moved

systematically from these habitats to fragmented deciduous forests, trees in cultivated areas, remote human settlements, suburban areas, and finally to parks in the cities between 1925 and 1940 (Peitzmeier in Hilden 1965). The change in habitat use was so rapid that genetic selection could not have been the main factor causing it. Hilden (1965) suggested that rapid colonization of new habitats may be facilitated by habitat imprinting. Experimental studies show that species have genetic preferences for habitat (Klopfer 1963), however early experience in some species may modify habitat preference (Klopfer 1963, Gluck 1984, Grunberger and Leisler 1990).

My study shows (Chapters 3 and 4) that breeding male Merlins hatched and raised in Saskatoon (residents) had significantly smaller hunting ranges than those presumed to have hatched outside the city (immigrants). I also found that immigrant birds generally included less urban habitat in their ranges (Chapter 3). First time breeding resident Merlins (males) also raised significantly more young than immigrants (unpubl. data). Thus, there are benefits for residents to return to Saskatoon to breed. I speculate that these benefits may be reinforced by habitat imprinting and have brought increasingly more birds to breed in Saskatoon in recent years. Perhaps, immigrant birds do better by nesting in Saskatoon than in their native habitats where they might face the option of not breeding at all. If so,

there would also be benefits for immigrants to colonize this urban area. Moreover, hunting range sizes of immigrant and resident males differed significantly only during the earlier part of the breeding season (Chapter 4). This suggests that perhaps immigrants modify their foraging activities as they become acquainted with the habitat. However, the effect of new habitat on the foraging activities of birds remains experimentally untested. Most similar experimental studies are restricted to the effect of habitat imprinting on the habitat selection (e.g., Grunberger and Leisler 1990).

House Sparrows (Passer domesticus) made up about 65% of the kills made by breeding Merlins (Chapter 2). Therefore, the Merlin can be broadly considered a specialist predator, although the degree of specialization on House Sparrows varied among individual Merlins as some birds specialized instead on the Horned Lark (Eremophila alpestris) (Chapter 2).

Specialization is favoured in a species when: 1) it exploits a stable and abundant food supply (Emlen 1966, Schoener 1971, Sherry 1984, Recher 1990), 2) it feeds in a large area (Orians and Pearson 1979, Schoener 1979), 3) it relies mainly on "pursuit" rather than "search" strategy to obtain prey (MacArthur and Pianka 1966, Schoener 1971), and 4) energy values (i.e., net energy gained by a predator) differ widely among prey species (Hughes 1979).

The food supply of Merlins is relatively stable and abundant in Saskatoon. A rough estimate from bird transect counts (Chapter 2; Appendix A) revealed that if all Merlins in the study area fed exclusively on House Sparrows, they would take only about 5% of the House Sparrow population. I also found that hunting ranges of Merlins were relatively large for the size of the bird, ranging up to 64.3 km² (Chapter 3).

The Merlin is a predator using the "pursuit" strategy to obtain prey since most of its foraging effort is spent pursuing, subduing, and consuming prey (i.e., it has higher handling times compared to predators feeding, for example, on insects). I did not measure prey energy values directly for different prey species. However, as prey species use cover differently (Chapter 2), they may offer different net energy values to foraging Merlins. It is hard to determine variation in the net energy values of different prey species from the available evidence. All-in-all, Merlins show most characteristics that favour specialization as predicted by foraging theory.

Depending upon ecological pressures, raptors exhibit different spacing patterns during the breeding season. For example, mutually exclusive hunting ranges have been recorded in the Golden Eagle (Aquila chrysaetos), Red-tailed Hawk (Buteo jamaicensis), and Swainson's Hawk (B. swainsoni) (Fitch et al. 1946, Palmer 1988, Collopy and Edwards 1989).

In contrast, the Peregrine Falcon (Falco peregrinus), Prairie Falcon (F. mexicanus), and Merlin have overlapping hunting ranges (Haak 1983, Palmer 1988, Chapter 3 of this study). Two main factors influencing spacing pattern during the breeding season are the number of competitors and prey characteristics (e.g., prey abundance, mobility, and stability) (Brown 1964, Brown and Orians 1970, Davies 1980, Davies and Houston 1984). I suggest that overlapping hunting ranges of Merlins in Saskatoon (Chapter 3) are due to their high nesting density and the abundance of prey.

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APPENDIX A. Abundance of potential prey species of Merlins in Saskatoon and surrounding areas (May-July). Data based on surveys of 6 urban and 6 rural 1-km transects. I = incubation, N = nestling, and F = fledging period.

Species	88			89			90		
	I	N	F	I	N	F	I	N	F
House Sparrow	168	207	89	146	176	100	94	95	53
Chipping Sparrow	19	24	9	8	18	22	22	15	17
American Robin	13	18	8	31	16	8	20	14	9
Cedar Waxwing	-	5	3	-	19	4	1	11	4
Yellow Warbler	18	12	3	-	11	11	6	9	2
Red-winged Blackbird	-	-	-	-	-	1	1	1	1
Black-capped Chickadee	1	3	2	1	-	1	-	-	2
White-throated Sparrow	1	-	-	-	-	-	3	-	1
House Wren	3	10	-	1	1	8	1	3	1
Western Meadowlark	5	4	4	2	1	1	6	5	4
Savannah Sparrow	3	2	1	1	1	1	2	3	3
Horned Lark	6	3	2	1	1	1	3	4	2
Vesper Sparrow	2	1	1	-	-	-	1	-	1
Brewer's Blackbird	7	10	4	5	3	1	3	7	6
Clay-colored Sparrow	22	20	4	1	8	2	5	2	2
Red-eyed Vireo	1	-	-	-	-	-	-	1	-
Swainson's Thrush	-	-	-	-	2	-	-	1	-

Killdeer	-	-	-	-	-	-	-	1	-
Red Crossbill	-	-	-	-	-	-	2	-	-
American Goldfinch	-	-	-	-	1	-	-	-	-
Hairy Woodpecker	-	-	-	-	1	-	-	-	-
Tree Swallow	1	3	-	-	-	-	-	-	-
Brown Thrasher	-	1	-	-	-	-	-	-	-
Red-breasted Nuthatch	2	-	-	-	-	-	-	-	-
Northern Oriole	1	-	-	-	-	-	-	-	-
Barn Swallow	1	-	-	-	-	-	-	-	-
Total	274	323	130	197	259	161	170	172	108

APPENDIX B. EFFECTS OF RADIO-TAGGING ON BREEDING MERLINS

Introduction

Radio-tracking is an important wildlife technique that enables researchers to obtain data otherwise difficult or impossible to collect. However, it is necessary to study the impact of transmitters on subjects to determine the reliability of the data collected and to ensure the well-being of study animals (White and Garrott 1990). Many researchers have used radio-tagging to study raptors (e.g., Marquiss and Newton 1981, Becker and Sieg 1987), but none has assessed the impact of radio-tagging (but see Taylor 1991). Most studies that have examined the effects of radio-tagging on birds have dealt with game birds (e.g., Erikstad 1979, Perri 1981, Hines and Zwickel 1985, Marks and Marks 1987). At least three negative effects of radio-tagging have been identified in the literature: 1) exhibition of abnormal behaviour during the postrelease period (Perri 1981), 2) decrease in reproductive success (Erikstad 1979), and 3) lower survival rate (Hessler et al. 1970, Johnson and Berner 1980, Warner and Etter 1983, Marks and Marks 1987).

I examined a population of breeding Merlins (Falco columbarius) in which some individuals were radio-tagged. My first objective was to determine if radio-tagged Merlins exhibit aberrant behaviour during the postrelease period.

My second aim was to compare the reproductive performance of males that were tagged during the pre-incubation period (their tags lasted through the nestling period or later) with untagged males. As males provide all the food for the females and young during most of the breeding cycle (unpubl. data), lower hunting success could affect reproductive success. For instance, clutch size, hatching success, and chick survival could decline due to lack of sufficient food, or to higher exposure to predation. Therefore, I compared both the number of chicks produced per breeding season and hatching success among tagged and untagged males. Last, I collated the return rates of the tagged and untagged birds to determine if radio-tagging had any detrimental impact on the long-term survival of the Merlins.

Methods

Radio-tagging methods and sample sizes are given in Chapter 3. The transmitters weighed about 4 g (2.4% and 1.6% of the male and female body mass, respectively) and those included in analyses lasted from 3 to 12 weeks.

The reproductive (the number of chicks at a bandable age [>8 d]; Warkentin et al. [1990]) and hatching success (number of eggs hatched/total number of eggs in a clutch \times 100) of twelve males (1988 = 3; 1989 = 5; 1990 = 4) tagged prior to the incubation were compared with 71 untagged males (1988 = 22; 1989 = 26; 1990 = 23). Data from different

years were pooled because the reproductive success did not differ significantly among the years in untagged (1988 = 4.0 ± 0.2 nestlings [SE]; 1989 = 3.8 ± 0.3 ; 1990 = 3.9 ± 0.3 ; Kruskal-Wallis ANOVA, $KW = 4.14$, $df = 2$, $0.05 < P < 0.10$) as well as in tagged male Merlins (1988 = 3.7 ± 0.9 ; 1989 = 3.2 ± 0.8 ; 1990 = 4.0 ± 0.7 ; $KW = 0.33$, $df = 2$, $P > 0.20$). Similarly, there did not appear to be large differences in the hatching success among different years within both tagged (1988 = 100%; 1989 = 90%; 1990 = 75%; $KW = 1.26$, $df = 2$, $P > 0.20$) and untagged males (1988 = 94%, 1989 = 84%; 1990 = 89%; $KW = 4.49$, $df = 2$, $0.05 < P < 0.10$).

The return rates during the subsequent breeding season were compared between 13 tagged and 46 untagged males, and 8 tagged and 66 untagged females. Because of low breeding dispersal among birds in general (Greenwood and Harvey 1982), and specifically among Merlins in this population (James et al. 1989), I assumed that the birds that did not return to Saskatoon during the following breeding season had died. Data from different years were pooled because the return rates of the untagged males (1988 = 5 of 14 returned; 1989 = 5/17; 1990 = 4/15; $\chi^2 = 0.16$, $df = 2$, $P > 0.20$) and females (1988 = 6/21; 1989 = 9/22; 1990 = 7/23; $\chi^2 = 0.43$, $df = 2$, $P > 0.20$) did not differ significantly across years. The small sample sizes on the tagged birds did not permit a similar statistical comparison (Males: 1988 = 1/3; 1989 0/5; 1990 = 2/5; Females: 1988 = 0/1; 1989 = 1/1; 1990 = 3/6).

To compare tagged and untagged Merlins, it was important that the two groups differed only in the method of marking (Hines and Zwickel 1985). First, differing body condition of the tagged and untagged birds could affect my results. I determined the body condition of the Merlins using the formula: $\text{body mass/wing cord length}^3 \times 100$, following Widen (1985). I compared the body condition of the tagged and untagged birds using two-tailed t -tests. Differential age distribution within the two groups could also bias my results (Erikstad 1979). Therefore I examined if there was evidence for age-biased mortality. The age of both untagged and tagged Merlins was known by year-specific colour and/or USFWS aluminium leg bands read during the nest investigation (see Warkentin et al. [1990], for details).

Results

Comparison Between Mounting Techniques

Out of four leg-mounts used, one was removed by the bird within 4 hours of attachment, and the antenna of another was pulled off on the third day following the attachment. I improved the remaining two leg-mounts by adding heat shrink over the antennas and leaving about one centimeter of leather near the attachment point for the birds to chew on. These two improved leg-mounts lasted for three and four weeks, respectively. The tail-mounts proved

to be more satisfactory as none were damaged by the birds and all lasted for a minimum of three weeks. However, two tail-mounts were prematurely moulted by two different males after three weeks of attachment.

Behaviour Upon Release

The usual response of Merlins following release was to stay perched at one spot and to peck at the transmitter package, and to preen frequently for about one to three hours. One male successfully hunted within two hours following release. The males performed all normal nesting activities; they successfully copulated, brought food for females and chicks, incubated, and defended their nests. The tagged females also hunted and fed chicks during the fledging period (i.e., when they normally hunt during the breeding season; Oliphant [1974]). I did not observe any unusual behaviour on the part of the tagged birds beyond the initial preening of the transmitter package. I did not collect much data on the food delivery rates of the untagged and tagged males, largely because of problems in obtaining adequate controls. However, comparison between two 2-years old males (one tagged and one untagged; with four similar aged chicks each), did not show a significant difference in the food delivery rates in 16 1-hr observation periods over two days during the nestling period (tagged = 10 deliveries, untagged = 13; Wilcoxon signed rank test, $T = 20$, $df = 14$, P

> 0.05).

Hatching and Reproductive Success

The hatching success of eggs of tagged males was, on average, 87% (43/48), whereas that of the untagged males was 91% (278/305) ($\chi^2 = 0.52$, $df = 1$, $P > 0.20$). The mean reproductive success of tagged (3.5 ± 0.4 [SE]) and untagged males (3.9 ± 0.1) did not differ significantly ($t = 0.75$, $df = 81$, $P > 0.05$). The mean age of known-aged tagged males was 2.0 ± 0.7 years ($n = 14$) whereas that of untagged males was 2.6 ± 1.4 ($n = 52$) ($t = 2.0$, $df = 64$, $P < 0.05$). This age difference between the two groups should not bias my results because in the study area the reproductive success was independent of age of males (Oliphant et al. unpubl. data).

Survival of the Tagged and Untagged Merlins

Return rates of tagged and untagged birds did not differ significantly. Three out of 13 (23%) tagged males returned during the following breeding season, while 14 of 46 (30%) untagged males returned (Fisher's exact test, $P = 0.25$). Four of 8 (50%) tagged females and 22 of 66 (33%) untagged females came back during the subsequent breeding season (Fisher's exact test, $P = 0.22$). Difference in body condition between tagged and untagged birds potentially could bias my results, but I found that body condition did

not differ significantly between the two groups within each sex at the time they were trapped (Males: $t = 0.01$, $df = 49$, $P > 0.05$; Females: $t = 0.1$, $df = 67$, $P > 0.05$).

Furthermore, body condition did not differ significantly between the birds that did return and those that did not (both categories and sexes; $P > 0.05$). Because age composition differed between groups, the age-biased mortality also could have an impact on my survival comparisons. However, among known-aged males, no significant difference was found between the return rates of males less than two years old ($n = 15$) and more than two years old ($n = 9$) ($\chi^2 = 1.04$, $df = 1$, $P > 0.20$). Similar comparison among females was not possible because few (26%, $n = 110$) breeding females were of known-age.

Discussion

Previous studies have documented permanent abnormal behaviour (e.g., nest desertion, reduced feeding efficiency) in tagged birds upon release (Boag 1972, Perri 1981, Gessaman and Nagy 1988, Massey et al. 1988, Wanless et al. 1989). Other studies have noted temporary changes in behaviour which appear to normalize after a period of acclimation (Herzog 1979, Nenno and Healy 1979, Sayre et al. 1981), or found no observable changes in behaviour (Brigham 1989).

Studies by Boag et al. (1973) and Lance and Watson

(1977) on Red Grouse (Lagopus l. scoticus) revealed no significant difference in the reproductive success among tagged and untagged birds. Similarly, Taylor (1991) did not find any significant difference in reproductive success among tagged and untagged Barn Owls (Tyto alba). However, Erikstad (1979) recorded lower reproductive success in tagged Willow Grouse (L. l. lagopus) than untagged, but suggested that this was due to the conspicuous colour of the tags used, which may have made the broods more vulnerable to predation. Although some researchers have noted no significant effect of radio-tagging on mortality (Boag et al. 1973, Lance and Watson 1977, Herzog 1979, Kalas et al. 1989), others have observed that radio-tagging is associated with significantly increased mortality (Hessler et al. 1970, Johnson and Berner 1980, Warner and Etter 1983, Marks and Marks 1987).

These studies are on different species, using different radio-mounting techniques, and transmitter package masses in proportion to the body mass of the study subjects, factors which might be important variables in causing effects (Small and Rusch 1985, Kenward 1987, Brigham 1989, Marcstrom et al. 1989). This makes comparison among different studies difficult. I conclude that transmitters I used weighing about 2% of the adult body mass had minimal negative impact on behaviour, reproduction, or survival of breeding Merlins.

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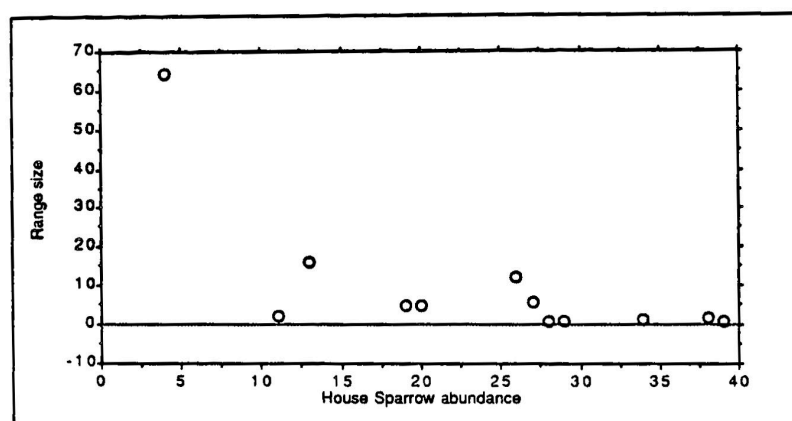
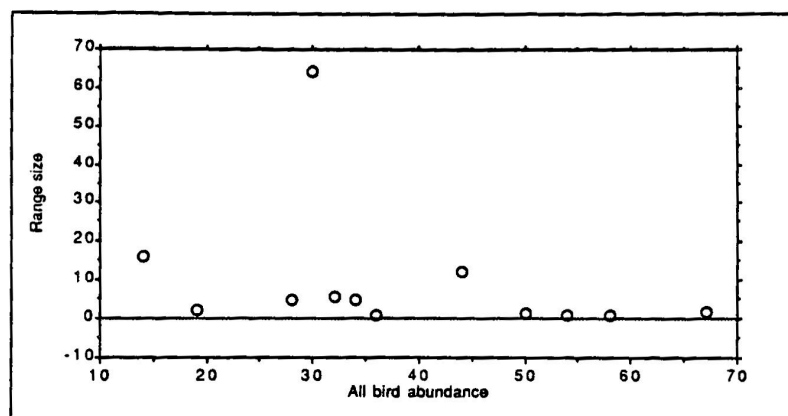
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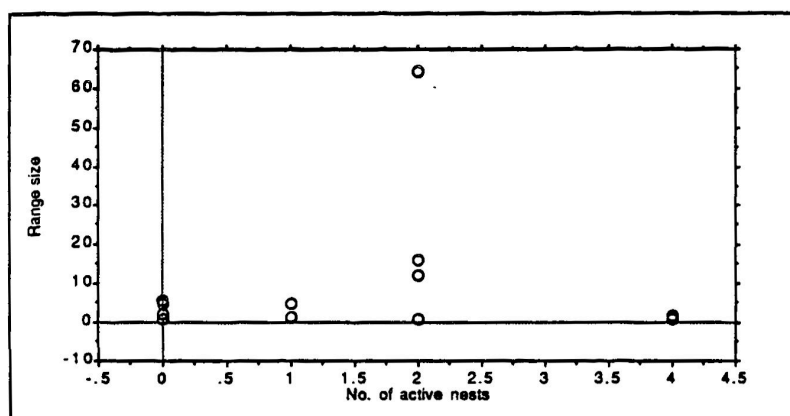
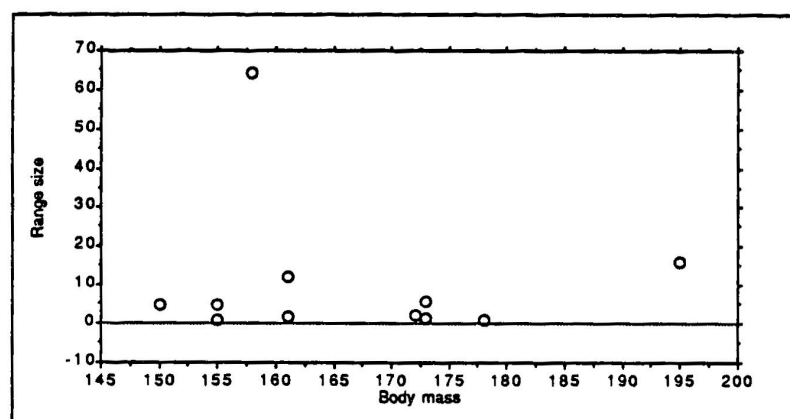
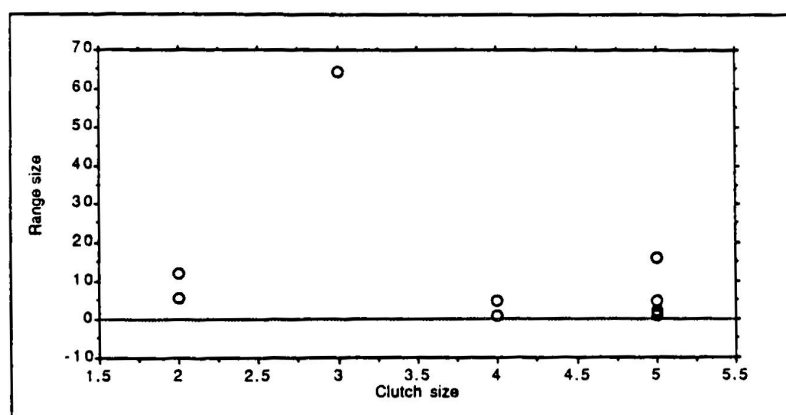
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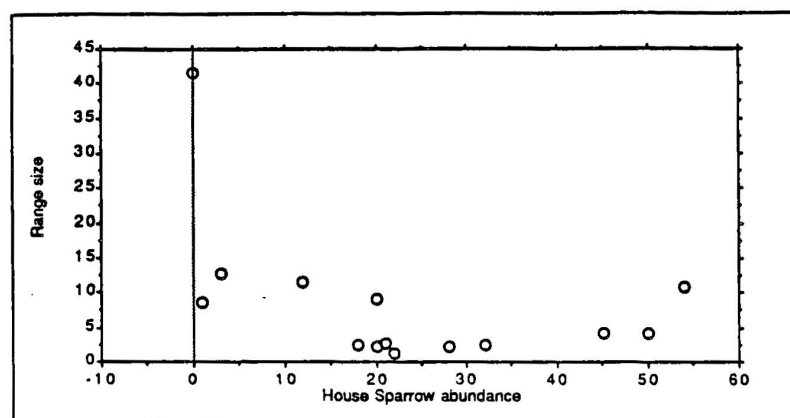
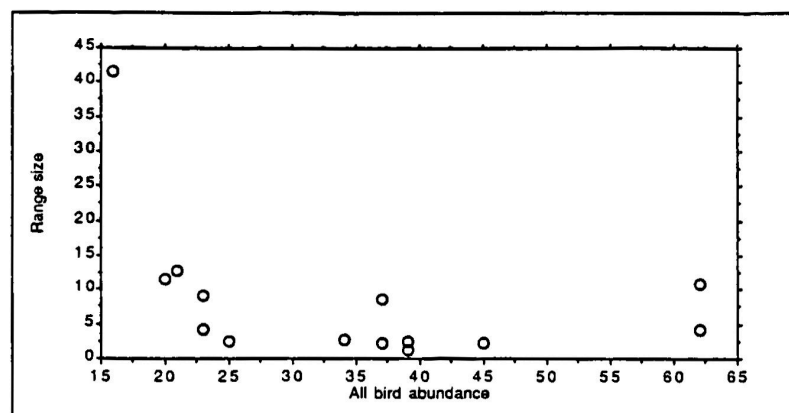
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APPENDIX C- CORRELATION PLOTS

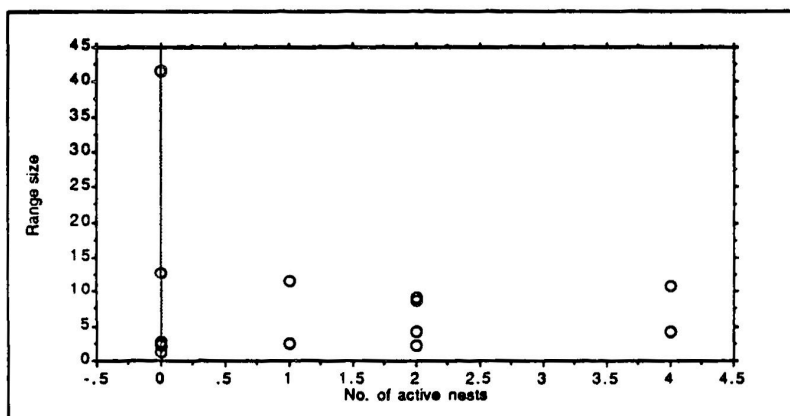
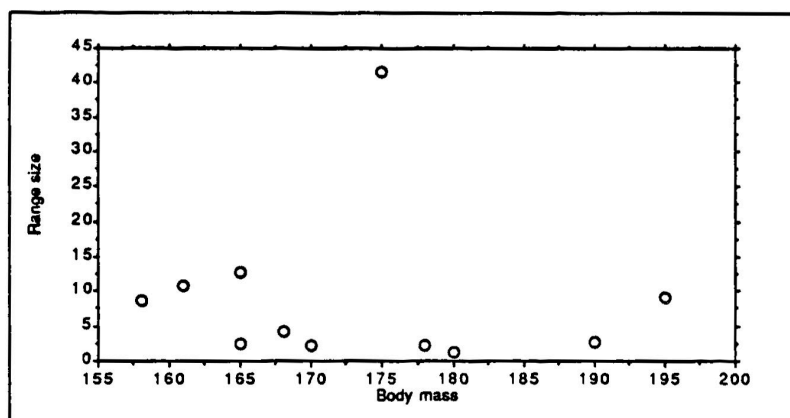
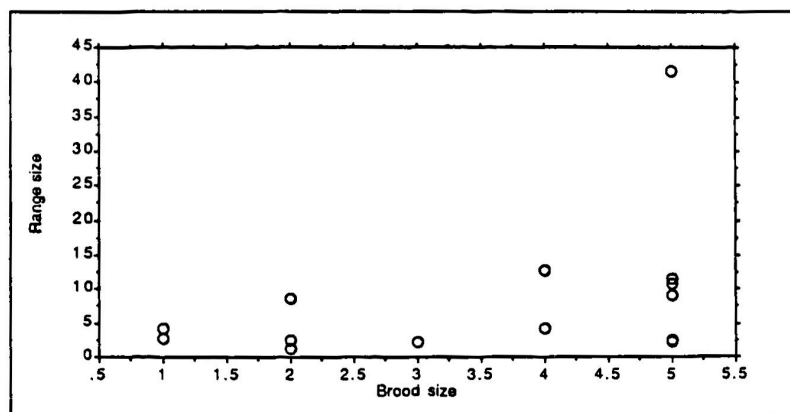


Chapter 4: The incubation period (males)

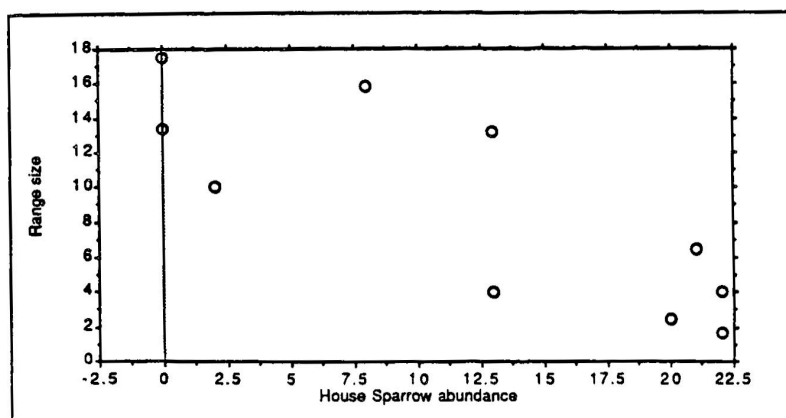
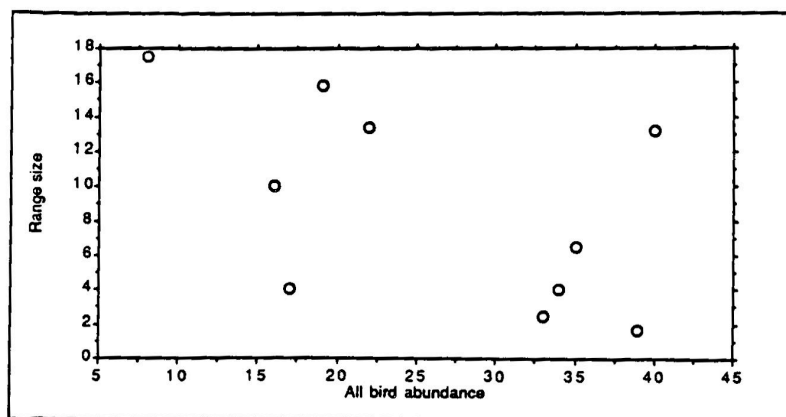




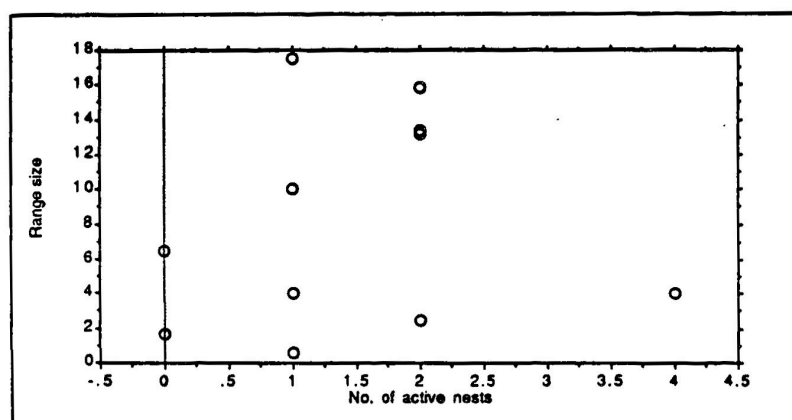
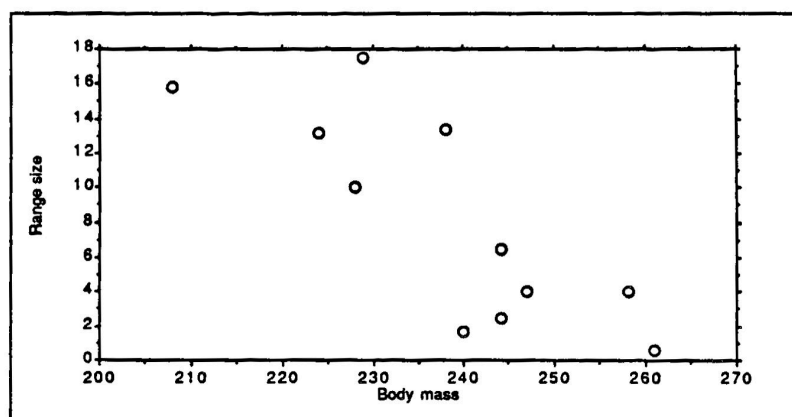
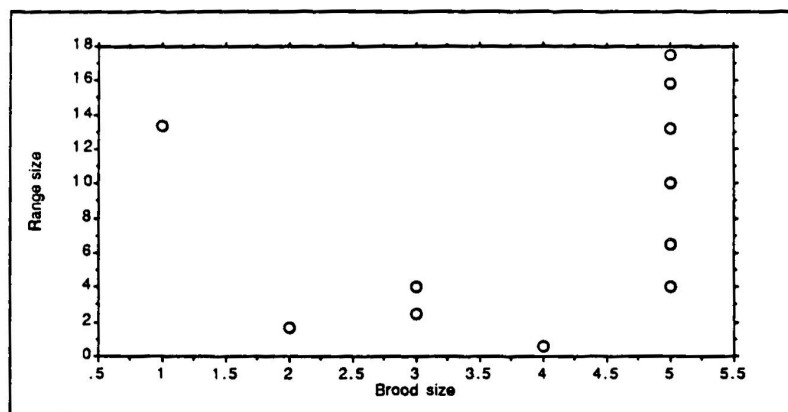
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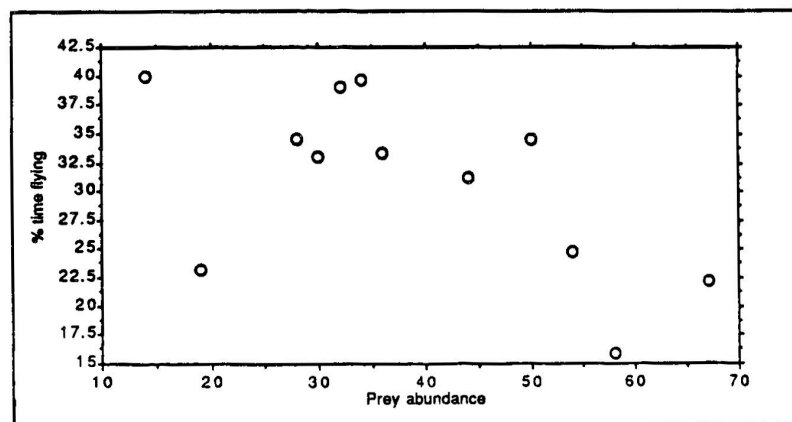
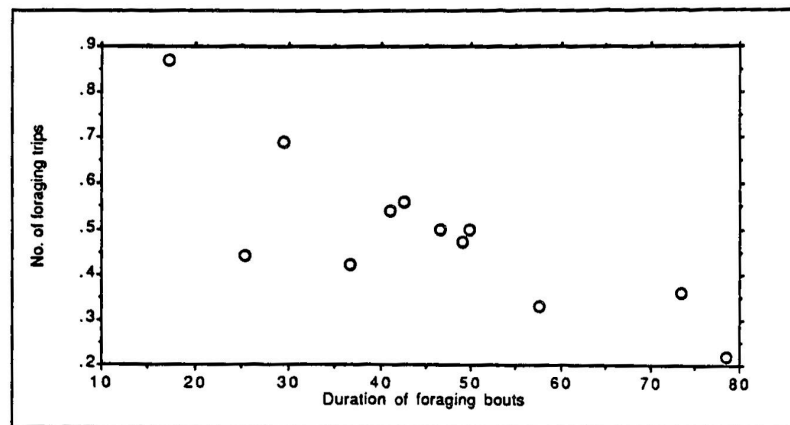


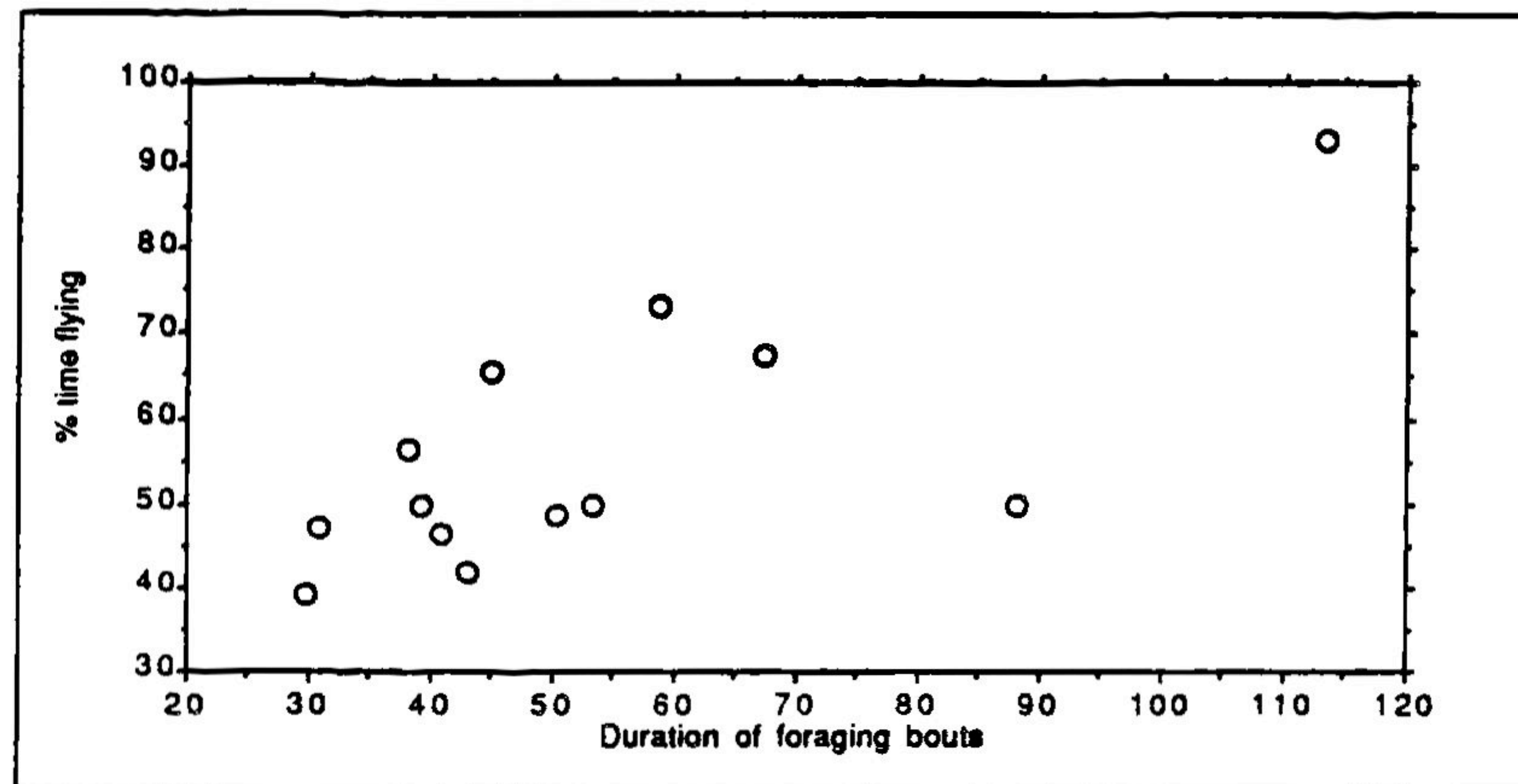
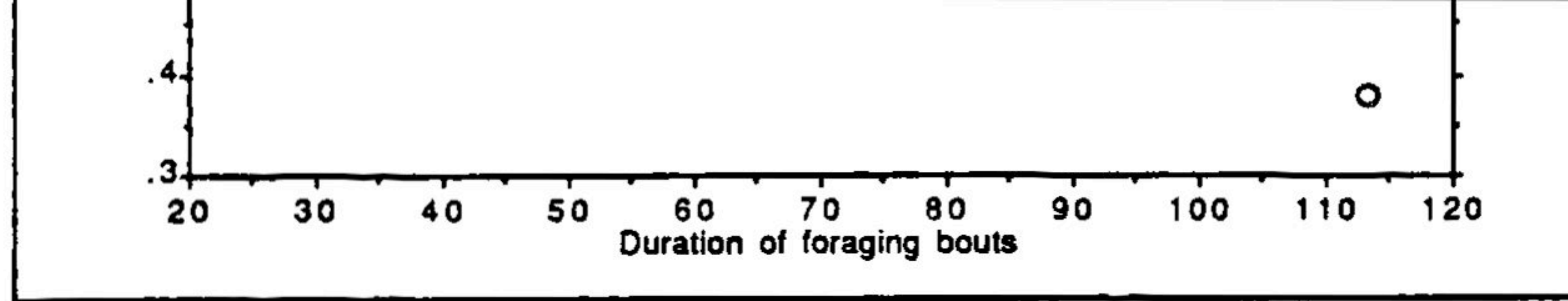
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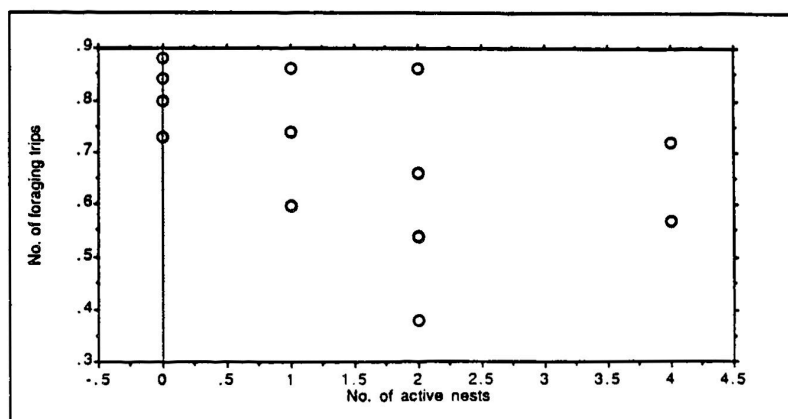
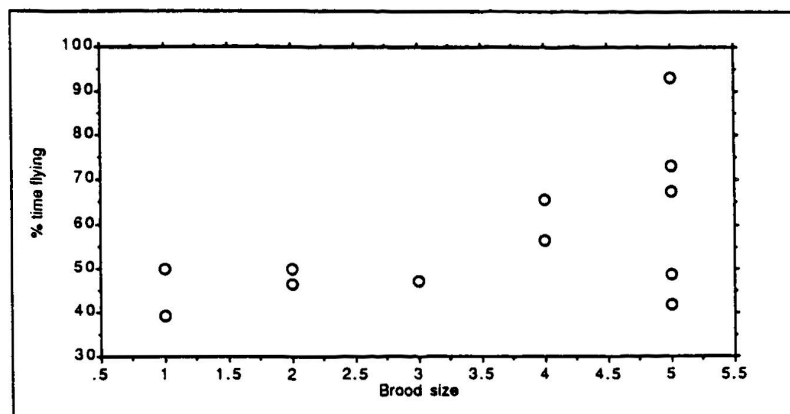
Chapter 4: The fledging period (females)







Chapter 5: The nestling period



Chapter 5: The nestling period