CENTRAL PLACE FORAGING AND PREY PREPARATION BY A SPECIALIST PREDATOR, THE MERLIN

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Abstract.—By discarding inedible body parts of prey at greater distances from a central place, a central place forager can reduce the cost of prey transport and thus increase net rate of energy delivery. This hypothesis was tested in a specialist predator, the Merlin (*Falco columbarius*). Fifteen male Merlins were radio-tracked in Saskatoon (Canada) for this study. Merlins were more likely to prepare prey at greater distances from their nests. The mean distance from where males transported prepared prey to the nests was significantly greater than from where they transported unprepared prey. Prey biomass delivered by males did not increase significantly with distance from the nests, however.

FORRAJEO DE UN PUNTO CENTRAL Y PREPARACIÓN DE LA PRESA POR UN DEPREDADOR ESPECIALIZADO: *FALCO COLUMBARIUS*

Sinopsis.—Al descartar las partes que no son comestibles, un forrajeador puede reducir el costo de la transportación de la presa de distancias mayores a un punto central, incrementando de esta manera la tasa neta de entrega de artículos que producen energía. Esta hipótesis fue puesta a prueba en un depredador especializado como lo es *Falco columbarius*. Para este estudio, 15 falcones machos, fueron rastreados con el uso de transmisores, en Saskatoon, Canada. Se encontró que a mayor distancia de sus nidos, más propensos fueron los halcones en limpiar sus presas. La distancia promedio desde donde las aves transportaron sus presas limpias resultó ser significativamente mayor que las distancias desde donde se transportaron presas sin preparar. Sin embargo, la biomasa de las presas entregada no aumentó significativamente con la distancia al nido.

Many birds bring prey items, one at a time to a central place (single-prey loaders). There are two principal models that predict how single-prey loaders should behave (Stephens and Krebs 1986). According to the size-distance model (Schoener 1979), the accepted range of prey sizes should decrease with increasing distance from the central place. The optimality model (Orians and Pearson 1979) predicts that the prey biomass brought to the central place should increase with increasing distance. The difference between these models are that the optimality model predicts that only larger prey is transported from greater distances, but if pursuit costs increase with prey size, the former model predicts the transport of smaller prey from greater distances (Stephens and Krebs 1986). Both these models assume that the central-place forager maximizes the net rate of energy delivery to the central place. These models, however do not make specific predictions about the impact on the behavior of a central-place forager of increased travel costs due to the load of the transported prey (Houston and McNamara 1985, Lessells and Stephens 1983, Tamm 1989). Foraging theory assumes that optimum parental foraging effort is that which maximizes fitness (Schoener 1987, Stephens 1990). As current breeding effort can influence future reproduction (Lifjeld 1989), it is

important to incorporate estimates of the amount of energy spent by the central-place forager while transporting prey in foraging models (Houston 1987).

The foraging behavior of a specialist central-place forager whose prey species do not differ greatly in size does not fit into either of the two main central place foraging models. If a specialist central-place forager can decrease the load carried during flight without decreasing the prey biomass delivered to the central place by discarding inedible body parts (e.g., feathers, head, scales), however, it could adjust its decision to prepare a prey in relation to distance from the central place. The prediction in this case is that the likelihood of prey preparation will increase as the distance from the central place increases.

I tested this prediction in breeding male Merlins (*Falco columbarius*). They are suitable for this test because: (1) during the breeding season they feed primarily on House Sparrows (*Passer domesticus*), which form 70% of the diet numerically (Oliphant and McTaggart 1977, Sodhi et al. 1990), (2) they bring one prey item at a time (single-prey loader) to the nest for the females and chicks during the entire breeding season (Sodhi, unpubl. data), and (3) they prepare (pluck) the prey before eating by discarding head, feathers and legs (Oliphant and Tessaro 1985, Warkentin and West 1990, pers. obs.).

METHODS

The data were obtained from 15 radio-tagged males between May and July 1988–1990, in Saskatoon (52°07′N,106°38′W), Canada. Each radio transmitter (model SS-1; Biotrack, Dorset, U.K.) weighed about 2% of the male's body weight and was attached dorsally on the tail by a method described by Kenward (1978). Data were collected after 1 d (to allow for acclimation to the transmitter) on each male. Two observers monitored each bird, one staying near the nest to note prey condition and species, and the other following the hunting bird to identify prey transport sites. The transport sites were kill sites when unplucked prey were transported to the nests. When males prepared prey, the plucking perches were considered to be transport sites, which were always within 100 m of the kill sites.

The data presented in this paper were collected during fair weather conditions (<10% cloud cover and <15 km/h wind speed; Sodhi 1991) and in the first and last 4 h of daylight when Merlins forage most intensively (Sodhi, unpubl. data). About 250 h were spent observing the males. On occasions (<25%) when it was not possible to identify prey transport sites exactly, these were estimated based on previous visual or radio contact, or by comparing notes between the observers. Distances of transport sites from the nests were measured from a 1:50,000 map of the city and surrounding areas by using a ruler to the nearest mm.

Based on dismembering and weighing House Sparrows (*n* = 10) found dead in the study area, I allocated the following approximate biomass values to the delivered prey: entire adult (100% of average weight), de-

capitated adult (90%), decapitated and partially plucked adult (85%), decapitated and fully plucked (80%), unplucked juvenile (90% of the average adult weight). The biomass of the decapitated or plucked juveniles was determined by computing values as above depending upon the degree of plucking. Average weights of prey species were obtained from Dunning (1984), Oliphant and Tessaro (1985), or the study skin collection at the Department of Biology, University of Saskatchewan.

Preliminary analysis showed that no one individual male brought only unplucked or plucked prey from every distance. Similarly, different breeding periods (incubation, nestling and fledging) appeared not to have influenced prey preparation. Therefore data from different birds and breeding periods were lumped. Data from different years were analyzed separately, if the same trend was observed in all years, they were lumped. Unless otherwise stated, most of the statistical tests are one-tailed because the results were based on directional predictions.

RESULTS

The males delivered 70 individuals belonging to seven species of passerines to the nests. Fifty-nine were House Sparrows, four Chipping Sparrows (*Spizella passerina*), two Cedar Waxwings (*Bombycilla cedrorum*), two Horned Larks (*Eremophila alpestris*), one American Robin (*Turdus migratorius*), one Yellow Warbler (*Dendroica petechia*), and one Clay-colored Sparrow (*S. pallida*). The prey were transported from distances ranging from 25 to 4800 m from the nests (Fig. 1). The mean transport distances were 1517, 1184 and 1681 m during 1988, 1989 and 1990, respectively (Kruskal-Wallis ANOVA, $KW = 1.3$, df $= 2$, $P > 0.05$, two-tailed test). Seventy-three individuals were captured by the males, but three (4.1%) House Sparrows were eaten entirely near the kill sites.

A correlation of the estimated prey biomass delivered with the transport distances was not significant ($r_s = -0.04$, $n = 70$, $P > 0.05$). The mean distance travelled when some prey preparation was done was greater in all years than the distance travelled when the prey was transported intact. The average distance from where the males did and did not prepare prey were 2030 and 927 m, 1395 and 611 m, 1771 and 1535 m during 1988, 1989 and 1990, respectively. Combining data from all years, the average distances where prey were plucked and not plucked were 1736 and 1025 m, respectively (Mann-Whitney $U = 376$, $Z = 2.4$, $P < 0.01$).

Generally, males were more likely to prepare prey at greater distances than near the nests (Fig. 1). Out of 30 times when males discarded 20% of the prey, five involved sites within 500 m and 25 more than 500 m from the nests ($\chi^2 = 12.0$, df $= 1$, $P < 0.05$; null hypothesis for this test was equal frequency distribution of prey preparation at <500 m and >500 m from the nests). There was some overlap in distances from where plucked or unplucked prey were transported (Fig .1). To test if hunger influenced the decision to prepare prey, I grouped two categories based on whether or not the males had captured at least one prey in the previous
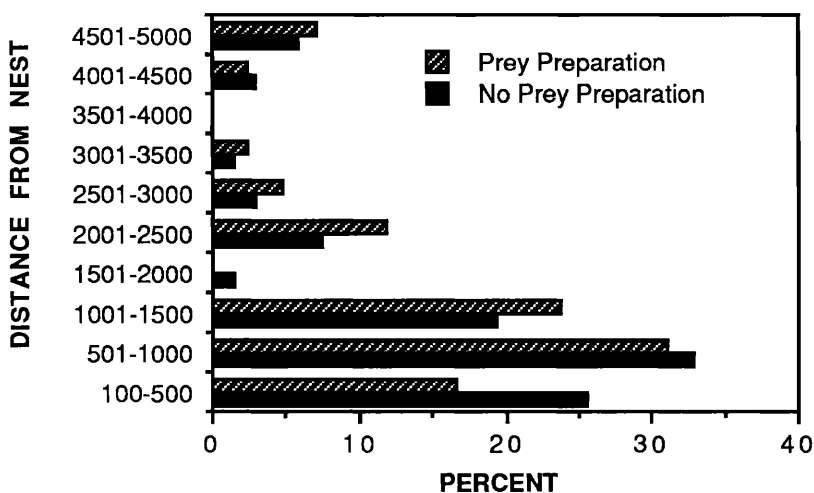
FIGURE 1. Percent of times prepared ($n = 43$) or unprepared ($n = 27$) prey were brought
   to the nests from different distances (m). Frequency distribution of each category is
   represented separately.

2 h. I compared the proportion of plucked and unplucked prey in these
two categories and found no significant difference ($x^2 = 1.5$, df $= 1$, $P >$
0.05).

DISCUSSION

Many generalist birds eat small prey away from the central place but
will transport larger prey items (e.g., Bull et al. 1989, Carlson 1985,
Krebs et al. 1987, Rudolph 1982, Sonerud 1989). In the Snail Kite
(*Rostrhamus sociabilis*), a specialist predator, Bourne (1985) noted that
larger snails were transported but smaller ones were eaten away from
the nest. These data, however, were based on only one pair of kites.

Many birds prepare prey before eating or bringing it to the central
place (Errington 1932, Gronlund et al. 1970). No study has examined
how the degree of prey preparation varies with distance from the central
place, however. The net rate at which a parent delivers energy at the nest
is: Gross energy gained minus energy spent (Houston 1987). The energy
spent by a central-place forager includes prey search, capture, preparation
and transport. It has been suggested that the flight cost varies linearly
with body mass (DeBenedictis et al. 1978, Schmid-Hempel et al. 1985,
Tamm 1989). Merlins can discard about 20% of the prey, which they
normally do not eat (head, feathers and legs; Oliphant and Tessaro 1985,
Warkentin and West 1990, pers. obs.). On average, House Sparrows
weigh 28.6 g during summer in Saskatoon (Oliphant and Tessaro 1985)
and 20% of their inedible parts make 5.7 g.

I used an equation given by Masman and Klaassen (1987) to estimate
flight costs of male Merlins:

$$\text{Flight cost} = 17.360 \; M^{1.013} \; b_w^{-4.236} \; S_w^{1.926},$$

where M is body mass (169.1 g in male Merlins), b_w is wing span (59.2 cm), and S_w is wing area (378.4 cm^2; average Merlin morphometric values were obtained from Warkentin and West [1990] or Warkentin et al. [1990]). This equation estimated the cost of flight for a male Merlin when carrying an unprepared House Sparrow to be 10.54 W and 10.23 W when carrying a fully prepared House Sparrow. This suggests that by discarding 5.7 g, males can reduce their flight costs by about 3%. The total energy savings will be proportional to the transport distance and therefore increase the net rate of energy delivery at the nests. There are some energetic costs involved in plucking prey, but it costs about 50% less than unloaded flight in Merlins (Warkentin and West 1990). Perhaps it is not profitable for males to prepare the prey at closer distances from their nests as they deliver prey to the females at the nests. The females prepare unprepared prey to feed themselves and chicks.

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