THE AUK
A QUARTERLY JOURNAL OF
ORNITHOLOGY

VOL. 106 JULY 1989 NO. 3

EFFECT OF PREY CONSUMPTION ON FORAGING ACTIVITY OF NORTHERN HARRIERS

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ABSTRACT.—Subsequent to feeding, territorial Northern Harriers (*Circus cyaneus*) curtailed hunting for short periods. I evaluated hypotheses for this behavior based upon resource depression, oxygen debt, satiation, or processing constraints. Lengths of inactive periods after prey consumption were uncorrelated with foraging time prior to prey capture, contrary to expectations if harriers had either depressed prey populations or incurred oxygen debts from their hunting activity. In contrast, lengths of inactive periods after prey consumption were highly correlated with time to consume prey. Presumably, harriers ceased hunting because of either a processing constraint or satiation. Because the regressions between lengths of inactive periods following meals and eating times did not change between the first and second meals of the day, harriers' inactivity following meals was probably due to a processing constraint. *Received 6 June 1988, accepted 23 January 1989.*

A CURRENT issue in behavioral ecology concerns an animal's foraging goals. Specifically discussed is whether the animal is either a foraging-time minimizer or an energy maximizer (Schoener 1971). A *time minimizer* acquires only enough food to satisfy a fixed minimal energy requirement, which maximizes the time available for other activities. In contrast, an *energy maximizer* maximizes the amount of energy gained beyond a fixed minimal energy requirement. Energy intake is limited by the total time available to feed. Correctly classifying an animal is necessary not only to describe how it selects prey items in its diet (e.g. Schoener 1971), but also to describe how it adjusts both its territory size and its patrol time in response to changes in food density, intruder pressure, or both (e.g. Schoener 1983, 1987; Hixon et al. 1983).

The relative proportion of available time spent foraging would seem to be the only data needed to classify an animal as either a time minimizer or an energy maximizer. However, a problem arises in determining the time actually "available" for foraging (Hixon 1982). For example, Rufous Hummingbirds (*Selasphorus rufus*) spend about 75% of the day sitting, and about 20% of the day foraging (Hixon et al. 1983). On the basis of time-budget analyses, they would be classified as time minimizers. Nonetheless, studies of Rufous Hummingbird digestive physiology indicated that their foraging time was constrained by the passage rate of nectar through the crop into the digestive tract (Diamond et al. 1986, Karasov et al. 1986). Thus, Rufous Hummingbirds are properly categorized as energy maximizers with a processing constraint (i.e. their energy intake is limited by the rate of food processing; Hixon 1982, Schoener 1983).

I studied wintering Northern Harriers (*Circus cyaneus*) defending feeding territories (Temeles 1986, 1987) and found that they foraged only 6.3-16.5% of daylight hours and sat 46.4-85.5% of daylight hours ($n = 11$ individuals; 4-9 h continuous observation per individual per day). Other studies of wintering harriers corroborated this (e.g. Craighead and Craighead 1969,

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Collopy and Bildstein 1987). These observations suggest that harriers may be foraging-time minimizers. However, time sitting does not always reflect time available to forage (Diamond et al. 1986, Karasov et al. 1986). Consequently, I examined whether or not harriers have a processing constraint on their foraging time similar to that of hummingbirds.

METHODS

I studied harriers in agricultural land located 3 km northeast of Davis, Yolo County, California (see Temeles 1986, 1987 for descriptions of the study area). The flat landscape allowed an unobstructed view in all directions of a minimum of 10 km. I collected data in the winters of 1984-1985 and 1985-1986, from late November to early February. During these periods, harriers defended winter feeding territories (Temeles 1986, 1987). I observed 132 h of harrier activities for 24 days in 1984-1985, and 80 h of harrier activities for 15 days in 1985-1986.

I made focal observations (Altmann 1974) of territorial harriers, and in any given focal period I watched a territorial individual continuously for an average of 6.6 h on days that averaged 9.5 h of daylight. I observed six territorial females in 1984-1985, and five territorial females in 1985-1986. Adult males typically did not defend winter feeding territories at the study area. Methods concerning the identification of territory owners and sex and age classes are given in Temeles (1986, 1987).

Observations were initiated from the moment a harrier was observed on its territory following first light (0645-0800). I used this procedure to decrease the possibility that a harrier had eaten before the start of my observations, which might affect foraging activity. For each territorial individual, I noted on a cassette recorder the date and time of each observation, the sex and age of the bird, the number of attempted prey captures and successful captures, the type of prey captured, and the time spent in foraging, perching, eating, or aggressively interacting. Harriers were observed at distances of 20-250 m, and 7 × 35 mm binoculars or a 15×-60× spotting scope were used when necessary. Elsewhere (Temeles 1986, 1987), I report methods concerning determination of capture attempts, capture successes, prey types, and time spent in various activities.

I used eating time as an estimate of prey size because I did not wish to disturb territorial harriers and influence their subsequent behavior by attempting to measure prey size directly. Two analyses indicated that eating time was a valid indirect measure of prey size. First, I compared eating times for prey of two size categories (*small prey* $\leq 1/2$ the length of a harrier's head or foot; *large prey* $> 1/2$ the length of a harrier's head or foot). Based on this criterion, prey categorized as "small" were eaten in <3.5 min ($\bar{x} \pm$ SE = 2.1 ± 0.3 min, range = 1.0-3.5 min, $n = 7$), whereas "large" prey required as long as 14 min to consume ($\bar{x} \pm$ SE = 10.1 ± 0.5 min, range = 8.0-14.0 min, $n = 12$). Second, I compared eating times for two prey species (*Mus musculus*, $\bar{x} \pm$ SE = 19.6 ± 1.1 g, $n = 27$; *Microtus californicus*, $\bar{x} \pm$ SE = 56.3 ± 2.4 g, $n = 4$) for the few instances where I could identify prey to species or locate prey remains after my observations were completed. Here, smaller *Mus musculus* required less time to consume (1.9 ± 0.1 min, range = 1.0-2.0 min, $n = 4$) than larger *Microtus californicus* (12.6 ± 0.9 min, range = 11.0-14.0 min, $n = 3$). Thus, eating time probably approximated prey size.

Statistical analyses were performed with BMDP statistical packages (Dixon et al. 1983).

RESULTS

Prey consumption and hunting activity.—Territory owners curtailed their hunting activities for a mean of 39.5 min (SE = 7.6 min, range = 0.25-183.00 min, $n = 30$ meals) subsequent to consuming prey. Temporary cessation of hunting occurred even after a harrier's first meal of the day.

Hypotheses for temporary cessation of hunting.—I hypothesized that inactive periods following prey consumption resulted from *processing constraints* (e.g. the passage rate of food through the crop into the digestive tract; Hixon 1982, Schoener 1983). I tested the processing constraint hypothesis against three alternative hypotheses for the temporary cessation of foraging after prey consumption. First, cessation of hunting after eating may have been due to *satiation*: territorial harriers simply are no longer hungry. The satiation hypothesis is distinguished from the processing constraint hypothesis by whether or not a bird's digestive tract is filled to capacity after feeding. According to the processing constraint hypothesis, cessation of hunting after eating represents a necessary period for crop-emptying before the bird can effectively forage again, and occurs even when the digestive tract has been only partially filled by feeding (DeBenedictis et al. 1978, Hixon et al. 1983). In contrast, under the satiation hypothesis, a bird ceases to forage after eating because its digestive tract has been filled to capacity, its daily energy requirements have been met or exceeded, or both. Second, harriers may sit after feeding to repay an *oxygen debt* (M. Hixon pers. comm.). In addition, they may have to flush lactate from their muscle tissues after actively foraging. Third, cessation of hunting by harriers after eating may result from *resource depression* (Charnov et al. 1976). This was observed for hummingbirds where removal of nectar depressed the food supply, and birds reduced their foraging activities until nectar levels were replenished (e.g. Ewald and Orians 1983). It is difficult, however, to envision how removal of one rodent could depress a territorial harrier's entire food supply. Thus, in contrast to hummingbirds for which the mechanism of resource depression is exploitative (i.e. physical removal of a resource), I hypothesized that the mechanism of resource depression for harriers might be behavioral where foraging harriers drive prey into hiding (Charnov et al. 1976, Temeles 1985).

Tests of processing constraint and satiation hypotheses.—Both the processing constraint and satiation hypotheses predict that hunting activity following prey consumption should depend upon meal size. The larger the meal, the longer it might take to pass through a bird's crop. Alternatively, the longer it might take until the bird is hungry again. I examined the relation between resumption of hunting and meal size by using the time spent eating as an indirect estimate of meal size (see Methods). Resumption of hunting activity was correlated strongly with the time it took for a harrier to consume a meal (Fig. 1; log [min until next hunt] = $-0.9 + 2.7$ log [min eating time]; $r^2 = 0.77$, $P = 0.002$, $n = 9$ meals; first meal of the day, 1985-1986). A similar correlation held in 1984-1985 (log [min until next hunt] = $-0.5 + 2.2$ log [min eating time]; $r^2 = 0.70$, $P = 0.009$, $n = 8$ meals; first meal of the day, 1984-1985). Analysis of variance of the regression coefficients over groups (Dixon et al. 1983) indicated that the differences between the two years were not significant ($F = 0.23$, $P = 0.79$).

The relation between subsequent hunting activity and eating time supports both the processing constraint and satiation hypotheses, but does not discriminate between the two. However, if territorial harriers ceased to hunt after prey consumption because they were satiated, then I expected the length of the inactive period following prey consumption to increase with each additional prey consumed. I assumed that harriers' digestive tracts become progressively more filled with each additional prey consumed, and energy requirements are closer to being met. I tested the satiation hypothesis by comparing the relation between time taken to consume a meal and time until the next hunting bout following prey consumption for the first and second meals of the day in 1985-1986. If harriers ceased foraging after a meal because they were satiated, I predicted that, for a given eating time, time until the next foraging bout would increase after a harrier's second meal, which would be reflected by a significantly more positive Y-intercept or slope. Contrary to the prediction of the satiation hypothesis, time until the next foraging bout did not increase after the second meal of the day. In fact, the relation of eating time to resumption of hunting for the second meal was virtually identical to the relationship for the first meal (log [min until the next hunt] = $-0.8 + 2.6$ log [min eating time]; $r^2 = 0.64$, $P = 0.009$, $n = 9$ meals; second meal of the day, 1985-1986). Differences between the two meals were not significant (ANOVA regression coefficients over groups, $F = 0.04$, $P = 0.96$).

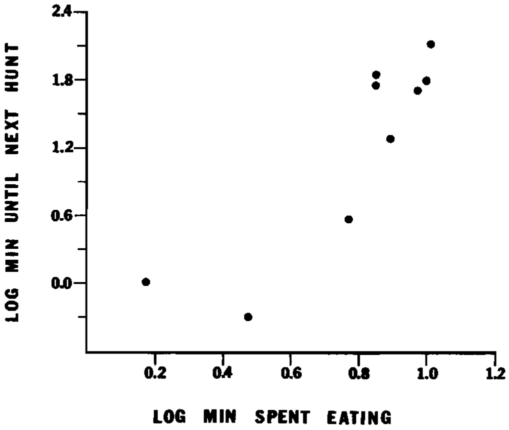

Fig. 1. Relation between minutes taken to consume prey (=log min spent eating) and minutes until the next foraging bout after prey consumption (=log min until next hunt) for territorial harriers, 1985-1986 data, first meal of the day. Log [min until next hunt] = $-0.9 + 2.7$ log [min spent eating]; $r^2 = 0.77$, $P = 0.002$, $n = 9$.

Tests of the resource depression and oxygen debt hypotheses.—If harriers behaviorally depressed their prey populations through their hunting activity, I predicted that how soon foraging resumed after prey consumption would depend on how long a bird had hunted prior to prey capture. The more time spent hunting, the more prey activity would be depressed. Similarly, if harriers temporarily ceased to hunt after eating to repay an oxygen debt, I predicted that lengths of foraging bouts prior to prey capture would be correlated with the length of sitting after prey consumptions. These predictions were not supported. I found no relation between sitting activity following prey capture and hunting activity prior to prey capture in either 1984–1985 or 1985–1986 (log [min until next hunt] = 1.07 + 0.16 log [min hunt before capture]; $r^2 = 0.004$, $P = 0.9$, $n = 9$ meals; first meal of the day, 1985–1986; log [min until next hunt] = 1.22 − 0.18 log [min hunt before prey capture]; $r^2 = 0.007$, $P = 0.9$, $n = 8$ meals; first meal of the day, 1984–1985).

DISCUSSION

Exclusion of competing hypotheses.—I suggest that harriers may have a processing constraint. The validity of this conclusion depends upon my ability to exclude competing hypotheses based upon resource depression, oxygen debt, and satiation. The harriers at my study area directed their attacks almost exclusively at rodents (93% of 531 capture attempts; Temeles 1987). Because these rodents used runways concealed beneath vegetative mats, it seems unlikely that harriers could have depressed the behavior of rodent populations by their hunting flights 3 m above the ground, and previous hunting activity certainly had no effect on subsequent hunting activity. Similarly, harrier activity patterns did not support the predictions of the oxygen debt hypothesis. However, I assessed resource depression and oxygen debt indirectly, and direct measurements on both behavioral depression of prey populations and oxygen debt of harriers are needed.

In contrast, satiation as an explanation for inactivity cannot be excluded completely. Because territory owners varied in their capture success, I had sufficient data to compare changes in activities following prey consumption only for the first and second meals of the day. A female harrier requires about 100 g of food per day for maintenance (Craighead and Craighead 1969), which is roughly equivalent to 4 small rodents. At my study area harriers' primary prey were rodents that weighed 10–60 g. Thus, if I had sufficient data on third and fourth meals, I might have observed some "satiation effect." However, I emphasize that it was improbable that any of the prey captured by the harriers weighed >100 g (their daily energy requirements), yet harriers were temporarily inactive even after their first meal of the day. Crop capacity of raptors is thought to be greater than their daily energy requirements (e.g. Brown and Amadon 1968, Stalmaster and Gessaman 1984), and it was unlikely that harriers' crops were filled to capacity.

Prey consumption might constrain harriers to cease hunting temporarily for a variety of reasons. Food in the crop increases body weight, which would increase flight costs and decrease maneuverability (Andersson and Norberg 1981). In contrast to many raptor species, harriers search for prey almost exclusively while in flight, increasing the importance of flight costs. Food in the crop also might increase a harrier's risk of injury during subsequent prey capture attempts. Finally, harriers are unusual among the Falconiformes by their possession of a facial ruff (Brown and Amadon 1968) which enhances hearing in a manner similar to owls (Rice 1982). Food in the crop might distort the shape of the facial ruff, and make it difficult for harriers to locate rodents beneath vegetation (G. Duke pers. comm.).

My observations underscore the problems in determining an animal's foraging goals (Hixon 1982). Harriers spend considerable time sitting on the ground, which would suggest at first that they are time minimizers (Schoener 1971). However, sitting bouts may actually facilitate crop-emptying between successive foraging bouts, and harriers may in fact be energy maximizers with a processing constraint (Hixon 1982, Schoener 1983). This problem could be resolved through behavioral and physiological analyses of harriers' time and energy budgets, and laboratory analyses of harriers' digestive physiology, as accomplished for hummingbirds (e.g. Hixon et al. 1983, Diamond et al. 1986, Karasov et al. 1986).

ACKNOWLEDGMENTS

I extend special thanks to G. Duke for consultation on raptor physiology that helped my interpretation, and to M. Hixon for a critical review of an earlier version of this paper. I also am grateful to A. H. Brush, K. Steenhof, T. Schoener, S. Pimm, J. Stamps, C. Toft, and an anonymous reviewer for suggestions. I especially value A. Hedrick for assistance beyond compare. I thank the Davis Audubon Society, Heidrick Farms, Inc., and Hunt-Wesson Foods, Inc., for granting me access to their lands. Supported by Graduate Student and Jastro-Shields Awards and Regents' and E. C. Anthony Fellowships from the University of

California, Davis, and a Science Alliance Postdoctoral Fellowship from the University of Tennessee.

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