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PREY HANDLING RELATIONSHIPS IN CAPTIVE OVENBIRDS

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ABSTRACT.—The effects of prey size, individual behavioral differences, satiation, and experience on handling time were tested experimentally on five captive Ovenbirds (*Seiurus aurocapillus*) feeding on *Tenebrio mollitor* larvae. While prey size and individual differences had the largest effects, all four factors significantly influenced handling times. For each bird, handling times were significantly correlated with prey mass. This relationship was best-portrayed as an exponential function. Handling times increased with satiation, but decreased with experience. Two of the birds that had relatively long bills got their highest foraging returns, in terms of prey mass ingested per unit handling time, when consuming large larvae. The shorter-billed birds displayed their highest returns on medium-sized prey. Our experiments suggest that small differences in bill size could significantly influence prey selection, ultimately producing divergent diets under natural conditions.

Handling time, the time required for a predator to eat a captured food item, is widely employed as a measure of time and energy investment for foraging animals (Krebs et al. 1983). This aspect of foraging behavior is particularly amenable to experimental manipulations (e.g., Kear 1962, Werner 1974, Krebs et al. 1977, Hughes and Elner 1979, Sherry and McDade 1982). Such experiments have generally focused on a single factor influencing handling time; they have used this factor to assess a predator's ability to maximize energy intake and to predict its diet in the laboratory or field.

We performed a series of experiments with captive Ovenbirds (*Seiurus aurocapillus*) that addressed the following questions: 1) How does prey size affect handling time? 2) Does satiation influence handling time? 3) Does experience affect handling time? 4) Do individual birds differ in their prey-handling relationships?

While prey size was of primary interest because of its role in dividing the food supply among species (Schoener 1965), we felt that all of these factors might influence the foraging behavior of Ovenbirds and other avian predators under natural conditions. In contrast to other studies that have used different prey species as the basis for different size classes (Zach and Falls 1978, Sherry and McDade 1982), we controlled for prey morphology and behavior by using various sizes of a single prey type, i.e., mealworms, the larvae of *Tenebrio mollitor.*

METHODS

We conducted experiments from 17 February–22 March 1978 at the University of Wisconsin–Madison using birds captured locally in September 1977. Ovenbirds were housed singly in 60 × 30 × 30 cm metal cages. They were maintained on a mixture of ground beef, egg, turkey starter mix, and vegetable materials (modified Lanyon recipe; J. Baylis, pers. comm.). Food and water were given twice daily, and once a day birds received one to three supplemental mealworms cut in halves or thirds.

Trials consisted of timing captive Ovenbirds as they ingested mealworms of five size classes. For each of five birds the following design was replicated four times: on each of five days the order in which five differently sized larvae were presented was randomized with the restriction that once a size class had been presented in a particular ordinal position (e.g., first, fourth) it could not be presented in that position on a succeeding day. During a single replicate we presented each individual bird with 25 larvae over the five-day period. The four replicates yielded 100 handling times per individual, 20 for each size class.

Experiments were run on successive days between 12:00–14:00, with 1–10 days separating replicates. Just before beginning a trial, we measured the mass and length of five mealworms, then assigned them to one of five size classes. The mean length (mm) and mean mass (g) for the five size classes (I–V) were as follows:

I = 14.0, 0.02; II = 17.5, 0.07; III = 20.0, 0.11; IV = 23.0, 0.16; V = 26.0, 0.21. We tested birds in their home cages, removing food and water a few minutes before a trial began. Larvae were presented singly, in the predetermined randomized order, in one-half of a petri dish placed on the floor of the cage. Handling time, the period from first contact to successful swallowing, was recorded to the nearest 0.01 min. Occasionally, after touching a larva, a bird either lost it on the cage floor or held it without swallowing. In such cases, if the interruption in handling was greater than 3 min, the larva and dish were removed from the cage and the presentation was immediately repeated.

We measured the length of the culmen, from the distal portion of the nares to the tip, on four of the five birds in June 1978. These lengths (mm) were as follows: Bird 1 = 10.3, Bird 2 = 9.0, Bird 3 = 8.7, Bird 4 = 8.5. Bird 5 was inadvertently released before its bill was measured.

We used linear regression and analysis of variance (ANOVA; Ryan et al. 1976) in conjunction with least significant difference tests (L.S.D.; Snedecor and Cochran 1967) to analyze our results. We performed a comprehensive ANOVA based on our experimental design that examined simultaneously the effects of prey size class, individual bird, trial replicate, and order of presentation nested within replicate on $\log_{10}$-transformed handling times. The ANOVA model included interactions between individual and size class and individual and replicate, since preliminary analysis of all possible pair-wise interactions showed these to be significant. Estimation and computation of sums of squares were carried out using regression on indicator variables in MINITAB (Ryan et al. 1976).

RESULTS

We performed preliminary linear regression analyses to assess the relationships of prey mass, length, and size class with handling time. Of the three measures of prey size, mass accounted for the largest amount of the variation in handling time. Prey mass was also significantly correlated with both prey length ($r = 0.894$, df = 530, $P < 0.01$) and prey size class ($r = 0.952$, df = 530, $P < 0.01$).

The relationship between prey mass and handling time appeared most linear, in an

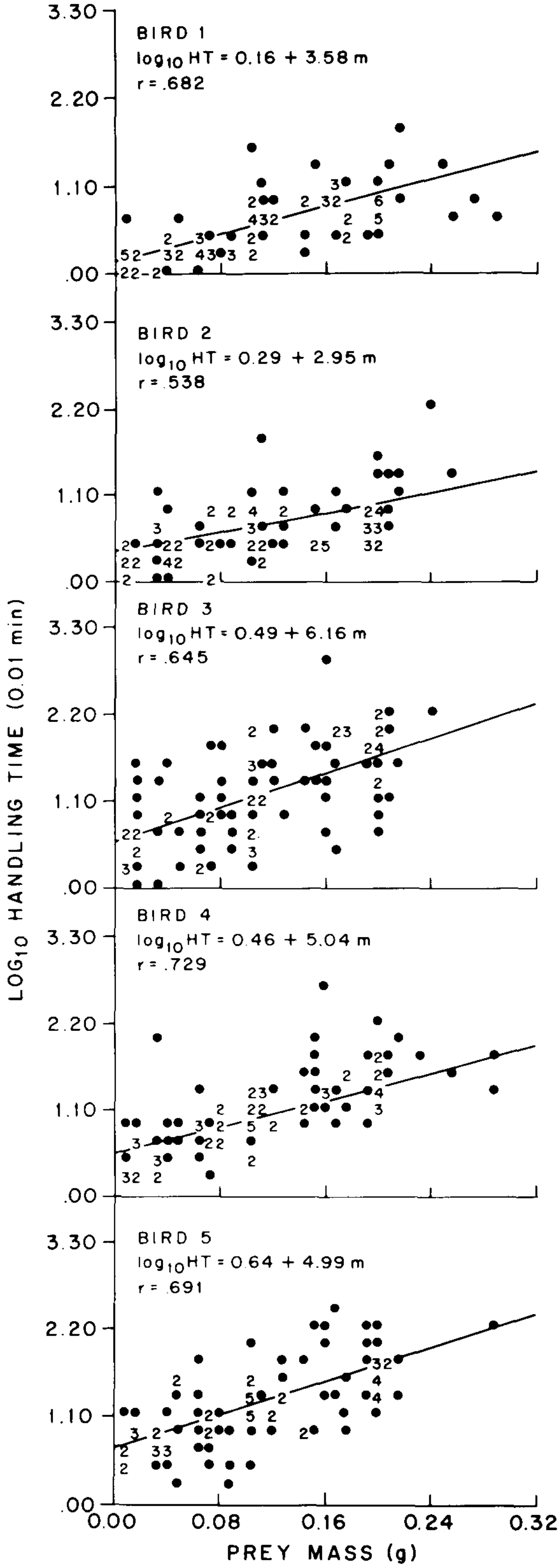

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FIGURE 1. Handling times (HT) for five captive Ovenbirds plotted against prey mass (m), including least-square regression equations and correlation coefficients. Samples consisted of 100 *Tenebrio* larvae for each bird. Circles represent single datum points. Arabic numerals represent multiple datum points, the numeral corresponding to the number of points plotted. The actual coordinates are located at the center of each numeral.

TABLE 1. Results of an ANOVA examining the effects of prey size, individual bird, trial replicate, and order of presentation nested within replicate on the handling times of five captive Ovenbirds feeding on *Tenebrio* larvae. Handling times were $\log_{10}$-transformed.

Source	df	SS	MS	F	P
Size	4	47.1879	11.7970	104.38	$\ll 0.001$
Individual	4	36.7391	9.1848	81.27	$\ll 0.001$
Replicate	3	3.4291	1.1430	10.11	<0.001
Order (replicate)	16	3.7482	0.2343	2.07	<0.01
Individual × size	16	3.8390	0.2399	2.12	<0.01
Individual × replicate	12	5.5087	0.4591	4.06	<0.001
Error	444	50.1793	0.1130		
Total	499	150.6313			

"eyeball" estimate, when a $\log_{10}$-transformation of the dependent variable (handling time) was employed, i.e., an exponential function. Additionally, the amount of total variation accounted for by the exponential model ($R^2 = 0.307$) was larger than for the arithmetic ($R^2 = 0.072$) or the power (log-log) models ($R^2 = 0.282$). For each bird, $\log_{10}$-transformed handling times were significantly correlated with prey mass (df = 98, $P < 0.01$; Fig. 1). On average, prey mass accounted for 43.6% (±9.1) of the observed variation in the handling times of individual Ovenbirds.

All four experimental factors (prey size class, individual bird, trial replicate, order of presentation) and both interactions (individual × size class, individual × replicate) significantly affected handling times, with prey size and individual bird accounting for the most variation (Table 1). L.S.D. tests, based on our comprehensive ANOVA, revealed the following patterns (Table 2):

1) In agreement with our linear regression analyses (Fig. 1), handling times increased with prey size. Handling times for all five size classes differed significantly from each other.

2) Individual Ovenbirds with longer bills (Birds 1 and 2) handled prey significantly faster than individuals with shorter bills (3 and 4).

3) Handling times tended to decrease with experience; i.e., Ovenbird performances improved with successive replicates.

TABLE 2. Results of L.S.D. tests, based on a comprehensive ANOVA (Table 1), comparing differences in handling times among prey size classes (I–V), individual birds (1–5), and trial replicates (A–D). Categories joined by a line did not differ significantly; $P > 0.05$.

	$\bar{x}$ handling times (0.01 min)				
Size classes	I	II	III	IV	V
(n = 100)	3.13	4.69	8.95	14.22	21.73
Individuals	1	2	4	3	5
(n = 100)	3.73	4.18	11.10	15.07	15.63
Replicates	D	C	A	B	
(n = 125)	6.55	7.73	8.73	11.04	

Because order of presentation was nested within replicate in our design, we did not perform an L.S.D. test for this factor. Inspection of our results indicated that handling times increased as a trial progressed, i.e., mean handling time (in 0.01 min) for first prey presented = 6.93, second = 7.59, third = 8.00, fourth = 9.44, fifth = 10.23; in each case n = 100). This pattern of increase, independent of prey size-class, was apparently due to gradual satiation.

We performed two sets of one-way ANOVAs to determine the causes of the significant interaction between individual and replicate. The handling time relationships among the individual birds did not vary across the four replicates; however, the rankings of the four replicates varied somewhat among individuals although the overall trend was maintained (i.e., all five birds tended to handle prey faster with experience).

The significant interaction between individual and prey size class reflected that, although the handling times of all birds increased with prey size, this increase was not equivalent across the five individuals (Fig. 1). We examined this relationship by calculating ratios of benefit:cost, in terms of mass of prey consumed per unit of handling time, for each Ovenbird for each prey size class. A one-way ANOVA and L.S.D. test indicated that for all prey sizes combined, Birds 1 and 2 had significantly higher benefit : cost ratios than Birds 3, 4, and 5 ($F_{4,495} = 57.20$, $P < 0.01$). For each individual, we performed one-way ANOVAs and L.S.D. tests comparing benefit:cost ratios among the five prey size classes (Fig. 2). For Birds 1 and 2, the smallest (I) and largest (V) size classes differed significantly in their ratios with the latter being more profitable. For Birds 3, 4, and 5, Classes I and V did not differ significantly. These birds achieved their highest benefit : cost relationships for medium-sized

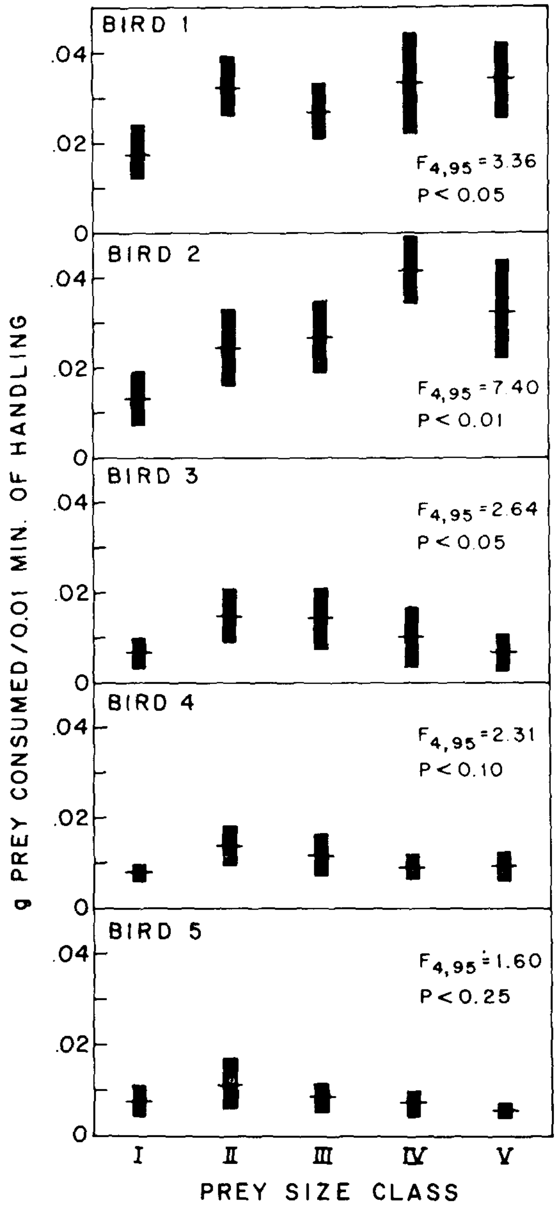

FIGURE 2. Summary of prey-handling patterns for five captive Ovenbirds, in terms of benefit (mass of prey consumed) : cost (time invested in handling), on five size classes of prey. Each record represents mean mass (g) consumed/0.01 min handling time and the corresponding 95% confidence interval based on 20 *Tenebrio* larvae. Included are the results of one-way ANOVAs comparing the benefit : cost ratios among the five size classes for each bird.

prey (II and III) with the pattern being significant for Bird 3 (Fig. 2).

DISCUSSION

As has been documented for a variety of predators (e.g., Goss-Custard 1977, Stein 1977, Thompson 1978), we found a strong positive relationship between handling time and prey size for Ovenbirds (Fig. 1, Tables 1 and 2). Sherry and McDade (1982) discussed whether this relationship is generally better portrayed as an exponential or a power function. They found that a power function more effectively described the relationship of prey size and handling time in White-fronted Nunbirds (*Monasa morphoeus*, Bright-rumped Attilas (*Attila spadiceus*), and Greater Roadrunners (*Geococcyx californianus*; based on Beal and Gilliam 1979). However, our observation of an exponential relationship for Ovenbirds agrees with the findings of Werner (1974) for centrarchid fishes, Hughes and Elner (1979) for crabs, and Pastorok (1981) for dipteran larvae. The causes and significance of these differences are unclear. For vertebrate predators, the relative sizes of predator and prey might be a factor: the birds examined by Sherry and McDade were given relatively large prey that required extensive manipulation before ingestion, while Werner's sunfishes and our Ovenbirds fed on small, easily handled prey.

The handling times that we measured for Ovenbirds feeding on mealworms fell within the range of values reported by Zach and Falls (1978) for this species foraging on natural prey varying in taxonomic affinities and size. Class I larvae, with a mean handling time of 1.86 s, were comparable to small spiders and millipedes. Class V larvae, with a mean handling time of 13.02 s, were similar to other large coleopteran larvae or adult beetles. Our results suggest that a predator can be confronted with some of the same foraging decisions when it exploits a single prey species, owing to growth stages in the prey (Thompson 1978, Pastorok 1981), that it faces with a diversified diet. Handling time differences can thus be linked, at least in part, to size alone rather than to sharper interspecific differences in prey morphology or behavior (Recher and Recher 1968, Sherry and McDade 1982).

The birds also appeared able to forage better with experience within this relatively simple system (Table 2). This learning pattern presents an adaptive behavioral response, occurring in the post-capture stage of feeding, roughly analogous to the development of a search image in the pre-capture stage (Hughes 1979, Dill 1983).

In an opposite trend, handling times tended to increase during individual trials, independently of prey size, presumably owing to declining hunger in the Ovenbirds. Similar patterns have been reported for other predators and might play a role in short-term shifts in prey selection (Krebs et al. 1977, Dill 1983).

The most interesting experimental results were perhaps the differences among the individual birds (Table 2). The birds fell into two groups with respect to their foraging patterns, and these groups differed in bill size. The two longer-billed individuals, Birds 1 and 2, were most successful, in terms of prey mass ingested per unit handling time, when consuming the larger size classes of larvae (particularly Classes IV and V; Fig. 2). The remaining birds, including those (3 and 4) with shorter bills, experienced their highest returns on intermediate-sized prey (Classes II and III), although the higher ratios were statistically significant only for Bird 3. The general observation that "optimal" prey size is correlated with the size of trophic apparatus has been widely used in interspecific dietary comparisons (Schoener 1965, Wilson 1975). This relationship is less well documented within species (Schoener and Gorman 1968, Werner 1977), particularly for species with determinant growth such as birds (Selander 1966, Grant et al. 1976, Herrera 1978).

Besides suggesting that the two groups of Ovenbirds might specialize on different sizes of prey, Figure 2 indicates that Birds 1 and 2 enjoyed higher return rates across all five prey size-classes. Thus, within our experimental system, Birds 1 and 2 fed more efficiently than Birds 3, 4, and 5. Of course, natural foraging success might not be simply correlated with experimental performances or observed morphological differences. Larger bill size may be associated with greater musculature, bony support, and body size (Abbott et al. 1975), so overall increases in energy requirements might counteract handling-time improvements. A larger bill might also be less efficient for handling prey other than coleopteran larvae, e.g., very small prey (Werner 1977) or prey requiring dismemberment (Zach and Falls 1978, Sherry and McDade 1982). Finally, handling is just one aspect of feeding. Other components that contribute to overall efficiency (e.g., locomotion, search pattern, prey detection) might be independent of predator or prey size.

In summary, our experiments have shown that prey size, even within a single prey species, can affect significantly one aspect of the foraging benefit:cost relationship of an avian predator. Furthermore, we have shown that small intraspecific differences in predator morphology correspond with differences in this benefit:cost relationship and could potentially produce dietary differences under natural conditions (e.g., Herrera 1978, Wiens and Rotenberry 1980). Comparable but larger-scale differences in predator morphology and foraging performance presumably contribute to interspecific differences in diet with respect to prey size and type.

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RECENT PUBLICATIONS

World inventory of avian anatomical specimens: geographical analysis.—D. Scott Wood and Marion Anne Jenkinson. 1984. American Ornithologists' Union and Oklahoma Biological Survey, Norman, Oklahoma. 290 p. Paper cover. $30.00. Source: Oklahoma Biological Survey, Sutton Hall, University of Oklahoma, Norman, OK 73019. This reference work is a companion to Wood, Zusi, and Jenkinson's two world inventories of avian skeletal and spirit specimens (noted in Condor 85:345). It divides the world into sixty discrete areas and lists the species of birds in each, together with an indication of their temporal occurrence. These avifaunal lists are tabulated with the data from the inventories, thereby showing the total numbers of anatomical specimens for each species, grouped by geographical area. The results are given in three multi-page tables, one each for the New World, Palearctic and Ethiopian Regions, and all remaining areas. Each table is preceded with a list of the references that were used to determine the occurrence and status of the species in each of the geographic areas. Additionally, shorter tables summarize data on museum holdings of anatomical specimens, and roughly indicate the geographical strengths and weaknesses of such material in each collection. The volume should be useful to researchers in avian distribution as well as curators and anatomists, for whom its preceding inventories were intended.

Body weights of 686 species of North American birds.—John B. Dunning, Jr. 1984. Western Bird Banding Association Monograph No. 1. 38 p. Paper cover. $3.75. Source: WBBA, Jolan Truan, Asst. Treasurer, 3314 W. Glenn Drive, Phoenix, AZ 85021. Although mean body weight is now recognized as a useful measurement for various kinds of avian research, it is used less than it might be because such information is hard to come by for many species. Addressing that problem, Dunning has summarized in tabular form the best weight data he could find for each species, based on sources with the largest and most complete samples. His list comprises the regularly occurring avifauna of the continental United States and Canada. Given for each species are the sample size, mean weight, standard deviation (for samples of 10 or more), range, season and place where the birds were collected (if known), and the source of the data. Values for males and females are reported separately, where possible. List of references, indexes. Dunning has put a lot of work into compiling this information from published and unpublished sources, and has admirably accomplished his purpose. Researchers should nevertheless heed his remarks on limitations in using the data he has gathered.