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DETERMINANTS OF DIETARY PREFERENCE IN YELLOW-RUMPED WARBLERS

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ABSTRACT.—Warblers are selective in what they eat, yet little is known about the dietary cues used by warblers as they decide what to eat. Semisynthetic diets may be useful for investigating how specific dietary cues, such as appearance or nutrient composition of food, influences diet preference of warblers because these dietary cues can be easily and systematically modified with semisynthetic diets. We offered Yellow-rumped Warblers (*Dendroica coronata*) paired choices of live waxworms (*Galleria mellonella*) and a waxworm mash, or waxworm mash and a semisynthetic mash. Birds strongly preferred live waxworms over waxworm mash, suggesting that natural appearance of food strongly influences diet preference of warblers when the nutrient composition of diets is similar. When birds initially were offered the two mash diets, they consistently preferred waxworm mash over semisynthetic mash within the first 15 min with food, suggesting that they were using dietary cues that provided rapid feedback as would be provided by a cue such as taste. This initial preference for waxworm mash was maintained for the first two days, but then the warblers ate similar amounts of waxworm mash and semisynthetic mash during the last two days of the experiment. The decrease in preference for waxworm mash over time probably occurred because at least some of the cues used by the birds in determining their diet preference(s) required days for reliable feedback. Thus, diet preferences of warblers apparently were influenced by dietary cues that provided immediate and delayed, postingestional feedback. These results support the use of semisynthetic diets in studies of avian diet preferences and highlight the importance of adequate acclimation time on test diets. *Received 19 June 2001, accepted 11 March 2002.*

Descriptive studies of the diet and foraging behavior of warblers (family Parulidae) have provided the foundation for testing important ecological theory related to niche partitioning (MacArthur 1958; Morse 1980, 1989), competition (Wiens 1989), and optimal foraging (Zach and Falls 1976, 1978). Most such descriptive studies have compared food use and availability, and have demonstrated that warblers are selective in what they eat (Morse 1989). However, predicting the diet of warblers also requires an understanding of their diet preferences which can be investigated by allowing an animal equal access to certain food types and measuring relative use (Johnson 1980, Litvaitis et al. 1996). Diet preference likely is related to the nutritional adequacy of foods whereas diet selection is a function of the interaction between diet preference and the availability of alternative foods. Thus, an understanding of the dietary cues used by warblers as they decide what to eat is necessary for accurately predicting both diet preferences and diet selection of warblers.

Free-living warblers and other passerine birds may use a variety of dietary cues to decide what to eat, including sensory cues such as appearance, taste, smell, and texture of the food (Willson et al. 1990, Willson 1994) and the nutritional adequacy of the food itself (Murphy and King 1987, Cipollini and Levey 1997, Lepczyk et al. 2000). The relative importance of certain cues in determining diet preferences can be inferred from measurements of temporal changes in diet choice since dietary cues differ in how rapidly they can be detected. For example, dietary cues such as color are immediately apparent to birds whereas postingestive cues related to the nutritional adequacy of the diets may take days for reliable feedback.

Since natural foods often differ markedly in nutrient composition and other dietary cues, we used semisynthetic diets to identify which dietary cues were important in determining diet preferences of Yellow-rumped Warblers (*Dendroica coronata*). Semisynthetic diets are useful in studies of avian diet preference and nutritional ecology because the exact nutrient composition of such diets is known, and because semisynthetic diets are easily and accurately replicated or manipulated (Murphy and King 1982). Although semisynthetic diets can be formulated to match the nutrient composition of the bird's natural diet, they often

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TABLE 1. Composition (per 100 g) of two mash diets and of whole waxworms[a] (*Galleria mellonella*). These three diets were used to determine how specific dietary cues such as appearance or nutrient composition of food influences diet preferences of Yellow-rumped Warblers (*Dendroica coronata*).

Experimental diet	Ingredients	Wet mass	Dry mass
Semi-synthetic mash	Carbohydrates (D-glucose)	1.13	10.04
	Protein (casein[b])	6.80	52.30
	Fat (olive oil)	2.61	20.08
	Vitamin mix[c]	0.22	1.67
	Salt mix[d]	0.76	5.86
	Agar	1.31	10.00
	Water	87.00	
Waxworm mash	Carbohydrates	0.70	6.92
	Protein	3.35	33.00
	Fat	4.42	43.63
	Calcium	0.01	0.03
	Ash	0.20	1.93
	Agar	1.47	14.49
	Water	89.85[e]	

[a] Composition of whole waxworms is the same as waxworm mash without agar and added water.
[b] Casein = (high N) Teklad, U.S. Biochemical Corp., Cleveland, Ohio.
[c] AIN-76 Vitamin Mix, ICN Biomedicals, Inc.
[d] Salt mix = ICN Biomedicals, Inc. (Spivey-Fox and Briggs 1960).
[e] 11.49% of water is from waxworms.

are quite different in appearance (e.g., mash diets used by Afik and Karasov 1995, Afik et al. 1995, McWilliams and Karasov 1998). In this study, we used live waxworms (*Galleria mellonella*), minced waxworms, and a semi-synthetic mash diet to determine how visual appearance and nutrient composition of diets influenced the warbler's choice of diets.

METHODS

Study subjects and maintenance.—We used mist nets to capture 20 Yellow-rumped Warblers in southern Rhode Island during October 1998. Prior to the experiments, birds were maintained in the laboratory for 15 weeks and were fed a semisynthetic mash (Table 1) and live waxworms. This semisynthetic mash is similar to the nutrient composition of insects (10% carbohydrates, 52% protein, and 20% fat; Bairlein 1987) and has been used to maintain Yellow-rumped Warblers in the laboratory for months (Afik and Karasov 1995, McWilliams and Karasov 1998). Birds were weighed and given fresh food and water between 07:30 and 09:00 EST each day. Birds were housed individually in stainless steel cages (60 cm × 20 cm × 35 cm) in a room with 10L:14D light and 21° C temperature regimes.

During February 1999, we acclimated all 20 birds to the paired dish protocol and the three food types used in the preference tests (Table 1). Throughout the 3-day acclimation period and during both experiments, birds always were offered food in two dishes on opposite sides of the cage (about 10 cm apart). During the 3-day acclimation period, one dish contained 20 g of waxworm mash and three live waxworms and the other dish contained 20 g of semisynthetic mash and three live waxworms. Each day we switched the location of the food types to ensure food position did not bias the preference results (see Jackson et al. 1998). This acclimation period was designed to reduce any effect of previous short term experience on diet preference of warblers. However, if diet preference is determined primarily by the duration of time spent feeding on a diet over months rather than days, then warblers should prefer the semisynthetic mash and live waxworms (fed to these birds for 3 months) over waxworm mash (fed to these birds for 3 days).

Preference tests.—In experiment 1, we offered 15 g of waxworm mash in one dish and 20 live waxworms (about 15 g) in another dish to each of the 20 birds. We weighed each dish with 20 waxworms to determine total mass of waxworms offered. For experiment 2, we offered 20 birds 15 g of waxworm mash in one dish and 15 g of semisynthetic mash in another dish. In both experiments, the food was available from 08:00–12:00. After the 4-h test period, the food dishes were weighed and then replaced with two dishes each containing 10 g of semisynthetic mash. Subsamples of food were dried at 100°C to estimate dry matter intake. All birds had food remaining after the 4-h test period and by morning, so that the feeding regime each day was *ad libitum.*

In both experiments, we observed some birds during the first hour (08:00–09:00) with food to determine which food type was eaten first and visited most frequently. For experiment 1, we randomly selected 10 of the 20 birds for observation on day 1 and then we observed the same 10 birds on day 2. For experiment

TABLE 2. Captive Yellow-rumped Warblers (*Dendroica coronata*; $n = 20$) ate predominately live waxworms when offered a choice of live waxworms and minced waxworms (experiment 1), and eventually ate similar amounts of each diet when offered a choice of minced waxworms and a semisynthetic diet (experiment 2). Values for food intake are means ± SE.

	Food intake (g dry/4 h) of warblers given a choice of two diets					
	Live waxworms	Waxworm mash	Semisynthetic mash	Total food intake[a]	t[b]	P
Experiment 1						
Day 1	1.48 ± 0.09	0.08 ± 0.01		1.56 ± 0.07	20.95	<0.01
Day 2	1.45 ± 0.06	0.16 ± 0.01		1.56 ± 0.06	24.45	<0.01
Experiment 2						
Day 1		0.64 ± 0.04	0.30 ± 0.04	0.94 ± 0.04	4.42	<0.01
Day 2		0.78 ± 0.04	0.28 ± 0.06	1.06 ± 0.05	5.73	<0.01
Day 3		0.74 ± 0.06	0.78 ± 0.25	1.52 ± 0.09	−1.10	0.77
Day 4		0.52 ± 0.04	0.68 ± 0.47	1.20 ± 0.17	−0.30	0.28

[a] Total food intake was similar between days in experiment 1 ($P > 0.90$), whereas total food intake increased across days in experiment 2 ($F_{3,57} = 5.75$, $P = 0.002$).
[b] Two-tailed paired t-test with 19 df comparing food intake of live waxworms and waxworm mash in experiment 1 or waxworm mash and semisynthetic mash in experiment 2.

2, we observed all 20 birds on day 1 and again on day 3. We made observations from behind a blind that had been in the room for two weeks prior to the experiment.

Food preference was determined by comparing the amount of food that had been consumed during the 4-h test period, the number of birds that visited each food type first, and the mean frequency of visits to each food type during the first four 15-min periods with food each day.

Statistical analysis.—For both preference tests, we used a two-tailed paired t-test to determine if there was a significant difference between days in the amount of each food type eaten. In experiment 1, we also used a two-tailed paired t-test to determine if there was a significant difference between days in the proportion of food intake composed of live waxworms. We used a chi-square test to determine if more birds fed first on one food type than the other, assuming no preference. In experiment 1 and experiment 2, we used a repeated measures ANOVA to determine if the preferences of birds changed during the first hour with food. For experiment 1, the dependent variable was the proportion of food intake composed of live waxworms. For experiment 2, the dependent variable was the proportion of food intake composed of waxworm mash. In experiment 2, we used a repeated measures ANOVA to determine if the preferences or total food intake of birds changed across days. For all statistical tests, a P value <0.05 was considered significant. All results are presented as mean ± SE.

RESULTS

In experiment 1, birds ate significantly more live waxworms than waxworm mash on both day 1 (95.09% ± 0.01) and day 2 (92.66% ± 0.01; Table 2). This difference between days was statistically significant ($t_{19} = 2.27$, $P = 0.018$) because birds ate slightly more of the waxworm mash on day 2 (Table 2).

In experiment 2, total food intake during the 4-h test period increased across days as more semisynthetic mash was consumed on days 3 and 4 (Table 2). The proportion of food intake composed of waxworm mash declined significantly across days ($F_{3,57} = 6.94$, $P < 0.0001$). Birds ate significantly more waxworm mash than semisynthetic mash on day 1 (68.53% ± 0.04) and day 2 (75.63% ± 0.04), but showed no significant difference on day 3 (53.34% ± 0.05) or day 4 (53.62%; 0.05; Table 2). We calculated the statistical power to detect a 0.10 g difference in food intake assuming $\alpha = 0.05$ and using the estimated within-group variance from our experiment. The power in this case was 95.5%. Thus, there was a 95.5% probability of detecting a 0.10 g difference in food intake between the two mash diets at the 5% level of significance.

In experiment 1, all 10 birds that were observed during the first hour with food ate a live waxworm first on both day 1 and day 2. In experiment 2, similar numbers of birds ate first from the waxworm mash (12 birds) and semisynthetic mash (8 birds) on day 1 ($\chi^2 = 0.80$, df = 1, $P = 0.39$), whereas significantly more birds ate waxworm mash first (19 birds) on day 3 ($\chi^2 = 16.25$, df = 1, $P < 0.0001$).

In each of the four 15-min periods during the first hour with food, birds in experiment 1 visited the dish with live waxworms more often than the dish with waxworm mash (time effect: $F_{3,54} = 1.36$, $P = 0.26$; day effect: $F_{1,18} = 0.06$, $P = 0.81$; day × time effect: $F_{3,54} = 0.23$, $P = 0.87$). On both day 1 and day 2, birds visited the dish with live waxworms 86% ± 9.3 of the time during the first 30 min with food compared to 68% ± 14.9 of the time during the next 30 min. During the first 15-min period on day 1, birds in experiment 2 visited the dish with waxworm mash as often as the dish with semisynthetic mash. However, during the next three 15-min periods on day 1 and during all four 15-min periods on day 3, birds visited the dish with waxworm mash a mean of 81% ± 5.2 of total visits compared to the dish with semisynthetic mash (time effect: $F_{3,114} = 3.06$, $P = 0.031$; day effect: $F_{1,38} = 2.61$, $P = 0.11$; day × time effect: $F_{3,114} = 2.74$, $P = 0.046$).

DISCUSSION

Yellow-rumped Warblers consistently ate live waxworms first, they visited the dish with live waxworms more frequently during the first hour with food, and >90% of their diet during each 4-h test period was live waxworms. Given that live waxworms and waxworm mash have the same nutrient composition, the preference for live waxworms is likely due to the familiar appearance of the live caterpillars to the insectivorous warblers. Similarly, granivorous White-throated Sparrows (*Zonotrichia leucophrys*) preferred a semisynthetic mash shaped like seeds to the powdery form of the same diet (Murphy and King 1982). Thus, natural appearance of food influences diet preference of birds, especially when the nutrient composition of alternative diets is similar.

When Yellow-rumped Warblers initially were offered a choice between the two mash diets, they sampled both diets during the first 15 min with food and then settled on a consistent preference for waxworm mash over semisynthetic mash. Such short term sampling of diets at first offering was not evident when the birds were offered live waxworms and waxworm mash. Denslow et al. (1987) also found that birds required more sampling time when offered mash diets compared to natural diets. Apparently when two mash diets are offered, the warblers must base their preference on properties of the foods that are not detectable prior to ingestion so that sampling is necessary. Such sampling of foods with similar appearance also has been observed in bumblebees (*Bombus* spp.) choosing flowers (Oster and Heinrich 1976) and in mammalian herbivores (e.g., equines, ungulates, and lagomorphs) choosing rangeland plants (Westoby 1974, 1978). Given that the warblers' diet choice did not change after the first 15 min with food, the postingestive cues used by the warblers provided rapid feedback as would be provided by a cue such as taste.

Despite a consistent preference for waxworm mash over semisynthetic mash during the first hour with food, Yellow-rumped Warblers did not consistently eat more waxworm mash than semisynthetic mash during the entire 4 h with the diets on all four days of experiment 2. Warblers preferred waxworm mash during the first two days of experiment 2, but they ate similar amounts of waxworm mash and semisynthetic mash during the last two days of experiment 2. The change in preference across days occurred primarily because warblers increased their consumption of semisynthetic mash as well as total intake between the first two and the last two days of experiment 2. Such a temporal change in diet preference across days may occur (a) if birds must become familiar with the diets (Greenberg 1983, Murphy and King 1987, Avery et al. 1995), (b) if birds can not satisfy their nutrient requirements on only one of the diets (Murphy and Pearcy 1993), or (c) if the process of sampling and choosing diets involves cues that require days for reliable feedback.

The first two hypotheses are unlikely to explain the temporal change in diet preference across days that we observed. In general, Yellow-rumped Warblers eat a diversity of foods in the wild (Hunt and Flaspohler 1998) and so are unlikely to exhibit feeding neophobia as observed in some species of warblers and sparrows that are feeding specialists (Greenberg 1983, 1990). In addition, the design of our experiment included at least three days of acclimation on the experimental diets so that birds were familiar with those diets. Furthermore, the warblers used in this experiment have maintained body mass for weeks when fed only semisynthetic mash (this study) or waxworm mash (SRM unpubl. data), both supplemented with several live waxworms. Thus, both diets apparently are nutritionally adequate, and both diets were familiar to these warblers prior to the experiments.

The similar appearance and consistency of the waxworm mash and semisynthetic mash apparently required warblers to extensively sample the diets offered and use cues that required days for reliable feedback. The birds initially may have preferred waxworm mash in experiment 2 because they had just completed experiment 1 in which they were offered live waxworms and waxworm mash. After two days of sampling both diets, however, warblers ate equivalent amounts of waxworm mash and semisynthetic mash, suggesting no preference. McPherson (1988) found that Cedar Waxwings (*Bombycilla cedrorum*) also changed their diet preference over time, from an initial preference for small, red, semisynthetic berries over large, nonred berries to no preference. Given that the warblers' and waxwings' diet choice changed only after two days, the postingestive cues used by these birds must have provided delayed feedback as would be provided by a cue such as maintenance of body mass or certain fat reserves.

Yellow-rumped Warblers always ate some of both diets offered, even when provided live insects that they strongly preferred. Such "partial preferences" (after Krebs and McCleery 1984) may occur because warblers are sampling to better assess their diet choices. During their sampling of the two mash diets, warblers used cues with both immediate and delayed feedback to determine their diet preferences as indicated by temporal changes in their diet choices.

If semisynthetic diets that appear different from natural foods are used to investigate the nutritional cues that determine diet preferences of birds (e.g., Murphy and King 1987, this study), then birds must be given adequate acclimation time so that the birds' preferences can be determined independent of the process of diet sampling. In the case of Yellow-rumped Warblers eating simple mash diets, an acclimation period of at least three days seems necessary. If color is added to the mash diets, then birds may use visual cues to determine diet type (Schuler 1983, Lepcyck 1993, Whelan and Willson 1994, Willson 1994) and this may reduce the time delay associated with using other cues that provide delayed feedback. In summary, these results support the use of semisynthetic diets in studies of avian diet preferences and highlight the importance of adequate acclimation time on test diets.

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LITERATURE CITED

Afik, D. and W. H. Karasov. 1995. The trade-offs between digestion rate and efficiency in warblers and their ecological implications. Ecology 76: 2247–2257.

Afik, D., E. C. Vidal, C. Martinez del Rio, and W. H. Karasov. 1995. Dietary modulation of intestinal hydrolytic enzymes in Yellow-rumped Warblers. Am. J. Physiol. 269R:413–420.

Avery, M. L., D. G. Decker, J. S. Humphrey, A. A. Hayes, and C. C. Laukert. 1995. Color, size, and location of artificial fruits affect sucrose avoidance by Cedar Waxwings and European Starlings. Auk 112:436–444.

Bairlein, F. 1987. Nutritional requirements for maintenance of body weight and fat deposition in the long-distance migratory Garden Warbler, *Sylvia borin* (Boddaert). Comp. Biochem. Physiol. 86A: 337–347.

Cipollini, M. L. and D. J. Levey. 1997. Secondary metabolites of fleshy vertebrate-dispersed fruits: adaptive hypotheses and implications for seed dispersal. Am. Nat. 150:346–372.

Denslow, J. S., D. J. Levey, T. C. Moermond, and B. C. Wentworth. 1987. A synthetic diet for fruit-eating birds. Wilson Bull. 99:131–135.

Greenberg, R. 1983. The role of neophobia in determining the foraging specialization of some migrant warblers. Am. Nat. 122:444–453.

Greenberg, R. 1990. Feeding neophobia and ecological plasticity: a test of the hypothesis with captive sparrows. Anim. Behav. 39:375–379.

Hunt, P. D. and D. J. Flaspohler. 1998. Yellow-rumped Warbler (*Dendroica coronata*). No. 376 *in* The birds of North America (A. Poole and F. Gill, Eds.). The Birds of North America, Inc., Philadelphia, Pennsylvania.

Jackson, S., S. W. Nicolson, and S. N. Lotz. 1998. Sugar preferences and "side bias" in Cape Sunbirds and Lesser Double-collared Sunbirds. Auk 115:156–165.

JOHNSON, D. H. 1980. The comparisons of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

KREBS, J. R. AND R. H. MCCLEERY. 1984. Optimization in behavioural ecology. Pp. 91–121. *in* Behavioural ecology: an evolutionary approach, 2nd ed. (J. R. Krebs and N. B. Davies, Eds.). Sinauer Associates, Sunderland, Massachusetts.

LEPCZYK, C. A. 1993. Assimilation efficiencies and preferences of lipids and reducing sugars in the American Robin (*Turdus migratorius*). Bios 64: 122–129.

LEPCZYK, C. A., K. G. MURRAY, K. WINNETT-MURRAY, P. BARTELL, E. GEYER, AND T. WORK. 2000. Seasonal fruit preferences for lipids and sugars by American Robins. Auk 117:709–717.

LITVAITIS, J. A., K. TITUS, AND E. M. ANDERSON. 1996. Measuring vertebrate use of terrestrial habitats and food. Pp.254–274 *in* Research and management techniques for wildlife and habitats (T. A. Bookhout, Ed.). The Wildlife Society, Bethesda, Maryland.

MACARTHUR, R. H. 1958. Population ecology of warblers in northeastern coniferous forests. Ecology 39:599–619.

MCPHERSON, J. M. 1988. Preferences of Cedar Waxwings in the laboratory for fruit species, colour and size: a comparison with field observations. Anim. Behav. 36:961–969.

MCWILLIAMS, S. R. AND W. H. KARASOV. 1998. Test of a digestion optimization model: effect of variable-reward feeding schedules on digestive performance of a migratory bird. Oecologia 114: 160–169.

MORSE, D. H. 1980. Foraging and coexistence of spruce-woods warblers. Living Bird 18:7–25.

MORSE, D. H. 1989. American warblers: an ecological and behavioral perspective. Harvard Univ. Press, Cambridge, Massachusetts.

MURPHY, M. E. AND J. R. KING. 1982. Semi-synthetic diets as a tool for nutritional ecology. Auk 99: 165–167.

MURPHY, M. E. AND J. R. KING. 1987. Dietary discrimination by molting White-crowned Sparrows given diets differing only in sulfur amino acid concentration. Physiol. Zool. 60:279–289.

MURPHY, M. E. AND S. D. PEARCY. 1993. Dietary amino acid complementation as a foraging strategy for wild birds. Physiol. Behav. 53:689–698.

OSTER, G. AND B. HEINRICH. 1976. Why do bumblebees major? A mathematical model. Ecol. Monogr. 46:129–133.

SCHULER, W. 1983. Response to sugars and their behavioral mechanisms in the starling (*Sturnus vulgaris* L.). Behav. Ecol. Sociobiol. 13:243–251.

SPIVEY-FOX, M. R. AND G. M. BRIGGS. 1960. Salt mixtures for purified-type diets: an improved salt mixture for chicks. J. Nutr. 72:243–250.

WESTOBY, M. 1974. An analysis of diet selection by large generalist herbivores. Am. Nat. 108:290–304.

WESTOBY, M. 1978. What are the biological bases of varied diets? Am. Nat. 112:627–631.

WHELAN, C. J. AND M. F. WILLSON. 1994. Fruit choice in migrating North American birds: field and aviary experiments. Oikos 71:137–151.

WIENS, J. A. 1989. The ecology of bird communities, vol. 1: foundations and patterns. Cambridge Univ. Press, New York.

WILLSON, M. F. 1994. Fruit choices by captive American Robins. Condor 96:494–502.

WILLSON, M. F., D. A. GRAFF, AND C. J. WHELAN. 1990. Color preferences of frugivorous birds in relation to the colors of fleshy fruits. Condor 92:545–555.

ZACH, R. AND J. B. FALLS. 1976. Ovenbird (Aves: Parulidae) hunting behavior in a patchy environment: an experimental study. Can. J. Zool. 54: 1863–1879.

ZACH, R. AND J. B. FALLS. 1978. Prey selection by captive Ovenbirds (Aves: Parulidae). J. Anim. Ecol. 47:929–943.