

FORAGING PROFICIENCY AND BODY CONDITION OF JUVENILE AMERICAN DIPPERS¹

ROARKE E. DONNELLY² AND KIMBERLY A. SULLIVAN
*Department of Biology, Utah State University, Logan, UT 84322-5305,
 e-mail: yejunco@cc.usu.edu*

Abstract. We quantified foraging proficiency in nine free-ranging American Dippers (*Cinclus mexicanus*) when they were 39–42 days post-hatching, and correlated foraging proficiency with body condition. Although all nine individuals foraged extensively on the smallest size class of prey, individuals with a relatively low rate of caloric intake (RCI) from the larger prey classes consumed a greater proportion of the smallest size prey. Body mass and hematocrit were significantly correlated with RCI. Mass and hematocrit are relative measures of body condition and the body condition of newly independent juveniles may predict survivorship through the first year. Thus, these data are consistent with the assumption that greater foraging proficiency confers fitness benefits for free-living birds. Alternatively, these data also support the interpretation that juvenile dippers in better physical condition forage more proficiently than birds in poorer condition.

Key words: *American Dipper, body condition, Cinclus mexicanus, foraging, hematocrit, juvenile.*

Optimality models have advanced the field of behavioral ecology by providing a framework for the analysis of animal behavior in terms of costs and benefits. Studies on birds were integral to the development of these models (Goss-Custard 1977, Pyke 1978) and continue to be instrumental in the refinement of optimal foraging theory (Bateson and Whitehead 1996, Waite and Ydenberg 1996). However, optimal foraging theory's assumption that the relevant currency, energy gain, is positively correlated with fitness has been tested only three times using birds: by directly measuring the fitness of captive Zebra Finches (*Taeniopygia guttata*, Lemon 1991) and free-living European Blackbirds (*Turdus merula*, Desrochers 1992) and by indirectly measuring the fitness of captive Wood Ducks (*Aix sponsa*, Demarest et al. 1997).

Testing the association of foraging proficiency and either direct or indirect measures of fitness in free-living birds is a formidable task because many bird species have large home ranges, exhibit little variation in foraging proficiency, and experience relatively low

mortality rates as adults. By studying juvenile birds, researchers may be able to reduce the difficulties inherent in the linking of fitness with foraging proficiency. The foraging proficiency of juvenile birds continues to improve for weeks or even years following the termination of provisioning by the parents (Orians 1969, Weathers and Sullivan 1991). During this period, it is highly probable that individuals improve their foraging proficiency at different rates. In addition, juveniles typically experience higher mortality rates than adults and several studies have suggested that body mass of recently independent juvenile birds predicts survival through the first year, an important component of fitness (Lack 1954, Patterson et al. 1988, Sullivan 1989).

In addition to body mass, other measures of body condition may provide insights into juvenile survival. Hematocrit value (volumetric proportion of packed erythrocytes) has been positively associated with body mass and fat scores in migrants, growth rate in nestling Cliff Swallows, and negatively associated with ectoparasite load in raptors (Chapman and George 1991, McFadzen and Marzluff 1996, Piersma et al. 1996).

We examined the assumed relationship between foraging proficiency and an indirect measure of fitness, body condition, in free-living, juvenile American Dippers (*Cinclus mexicanus*). We quantified foraging proficiency as gross rate of caloric intake (RCI) and used two measures of body condition to estimate fitness. American Dippers proved to be excellent subjects for this study. They may be observed for 1 week following independence when they remain on the natal territory and are relatively insensitive to the presence of observers (Yoerg 1994, Donnelly 1997). In addition, juveniles of this species dive for prey less often than adults, facilitating the identification and quantification of captured prey items.

METHODS

We monitored a population of dippers breeding along the Logan River (elevation 1,466–2,023 m) in northern Utah from March to August of 1994 and 1995. Young dippers were banded with a unique combination of a U.S. Fish and Wildlife Service band and three colored bands when they were 11 days post-hatching or on the day of fledging. Fledglings were provisioned by their parents until 35 days post-hatching and then dispersed from their natal territory after 44 days post-hatching. Therefore, foraging observations were made 39–42 days post-hatching. If the hatching date was unknown, we assigned the bird the average age at fledging (mean

¹ Received 21 July 1997. Accepted 10 December 1997.

² Present address: College of Forest Resources, University of Washington, Box 352100, Seattle, WA 98195, e-mail: roarked@u.washington.edu

TABLE 1. Prey items consumed by juvenile dippers. Prey items were assigned to a size class based on their length relative to the dipper's bill length. Representative prey in each size class were sampled, identified, dried and weighed to determine mean energy per prey item in the calculation of rate of caloric intake by each dipper.

Prey size class	Prey length (relative to bill)	Representative taxon	Developmental stage	Sample size	Mean energy value per item (cal)
Crumbs	<0.25	Simuliidae	Larva	400	3.3
Small	0.25–0.49	Ephemeroptera	Nymph	101	10.4
Medium ^a	0.5 ≤ x < 0.9	Trichoptera	Adult	28	48.4
		Ephemeroptera	Nymph	112	
Large ^a	≥1	Tipulidae	Adult	10	161.0
		Plecoptera	Nymph	10	

^a Size classes consisting of two types of insects.

± SD = 25 ± 1.7 days, $n = 93$) on the day it left the nest and observed its foraging behavior 14 days later. All birds ($n = 9$) were observed on at least two days of the four-day observation period, with two birds observed on day 39, seven on day 40, all nine on day 41, and seven on day 42. All foraging observations were conducted by the senior author during 1995 in the morning (07:00–11:00) and evening (13:00–19:30) using 10×42 binoculars from a distance of < 20 m. In order to avoid recording foraging rates when birds were resting but occasionally lunging at prey items, individuals were assumed to be foraging if they actively searched for or pursued prey for > 15 sec. Data collection was terminated for a bout of foraging if the individual stopped foraging for > 8 sec or spent > 8 sec traveling to another site. Foraging birds usually were observed in the order in which they were encountered; occasionally birds were sought out to increase the total amount of foraging time recorded for a specific individual. High water flows during the spring of 1995 prevented access to many foraging sites along the river; thus we have foraging data for only 9 of 109 banded juveniles. These nine birds fledged from four broods.

Once a foraging juvenile was located, the observer waited for 1 min before collecting data to allow the bird to adjust to his presence. The following data were recorded on cassette tapes and later transcribed with the aid of a stopwatch: prey size (relative to bill length), taxa and developmental stage of ingested prey, and the time spent foraging. Foraging bouts for each individual were numbered and individuals were observed for 8–18 foraging bouts totaling 47–145 min bird⁻¹ (mean ± SD = 87.9 ± 29.5 min bird⁻¹). None of the dippers we observed showed dramatic improvements in RCI over the 4-day observation period. For seven of the dippers there was little, if any, association between foraging bout order and RCI (P values ranged from 0.6 to 1.0). Moreover, only one bird had a significant association of foraging bout order and RCI ($d = 0.07$, $P < 0.05$). We therefore decided to use all foraging bouts in calculating RCI for each individual.

Prey items were placed in one of four prey size classes based upon their length in relation to bill length (Table 1; see Yoerg 1994). Bill length was defined as the distance from the tip of the bird's bill to the proximal end of the commissure (Proctor and Lynch 1993). Because items in the smallest size class, hereafter

crumbs, were too small to be visible in the bill from the typical observation distance of 15–20 m, their ingestion was inferred from esophageal contractions. When possible, the taxon and developmental stage of prey were identified at capture or at sites where birds had been foraging. Crumb and small size classes each consisted of one prey type, whereas the two larger size classes each consisted of two prey types (Table 1). Approximately one medium Trichopteran adult was captured for every four Ephemeropteran nymphs. Large Tipulid adults and Plecopteran nymphs were taken in nearly equal proportions.

In order to transform the foraging observations for an individual into RCI, it was necessary to calculate the mean energy content of prey in each size class. Adult and larval insects were collected from the Logan River with a dip net and a Surber Sampler. Specimens were sorted into four prey size classes according to three criteria: length, expressed as a fraction of mean juvenile bill length (mean ± SD = 22.0 ± 1.6 mm, $n = 8$), taxon, and developmental stage. Samples were dried for 48 hr at 40°C and weighed to the nearest 0.1 mg. Finally, the mass of each sample was divided by the number of individuals in the sample and the quotient was multiplied by Saether's (1994) conversion value of 5.5 Kcal g⁻¹ dry mass. The gross RCI for each bird was calculated by totaling prey from each size class that were ingested during all bouts, multiplying these totals by class-specific energy values, totaling the products, and dividing the sum by the sum of all bout lengths (min). Partial RCI's also were calculated to indicate the rate at which an individual gained calories from one size class over the course of all observations.

Eight of the dippers were captured in mist nets within 2 days of the completion of foraging observations. Birds were weighed to the nearest 0.1 g, bill length and wing chord were measured to the nearest 0.1 mm using calipers and a wing rule, and 75 µl of blood was drawn from the brachial vein into a heparinized capillary tube. Wing chord was not used to calculate a condition index (body mass/wing chord) because birds struggled while being held, reducing the reliability of this measure. Within 4 hr of collection, blood samples were centrifuged at 1,500 rpm for 5 min. Immediately thereafter, a hematocrit value was determined using a micro-capillary hematocrit reader (Daemon/International Equipment Company).

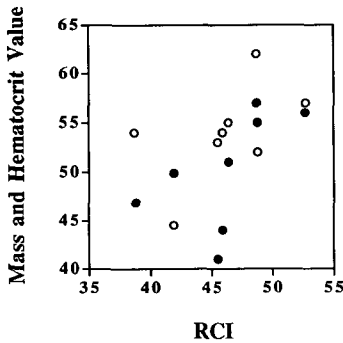


FIGURE 1. Association of RCI (cal min⁻¹) with body mass (g, open circles) and hematocrit value (solid circles).

Values are reported with an n of 9 for the foraging observations and n of 8 for the condition measures. Hoeffding's independence statistics (d) are reported for tests of association (Hoeffding 1948, SAS Institute 1994). For all analyses, statistical significance was set at $P < 0.05$.

RESULTS

Juvenile dippers specialized on the crumb-sized Simuliid larvae; crumbs represented 91–96% of captures by individual birds. Overall the nine dippers captured 8,269 crumb-sized, 441 small-sized, 44 medium-sized, and 8 large-sized prey. Although small, medium, and large-sized prey constituted only 4–9% of prey captures, because of their high caloric content they made up 12–35% of the calories individuals consumed. Dippers with a relatively low RCI from small, medium, and large-sized prey captured a greater proportion of crumb-sized prey ($d = 0.58$, $P < 0.01$). We failed to find significant associations between the RCI from the different size classes of prey (all P s > 0.1), although the power of these tests was low and may have prevented the detection of actual trends.

Both body mass and hematocrit value were significantly correlated with RCI (mass $d = 0.14$, $P < 0.05$; hematocrit $d = 0.32$, $P < 0.02$, Fig. 1). Hematocrit values varied significantly among broods (ANOVA $F_{2,5} = 11.2$, $P < 0.02$), whereas body mass ($F_{2,5} = 0.1$, $P > 0.9$) and RCI ($F_{3,5} = 2.5$, $P > 0.1$) did not.

DISCUSSION

The foraging proficiency of juvenile American Dippers, estimated by RCI, was positively associated with body mass and hematocrit value, two measures of body condition. An individual's RCI may depend upon many factors including morphology, foraging skills and decisions, and territory characteristics (Marchetti and Price 1989, Wunderle 1991). Like other bird species, juvenile dippers specialized on prey that were smaller, easier to capture and handle, but contained less energy, than those selected by adults (Wunderle 1991). Although all individuals foraged extensively on Simuliid larvae, the proportion of Simuliid prey in an individual's diet was negatively associated with the RCI from noncrumb prey. Juvenile Eurasian Dippers

(*Cinclus cinclus*, Yoerg 1994) improved their rate of prey capture between 9 and 21 days post-fledging, suggesting that capturing even the smallest prey required the development of foraging skills. Thus, it appears that each individual's prey choice was based in part upon its ability to detect, capture, and handle relatively large prey and that same age individuals may be at different stages in the transition from a diet of easy-to-capture, energy-poor prey to the adult diet requiring greater foraging skills.

Despite the abundance of crumb-sized prey on all territories (Brown 1935, Donnelly, pers. observ.), territory characteristics may have contributed to the observed variance in foraging proficiency. Three members of one brood hawked medium-sized caddisflies (order Trichoptera) from the concrete walls of a dam on their territory and had the highest RCI of the nine birds studied here. A fourth member of this brood was not observed foraging on the dam walls and had a lower RCI.

We used body mass and hematocrit as indirect measures of fitness. The few available studies on the mortality of juvenile birds have concluded that the body mass of recently independent juveniles indicates an individual's body condition and consequently its risk of mortality from starvation during the first year of life (Lack 1954, Patterson et al. 1988, Sullivan 1989). The body mass of juvenile dippers studied here was significantly associated with RCI (Fig. 1). This relationship can be interpreted in two ways: birds with relatively high foraging proficiency attained better condition or large birds in better physical condition foraged faster than birds in poorer condition. With either interpretation, foraging proficiency and body condition are linked.

Hematocrit values fell within the range reported for other species of wild birds (Bennett and Chisholm 1964, Sturkie 1986). Few studies of avian hematocrit exist for nondomesticated species, but there is a growing body of evidence that hematocrit, as well as body mass, is related to body condition (Chapman and George 1991, McFadzen and Marzluff 1996, Svensson and Merila 1996). Dehydration and changes in plasma osmolality, such as during vitellogenesis, may affect plasma volume (Morton 1994), but are unlikely to affect dippers because they consume prey high in water content, have ready access to drinking water, and are not reproductively mature. The three brood members that hawked caddisflies had the highest hematocrit values, in fact this brood had significantly higher hematocrit values than the other broods. The fourth brood member that was not observed hawking caddisflies had a lower hematocrit value, similar to individuals from the other broods. An individual's foraging proficiency, genotype, or parental provisioning rate as a nestling or fledgling may constrain hematocrit values during independence. However, it also is possible that an individual's hematocrit at independence influences foraging proficiency by limiting activities requiring high rates of gas exchange.

Although our results are based upon a small sample, and so should be interpreted with caution, they are consistent with the positive correlation of foraging proficiency with fitness reported for Zebra Finches (Lem-

on 1991) and with indirect measures of fitness in Wood Ducks (Demarest et al. 1997). In contrast, European Blackbirds (Desrochers 1992) did not show an association between foraging proficiency and fitness, perhaps because they were observed while foraging on mowed lawns and in ornamental hedges where little skill was required to detect food. By estimating foraging proficiency with gross caloric intake rate (RCI), our study assumes a positive relationship between gross and net energy intake. Individuals can vary in assimilation rates and energy expenditure and we did not measure these parameters. Additional studies measuring body condition, survival, and reproductive success are needed to definitively test the assumption that fitness is a function of foraging proficiency.

This study was conducted as part of a Master's thesis at Utah State University under the direction of Kimberly Sullivan, Mark Ritchie, and Edward Evans. We are grateful for advice on field methods from Carl Bock, Keith Dixon, Carl Marti, and Sonja Yoerg, banding assistance from Megan Donnelly, statistical consultation from Christl Donnelly, and insightful comments from two anonymous referees.

LITERATURE CITED

- BATESON, M., AND S. WHITEHEAD. 1996. The energetic cost of alternative rate currencies in the foraging starling. *Ecology* 77:1303-1307.
- BENNETT, G., AND A. CHISHOLM. 1964. Measurements on the blood cells of some wild birds. *J. N. Am. Wildl. Disease* 38:1-22.
- BROWN, C. 1935. A survey of the waters of the Cache National Forest, Utah. USDA Tech. Rep. 260167, Washington, DC.
- CHAPMAN, B. R., AND J. E. GEORGE. 1991. The effects of ectoparasites on Cliff Swallow growth and survival, p. 49-68. *In* J. E. Loye and M. Zuk [eds.], *Bird-parasite interactions: ecology, evolution and behaviour*. Oxford Univ. Press, Oxford.
- DEMAREST, D. W., R. M. KAMINSKI, L. A. BRENNAN, AND C. R. BOYLE. 1997. Body-mass, survival, and pairing consequences of winter-diet restriction in Wood Ducks. *J. Wildl. Manage.* 61:822-832.
- DESROCHERS, A. 1992. Age and foraging success in European Blackbirds: variation between and within individuals. *Anim. Behav.* 43:885-894.
- DONNELLY, R. 1997. The behavior of dippers (family Cinclidae) in relation to food acquisition. M.Sc. thesis. Utah State Univ., Logan, UT.
- GOSS-CUSTARD, J. 1977. Optimal foraging and the size selection of worms by Redshanks, *Tringia totanus*, in the field. *Anim. Behav.* 25:10-29.
- HOEFFDING, W. 1928. A non-parametric test of independence. *Ann. Math. Statist.* 15:546-557.
- LACK, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.
- LEMON, W. 1991. Fitness consequences of foraging behaviour in the Zebra Finch. *Nature* 352:153-155.
- MARCHETTI, K., AND T. PRICE. 1989. Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. *Biol. Rev.* 64:51-70.
- MCFADZEN, M., AND J. M. MARZLUFF. 1996. Mortality of Prairie Falcons during the fledging dependence period. *Condor* 98:791-800.
- MORTON, M. 1994. Hematocrits in montane sparrows in relation to reproductive schedule. *Condor* 96:119-126.
- ORIAN, G. 1969. Age and hunting success in the Brown Pelican (*Pelicanus occidentalis*). *Anim. Behav.* 17:316-319.
- PATTERSON, I., G. DUNNET, AND S. GOODBODY. 1988. Body weight and juvenile mortality in Rooks *Corvus frugilegus*. *J. Anim. Ecol.* 57:1041-1052.
- PIERSMA, T., J. EVERAARTS, AND J. JUKEMA. 1996. Build-up of red blood cells in refueling Bar-tailed Godwits in relation to individual migratory quality. *Condor* 98:363-370.
- PROCTOR, N., AND P. LYNCH. 1993. *Manual of ornithology: avian structure and function*. Yale Univ. Press, New Haven, CT.
- PYKE, G. 1978. Optimal foraging in hummingbirds: testing the marginal value theorem. *Am. Zool.* 18:739-752.
- SAETHER, B. 1994. Reproductive strategies in relation to prey size in altricial birds: homage to Charles Elton. *Am. Nat.* 144:285-299.
- SAS INSTITUTE. 1994. *SAS procedures guide*. Version 6. SAS Institute, Inc., Cary, NC.
- STURKIE, P. 1986. Body fluids: blood, p. 62-73. *In* P. Sturkie [ed.], *Avian physiology*. Springer Verlag, New York.
- SULLIVAN, K. 1989. Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaeonotus*). *J. Anim. Ecol.* 58:275-286.
- SVENNENSON, E., AND J. MERILA. 1996. Molt and migratory condition in Blue Tits: a serological study. *Condor* 98:825-831.
- WAITE, T., AND R. YDENBERG. 1996. Foraging currencies and the load-size decision of scatter-hoarding Grey Jays. *Anim. Behav.* 51:903-916.
- WEATHERS, W., AND K. SULLIVAN. 1991. Foraging efficiency of parent juncos and their young. *Condor* 93:346-353.
- WUNDERLE, J. M., JR. 1991. Age-specific foraging proficiency in birds. *Current Ornithol.* 8:273-324.
- YOERG, S. 1994. Development of foraging behaviour in the Eurasian Dipper, *Cinclus cinclus*, from fledging until dispersal. *Anim. Behav.* 47:577-588.