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FOOD DISPERSION AND FORAGING ENERGETICS: A MECHANISTIC SYNTHESIS FOR FIELD STUDIES OF AVIAN BENTHIVORES¹

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Abstract. Much effort has focused on modeling and measuring the energy costs of free existence and the foraging strategies of animals. However, few studies have quantitatively linked these approaches to the patch structure of foods in the field. We developed an individual-based model that relates field measurements of the dispersion of benthic foods to search costs and foraging profitability of diving ducks.

On Lake Mattamuskeet, North Carolina, Canvasback ducks (*Aythya valisineria*) eat only the belowground winter buds of the submerged plant *Vallisneria americana*. We measured and modeled the patch structure of winter buds at the level of potential foraging "loci," defined as contiguous circles 1 m in diameter. In the field and in the model, Canvasbacks make repeated vertical dives in such loci, foraging in the sediments by touch, before surface-swimming to another locus. We quantified first-order patchiness by fitting a negative binomial distribution to core samples taken at 50-m intervals along transects, to yield the frequencies of loci with different bud densities. Second-order patchiness was measured by taking cores at 1-m increments radiating from each sampling point, and regressing bud density at each sampling point on densities at these increments. No significant correlations were found, indicating that Canvasbacks could not predict food densities based on densities in nearby foraging loci. For the model, we generated food grids from the negative binomial distributions of core samples.

Energy costs of diving were calculated by applying aerobic efficiencies (mechanical power output ÷ aerobic power input) to biomechanical models. Unlike respirometry alone, this method accounts for effects on dive costs of varying water depth and dive duration. We used measurements of Canvasback intake rates at different bud densities to calculate profitability (energy intake minus expenditure) for each dive. Multivariate uncertainty analyses (Latin hypercube) indicated that profitability for Canvasbacks foraging on *Vallisneria* buds is determined mainly by food-item size and locomotor costs of descent. Bud metabolizable energy, water temperature, bud dispersion, and search and handling time coefficients of the functional response for intake rate have relatively minor influence. Individual-parameter perturbations indicated that to maintain the same foraging benefits, the total area of *Vallisneria* habitat would have to increase by 1.4-fold if dry mass per bud decreased from 0.10 to 0.03 g, and by 2.1-fold if water depth increased from 0.5 to 2 m.

Our method allows study of interactions between patch structure and foraging energetics without detailed spatial mapping of foods, which is not feasible at appropriate scales for highly mobile benthivores. The model yields estimates of energy balance, contaminant intake, and amount and quality of foraging habitat required to sustain diving duck populations under varying environmental conditions. More accurate prediction of giving-up times and giving-up food densities will require better understanding of the time scale over which ducks balance their energy budgets.

Key words: *Aythya valisineria*; biomechanics; Canvasback duck; diving; food dispersion; foraging energetics; *Vallisneria americana*.

INTRODUCTION

Considerable data and methodology have developed around modeling and measuring both the energy costs of free existence in animals (Nagy 1987, Costa 1988, Goldstein 1988, Birt-Friesen et al. 1989) and their for-

aging strategies (Tome 1988, Beauchamp et al. 1992, Houston and Carbone 1992, Ball 1994). Likewise, much effort has recently focused on refining concepts and measurements of patch structure, and identifying appropriate spatial scales for different ecological analyses (O'Neill et al. 1988, Kotliar and Wiens 1990, Malatesta et al. 1992). However, few studies have linked these disciplines mechanistically to analyze effects of resource dispersion on rates of energy expenditure and intake (Mason and Patrick 1993, Turner et al. 1993, Lovvorn 1994a). In this paper, we develop and explore

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an individual-based model that relates field measurements of the dispersion of benthic foods to search costs and foraging profitability (energy intake minus expenditure) of diving ducks.

From an autecological perspective, a number of studies have sought to quantify the energy cost of foraging in a given species (Croll 1993, Wilson and Culik 1993 and references therein). For example, the cost of diving (including pauses between dives) in Tufted Ducks (*Aythya fuligula*) in water at 7.4°C has been reported as 18.9 W/kg or 1.7 times the cost of resting at the surface (Bevan and Butler 1992). However, this cost was measured at a single depth (0.6 m); and because of depth-dependent differences in mechanical power required for descent vs. bottom foraging, both depth and dive duration can appreciably affect the energy cost of a dive (Lovvorn et al. 1991, Lovvorn and Jones 1991, 1994, Lovvorn 1994a). Analyses of trade-offs among different foraging strategies must account for such variations in energy costs under different conditions (Beauchamp et al. 1992). However, it is difficult to measure oxygen consumption in chambers at the water surface for all combinations of dive depth and duration observed in different species in the field. A synthesis of biomechanics and respirometry, whereby values of aerobic efficiency (mechanical power output ÷ aerobic power input) are applied to calculations of mechanical energy cost, offers the capability of estimating dive costs under different conditions as has been done for aerial flight (Pennycuik 1989, Lovvorn and Jones 1994).

From a resource management perspective, we often need to know how much habitat is required to support a population of animals, in order to set habitat protection priorities, acceptable levels of impact, and standards for restoration (Goss-Custard 1977, Korschgen et al. 1988). Past studies have calculated the average energy requirements of birds, and then compared these estimates to total food biomass present to infer sustainable population levels (Anderson and Low 1976, Cornelius 1977, Korschgen et al. 1988, Lovvorn and Baldwin 1996), impacts on the food base (Grant 1981, Howard and Lowe 1984, Baldwin and Lovvorn 1994), or competition with other species (Eadie and Keast 1982). However, food dispersion affects the biomass that can be fed upon profitably, and thus the fraction of food organisms subject to depletion (Lovvorn 1994a). Moreover, models using parameters averaged over entire populations might yield different results from individual-based models that simulate the foraging energetics of many individuals (Huston et al. 1988). The latter distinction is especially important to evaluating spatial effects, because foraging economics often vary widely among individuals depending on their specific locations in heterogeneous habitats (Roese et al. 1991). Individual-based models are needed to analyze how food requirements vary with food dispersion and consequent search costs, and how to

sample food organisms in ways that reflect their economic availability to foragers.

From an ecosystem perspective, the role of vertebrates in structuring prey communities and in nutrient regeneration depends on spatial and temporal patterns of predation, grazing, and excretion. Such patterns depend in turn on foraging profitability relative to food dispersion, i.e., search effort and food densities for which energy costs exceed gains and foraging ceases. Estimates of food requirements that do not consider the spatial pattern of food intake have unclear ecological implications, especially for animals that forage over large areas. For example, nutrients excreted by eiders and gulls in the Gulf of St. Lawrence are unimportant to the Gulf's total nutrient budget, but input by birds at aggregation sites can be locally significant (Bedard et al. 1980; see also Ruess et al. 1989, Powell et al. 1991, Manny et al. 1994). Shorebirds switching prey as profitability changes with prey depletion can alter the structure of invertebrate communities (Schneider 1978); and patchy herbivory can affect plant dispersion quite differently from more continuous grazing (Andrew and Jones 1990, Hyman et al. 1990). Thus, linking foraging energetics to the patch structure of food organisms can allow "scaling up" of organismal physiology and biomechanics to effects at community and ecosystem levels (Huston et al. 1988, Ehleringer and Field 1993). However, most spatial foraging models have used simple constants for quite variable physiological values such as locomotor costs, without comparing the consequences of physiological variability to that of other parameters at larger scales (Hyman et al. 1990, Roese et al. 1991, Mason and Patrick 1993, Turner et al. 1993).

Finally, computer mapping technologies have encouraged the development and testing of a growing body of ecological theory involving animal movements relative to resource dispersion (e.g., Wiens and Milne 1989, Clark et al. 1993, Turner et al. 1993). However, new capabilities for manipulating data have not decreased the difficulty of *obtaining* dispersion data on many important scales. For example, detailed mapping of benthic foods on a scale relevant to the foraging energetics of highly mobile birds is currently not feasible, despite the importance of food dispersion to their foraging profitability and sustainable population levels. A critical challenge is to develop alternative methods of sampling and analysis that allow consideration of resource dispersion effects without detailed and comprehensive mapping.

In this paper, we develop and explore an individual-based model of foraging energetics in Canvasback ducks (*Aythya valisineria*) that includes effects of food dispersion. We especially evaluate effects of variation in physiological parameters on foraging energetics, because such factors have received little emphasis in spatial models. Our model accounts for dive depth, dive duration, thermoregulation, search costs, and food in-

take as functions of the spatial pattern of belowground winter buds of the submerged plant *Vallisneria spiralis*. Our analyses indicate that (1) foraging profitability and amount of viable habitat are most affected by variations in food-item size and in locomotor costs of descent as influenced by water depth; (2) variations in water temperature above 0°C have relatively little effect on foraging costs; (3) variations in mass per bud alter profitability much more than do variations in bud metabolizable energy, mean bud density, or intake rates at different bud densities; and (4) variations in bud dispersion (as indicated by the negative binomial parameter k) have relatively minor effects on profitability in this habitat. These results have important implications for estimating energy balance, contaminant intake, and the amount and quality of habitat needed to sustain Canvasback populations under varying environmental conditions.

METHODS

We based our foraging energetics model on field and laboratory studies of Canvasbacks and other diving ducks. Model food grids of *Vallisneria* winter buds were generated from core samples in Lake Mattamuskeet, North Carolina. In the model, written in QuickBasic 4.5, an individual Canvasback was randomly placed on a food grid and began foraging. A foraging bout (sequence of dives in one or more foraging "loci" as defined below) ended when the duck either filled its esophagus or dropped below a certain energy deficit. Criteria used to evaluate foraging bouts included the mean profit (energy intake - energy expended) per dive, percentage of profitable foraging loci, and percentage of time spent surface-swimming between loci. We compared model results between early (early November) and late (late November-early December) periods of waterfowl staging on Lake Mattamuskeet, and assessed the correspondence between field observations and model simulations. We also performed uncertainty analyses (both multiple and individual parameter perturbations) to evaluate the relative contribution of selected parameters to variation in model output.

Study site

Lake Mattamuskeet, North Carolina, is ≈ 300 km² in area and <1 m deep throughout, with abundant stands of the submerged plants *Vallisneria spiralis* and *Potamogeton perfoliatus* (Lovvorn 1989a). Canvasbacks arriving in early November concentrate on Lake Mattamuskeet, where they eat exclusively the belowground winter buds of *Vallisneria*. In early December, they move 5-45 km away to Pamlico Sound where they remain until departing north beginning in late February (Lovvorn 1989a).

Time-activity budgets, distances moved, and dive and pause durations

Procedures for observing behavior of Canvasbacks on Lake Mattamuskeet were described in detail by Lov-

vorn (1989b). Five-minute, focal-individual samples of equal numbers of males and females were taken throughout daylight hours in fall 1982 and 1983. During the prewinter fattening period on Lake Mattamuskeet (Lovvorn 1994b), Canvasbacks foraged continuously and did not appear to leave the lake at night; thus, daytime behavior patterns are assumed to extend through the night (see also Perry and Uhler 1988, Hohman et al. 1990, and Howerter 1990 for evidence of consistent night feeding by Canvasbacks). Canvasbacks almost always dived and surfaced without significant lateral movement underwater, allowing continuous observation of individuals. Behavior at 20-s intervals, and the durations of all dives and pauses between dives, were recorded on a cassette recorder and later transcribed. Dive and pause durations used in this paper are from November to December 1983 only. Distances moved on the water surface were estimated assuming three body lengths per metre.

Percent time spent by Canvasbacks in activities other than surface-swimming and diving were assumed constant in all model simulations. Values based on observations at Lake Mattamuskeet from 11 November to 13 December 1982 and 7 November to 31 December 1983 were 3.2% for resting on the water surface (including alert behaviors), 30.2% for sleeping, and 7.6% for comfort movements such as preening and bathing (Lovvorn 1989b). Percent time spent flying, which has not been well documented for ducks, was estimated at 3% (Lovvorn and Jones 1994).

Regressions relating the duration of pauses between dives, D_p , to the duration of the dive preceding each pause, D_d , differed between early (11-15 November) and late (18 November-19 December) observation periods in 1983 (general linear test, $P < 0.001$, Neter and Wasserman 1974:160-167). For the early period the equation was $D_p = 2.822 + 0.165D_d$ ($r^2 = 0.086$, $P < 0.001$, $n = 1872$ dives), and for the late period $D_p = 3.579 + 0.141D_d$ ($r^2 = 0.077$, $P < 0.001$, $n = 1873$). In model simulations, we used these equations to estimate a pause duration to follow each dive that was randomly chosen from the frequency distribution of observed dive durations (Fig. 1).

Mechanical energy costs of diving

Mechanical costs of diving to different depths for different durations were calculated from the model of Lovvorn et al. (1991) and Lovvorn and Jones (1991) for diving ducks (*Aythya* spp.). For that model, hydrodynamic drag of ducks frozen in a diving posture was measured in a tow tank. Buoyancy was calculated as the difference between body weight and the weight of water displaced by restrained ducks submerged head-down in a water-filled cylinder. In model calculations, buoyancy was adjusted for compression of respiratory and plumage air spaces with depth. Ducks descending in a tank 2 m deep were filmed at 100 frames/s to determine linear displacement at 0.01-s intervals dur-

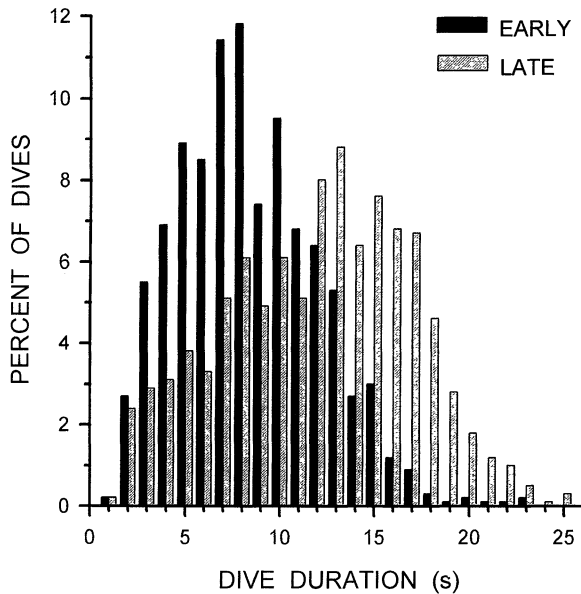


FIG. 1. Observed dive durations of Canvasbacks during early and late periods in 1983 on Lake Mattamuskeet. For the early observation period (11–15 November) $n = 2199$ dives, and for the late period (18 November–19 December) $n = 2330$ dives.

ing a stroke cycle (including power and recovery phases). Work during these intervals was calculated by multiplying drag and buoyancy by displacement, and then adding inertial work done in accelerating the body and the added mass of entrained water. Work during all intervals was then integrated over the power phase to yield work per stroke during descent. Work per stroke at the bottom was calculated by multiplying the buoyant force by the distance the bird would float upward during the time required for a stroke (Lovvorn et al. 1991). Counts of strokes needed to reach the bottom and remain there (from video films, see Lovvorn 1994a) allowed calculation of total work during dives.

Stroke rates and speeds of descent and ascent at water depths from 1.2 to 2 m were interpolated from video measurements at those two water depths (Lovvorn 1994a). Stroke rates and speeds for 1.2 and 2 m were used for shallower and deeper depths, respectively. Work during descent was calculated twice for each depth, once with buoyancy equal to that measured at the surface and once with buoyancy adjusted for hydrostatic pressure at the bottom. These two work values were then averaged for dives to given depths (Lovvorn and Jones 1991).

Aerobic energy costs of activities and nutrient storage

Activity costs can be affected by the thermal environment. Water temperature in shallow (<1 m) Lake Mattamuskeet closely tracks air temperature (J. R. Lovvorn, unpublished data). When daily mean air tem-

peratures from nearby Cape Hatteras, North Carolina, in 1983 were weighted by the number of dives observed on each day for which dive parameters were calculated, temperatures did not differ between early (11–15 November) and late (27 November–19 December) periods (t test, $P = 0.46$, data from the National Climatic Data Center, Asheville, North Carolina). For simulating early vs. late periods on Lake Mattamuskeet, we used the weighted mean air temperature for all observation days (mean \pm 1SD = $11.4 \pm 2.4^\circ\text{C}$, $n = 9$ d) for both air and water temperature.

We applied mass-specific respirometry data (\dot{V}_{O_2}) for congeneric Tufted Ducks to Canvasbacks. For Tufted Ducks, the relation between aerobic energy cost of resting on the surface (P_r , in watts per kilogram) and water temperature (T_w) was $P_r = 12.67 - 0.3069T_w$ ($r^2 = 0.61$, Bevan and Butler 1992). We assumed that costs of sleeping, alert behavior, comfort movements, and passive ascent during dives were equal to that for resting at given water temperatures. For descent and bottom foraging, we calculated aerobic efficiencies ($\eta = \text{mechanical power output} \div \text{aerobic power input}$) from the mechanical model described above and respirometry of Tufted Ducks diving to a depth of 0.6 m in water at 7.4°C ($\eta = 0.2337$) and 22.9°C ($\eta = 0.1438$, Bevan and Butler 1992). We linearly interpolated aerobic efficiencies for water temperatures between these two values, and applied them to mechanical work estimates for descent and bottom foraging. The lower \dot{V}_{O_2} (11.59 vs. 13.91 W/kg) and resulting higher η during submergence at the lower temperature was offset by higher \dot{V}_{O_2} during pauses between dives. For pauses, we linearly interpolated between \dot{V}_{O_2} of 17.47 W/kg at 7.4°C and 12.28 W/kg at 22.9°C (Bevan and Butler 1992).

Aerobic cost of surface-swimming in Tufted Ducks, measured only in water at 17.8°C , increased curvilinearly from 6.46 W/kg at 0.40 m/s to 20.99 W/kg at 0.78 m/s (Woakes and Butler 1983). The speed of wild ducks swimming on the water surface is variable; we used 0.6 m/s at a cost of 11.48 W/kg. Energy costs of flight were estimated by applying an aerobic efficiency of 0.23 to mechanical costs calculated from the aerodynamic model of Pennycuick (1989; see Lovvorn and Jones 1994). The aerobic power of flying was 230 W at the maximum range speed (V_{mr}) of 23 m/s for the mean (\pm 1 SD) body mass (1.395 ± 0.128 kg) and wingspan (0.873 ± 0.029 m) of 21 adult male Canvasbacks collected on Lake Mattamuskeet in November 1982–1983 (Lovvorn 1994b).

Canvasbacks on Lake Mattamuskeet in November 1982–1983 gained ≈ 1.66 g of body fat and 0.23 g of body protein per day (all sex-age classes combined, Lovvorn 1994b). Considering digestive and conversion efficiencies, nutrient deposition required an intake of ≈ 4.6 g dry mass of buds per g of body fat, and 14.8 g of buds per g of body protein (Lovvorn 1987:38). At a metabolizable energy of 11.568 kJ/g dry mass of buds

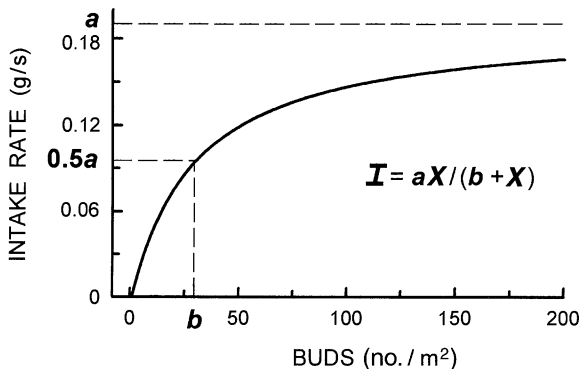


FIG. 2. Example of the functional response of the intake rate of Canvasbacks diving for *Vallisneria* winter buds, based on the data of Takekawa (1987). In the equation, I is the number of buds consumed per second at the bottom, x is the number of buds per m^2 , and a is the handling time coefficient, or the asymptote for the maximum rate at which Canvasbacks can handle buds regardless of bud density. The search time coefficient b is the bud density at an intake rate of $0.5a$, and thus indicates effects of search time on how quickly the curve for intake rate rises and becomes limited by the asymptotic handling time.

(Lovvorn 1987:33), nutrient storage increased the daily energy requirement of Canvasbacks by 127.71 kJ/d.

Daily costs of all activities, excluding work done underwater and surface-swimming between feeding loci, and including nutrient storage, were prorated to work on a per second basis. To distribute this overhead cost of daily nondive activities to the time required for each dive, this prorated work per second was multiplied by dive duration. This work was then added to the (prorated) energy expended during surface-swimming to that locus, and during the pause after that dive. This total abovewater cost was added to the work done underwater for comparison with energy intake during the dive.

Energy intake

Intake of *Vallisneria* winter buds per second spent at the bottom was estimated from a Michaelis-Menten equation fit to the functional response data of Takekawa (1987) (Marquardt method, PROC NLIN; SAS, Cary, North Carolina). In the equation $I = ax/(b + x)$, I is the number of buds consumed per second at the bottom, x is bud density (number per square metre), and a is the handling time coefficient, or the asymptote for the maximum rate at which Canvasbacks can handle buds regardless of bud density (Fig. 2). The search time coefficient b is the bud density at an intake rate of $0.5a$, and thus indicates effects of search time on how quickly the curve for intake rate rises and becomes limited by the asymptotic handling time. In Takekawa's (1987) experiments, in a tank $3 \times 3 \times 1$ m deep, Canvasbacks fed from an array of six trays, each 0.82 m^2 in area, in which *Vallisneria* buds were buried in sand at depths of 2.5–6.4 cm. Intake rates were reported only for entire

dives, so we calculated intake per second at the bottom based on the mean bottom time per dive during the experiments (5.7 s, Takekawa 1987:135). For seven bud densities (x) ranging from 10 to 110 buds/ m^2 , intake of buds per second at the bottom (I) was estimated by the equation $I = 0.193x/(29.5 + x)$, $R^2 = 0.98$.

The maximum number of *Vallisneria* winter buds a Canvasback could eat in a given foraging bout was taken to be the maximum number of buds found in esophagi among 119 Canvasbacks collected while feeding on Lake Mattamuskeet (see Lovvorn 1994b). In 1983, the mean dry mass of individual buds in esophagi was greater in Canvasbacks collected 4–14 November (0.0451 g/bud, $n = 773$) than 21 November–2 December (0.0296 g/bud, $n = 473$). The maximum dry mass of buds in any esophagus was 4.649 g in a juvenile male collected on 30 November 1983. Thus, we estimated the maximum number of buds ingestible in one foraging bout to be 103 in the early period and 157 in the late period. Metabolizable energy of *Vallisneria* winter buds (66.7% water) is ≈ 11.568 kJ/g dry mass (Lovvorn 1987:33).

Patch structure of *Vallisneria* winter buds

In a hierarchical model of patch structure, Kotliar and Wiens (1990) defined first-order patchiness as equivalent to "grain," the smallest scale at which an organism differentiates among patches. First-order patches are therefore internally homogeneous from that organism's perspective. Second-order patches are composed of clusters of first-order patches (Kotliar and Wiens 1990). We modeled the patch structure of winter buds with grain equal to potential foraging "loci," defined as contiguous circles 1 m in diameter. These loci approximate the area within which a Canvasback makes one or more vertical dives until surface-swimming to a different locus to begin a new series of vertical dives (Lovvorn 1989b).

First-order patchiness.—In fall 1983, transects for sampling *Vallisneria* winter buds were established in four areas of Lake Mattamuskeet that were heavily used by Canvasbacks the previous fall (see Fig. 2 in Lovvorn 1989a). Sediment cores were taken from 20 September to 5 October 1983 before Canvasbacks arrived, and again from 7 January to 2 February 1984 after they moved to Pamlico Sound.

Seventy sampling stations were marked with stakes at 50-m intervals along the transects, and three replicate cores were taken within 0.5 m of each stake during each sampling period (early vs. late). The sampler was a hand-held plunger device made of galvanized pipe and a 40-cm length of metal tubing with inside cross-sectional area of 92 cm^2 . The sampler was pushed as deep into the substrate as possible, depending on sediment hardness. Winter buds >10 cm deep in the firm sediments of Lake Mattamuskeet apparently were not used by Canvasbacks (Lovvorn 1989a). Cores from the early (first) sampling period were divided into upper

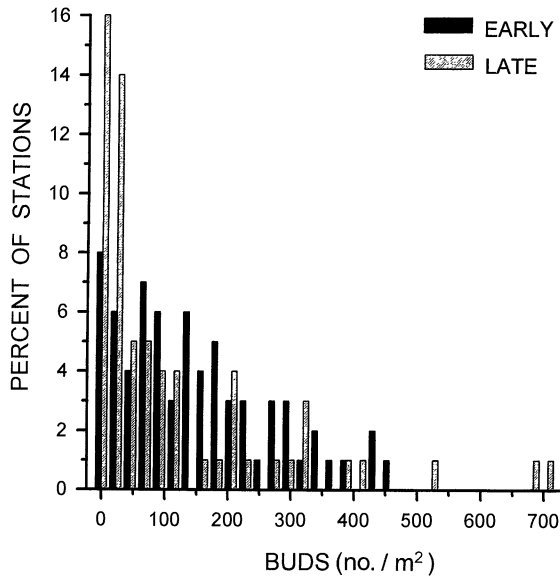


FIG. 3. Negative binomial distributions of the numbers of *Vallisneria* winter buds at 70 stations (means of three replicate cores per station) before and after the Canvasback staging period on Lake Mattamuskeet. For the early period (20 September–5 October 1983) the mean = 149 buds/m² and the negative binomial parameter $k = 1.504$; for the late period (7 January–2 February 1984) the mean = 111 buds/m² and $k = 0.930$.

(top 10 cm) and lower sections only at Transect 4, whereas all cores from the late (second) sample were divided. For analyses in this paper, numbers of *Vallisneria* winter buds in the upper 10 cm of cores from Transects 1–3 in the early sample were estimated by multiplying total buds in each core by the average proportion of buds in the upper 10 cm of cores from Transect 4 (93%, see Lovvorn 1994a). Owing to changes in lake water level, water depths at the same sampling stations ($n = 70$) averaged 39 ± 9 cm (± 1 SD) during the early sample and 68 ± 8 cm during the late sample.

We quantified first-order patchiness among individual foraging loci by using the FORTRAN program NEGBINOM of Krebs (1989:505–513) to fit negative binomial distributions to the above core samples (means of three replicate cores per station for 70 stations, Fig. 3). These distributions yielded the frequencies of possible loci with different bud densities, i.e., first-order patchiness.

Second-order patchiness.—From 18 to 20 October 1993, we took additional cores to describe the second-order spatial pattern (as opposed to negative binomial frequencies) of *Vallisneria* buds in Lake Mattamuskeet. Sixteen sampling stations were marked with stakes at 50-m intervals along a transect corresponding approximately (within a few hundred metres) to Transect 3 of the 1983 sample (see Fig. 2 in Lovvorn 1989a). At each station, three replicate cores were taken at the transect stake, and at each 1-m increment to a distance of 6 m in a random direction from the transect stake.

The distance of 6 m encompassed most surface movements by foraging Canvasbacks during early (94.2%) and late (91.5%) observation periods (Fig. 4). Mean ($n = 3$ replicates) number and dry mass of buds at each 1-m increment were then regressed on values at the focal transect stakes ($n = 16$ stations for regressions done separately for each of the six distance increments). None of these regressions were significant for bud numbers (all $r^2 < 0.11$, $P > 0.20$) or bud dry mass (all $r^2 < 0.15$, $P > 0.14$), indicating a lack of predictable spatial pattern at these scales. Probably because salinity was $\approx 5\%$ lower, mean bud density (± 1 SE) along this transect was 87% higher during 18–20 October 1993 (366 ± 20 buds/m²) than during 20–22 September 1983 (196 ± 15 buds/m²), and bud dry mass was 466% higher in 1993 (32.8 ± 2.1 g/m²) than in 1983 (5.8 ± 4.0 g/m²). Patch structure might differ with such changes in overall bud density, but we were unable to evaluate such effects.

In this habitat, lack of second-order patchiness indicates that Canvasbacks foraging by touch cannot predict how far or in what direction they should move between foraging loci, but rather must search by trial and error for loci with high enough food densities for profitable foraging.

Computer simulation of food grids

Because we detected no second-order patchiness on the scales of 1-m foraging loci and observed foraging movements of Canvasbacks (Fig. 4), we simulated 40×40 m grids of *Vallisneria* winter buds (Fig. 5) by rejecting only those randomly generated coordinates

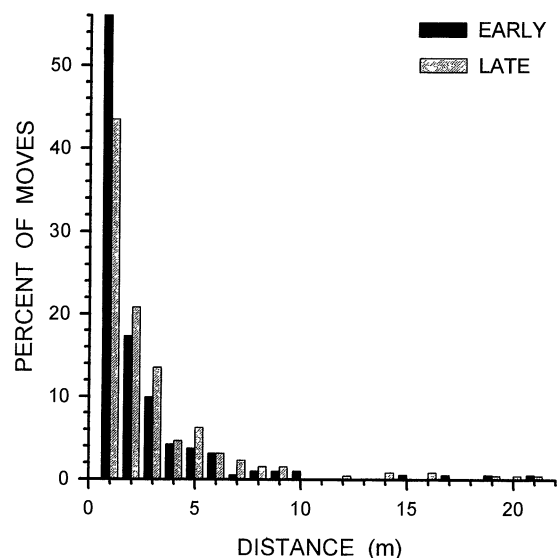
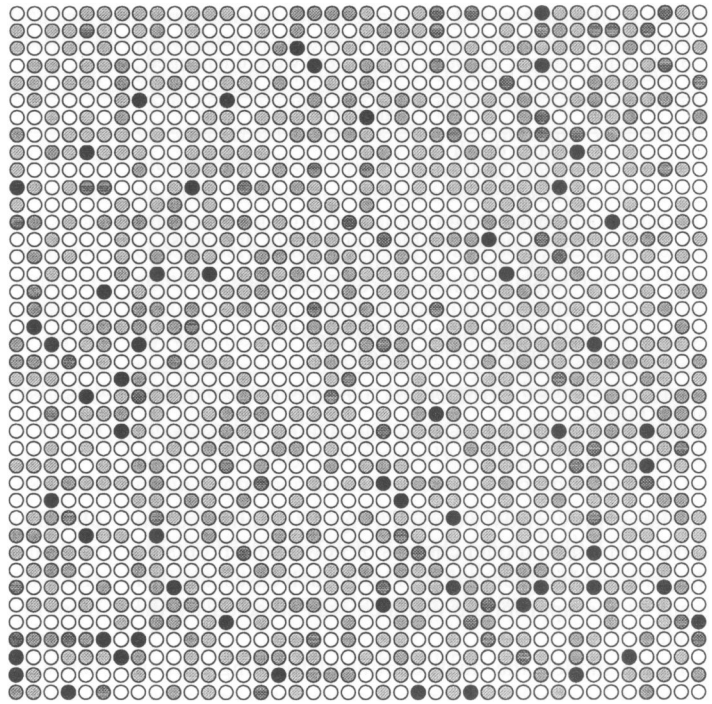


FIG. 4. Observed distances moved on the water surface between foraging loci by Canvasbacks during early ($n = 191$ moves) and late ($n = 269$ moves) observation periods in 1983–1984 on Lake Mattamuskeet. Medians (and 15–85% quantiles) were 1 m (1–4 m) in the early period and 2 m (1–5 m) in the late period.

FIG. 5. Example of a simulated grid (40×40 m) of the numbers of *Vallisneria* winter buds in circular foraging loci 1 m in diameter, based on core samples taken before (20 September–5 October 1983) the Canvasback staging period on Lake Mattamuskeet (mean = 149 buds/m², negative binomial $k = 1.504$, see Fig. 3). For symbol darkness ranging from white to black, bud density classes are 0–114, 115–228, 229–342, 343–456, and 457–1026 buds/m². In field samples, the highest density recorded at any station was 1140 buds/m².



that did not fall within the negative binomial distributions of first-order patchiness (Rejection Method, Press et al. 1989). Our algorithm for generating 40×40 prey grids from negative binomial distributions, when described by the program NEGBINOM of Krebs (1989), yielded coefficients of variation of 2.3% for mean number of buds/m² and 10.3% for parameter k ($n = 10$ grids).

Giving-up rules and movement distances

By the above definition of first-order patches, the assumption is that from the perspective of foraging Canvasbacks, *Vallisneria* bud density was homogeneous within a feeding locus 1 m wide. Canvasbacks can probably detect heterogeneity at smaller scales. However, in our application, the assumption is actually not that bud density is homogeneous within a foraging locus (0.8 m^2), but rather that Canvasbacks can assess average bud density within a locus on a single dive. In other words, a locus is a single foraging unit (first-order patch) during each foraging attempt (dive). Based on studies of captive Canvasbacks searching for food in trays of sand (Ball 1994), these birds are capable of assessing mean food density in a 0.8 m^2 area in a single dive. They might not always do so in the field, where the area searched during single dives probably varies even in the same habitat. However, discriminating spatial selection by diving ducks of areas less than 1 m in diameter is usually not possible during field observations. Our objective was to relate field observations of foraging behavior to food dispersion. Consequently, we feel that defining a foraging locus in terms of (1)

sampling radii that are feasible during a single foraging attempt, and (2) movements detectable in the field, is the most reasonable alternative for our purposes.

During the study period, aboveground parts of *Vallisneria* had senesced and detached, so Canvasbacks searched for belowground winter buds by touch (see Tome 1989a, Ball 1994). In model simulations, Canvasbacks decided when to stop foraging in a given locus and move to a different locus based on their energy balance. After each dive, energy intake was compared to energy expended, including work underwater, surface-swimming between loci, pausing between dives, and the overhead cost of all other daily activities prorated on a per second basis. If expected energy balance on a subsequent dive in the same locus was positive, based on the functional response for the decremented food density and the energy cost of the preceding dive, the duck dove again.

If the expected energy balance from another dive in the same locus was negative, the duck moved to another locus. As noted above, core sampling revealed no second-order patchiness of *Vallisneria* buds at the scale of foraging loci; thus, Canvasbacks moving to a new locus had the same negative binomial expectation of food density regardless of direction or distance moved. (Negative binomial probabilities of encountering individual loci with different bud densities do not vary spatially.) Any criteria used by Canvasbacks to vary distance moved between loci were unknown to us, so we randomly sampled from frequency distributions of movement distances observed in the field (Fig. 4). Direction moved was assumed random. In simulations,

TABLE 1. Parameters and their ranges used in uncertainty analyses of the foraging energetics model for diving ducks. For parameters having two specified ranges, the second range was used in a second set of simulations (Simulation 2 in Table 3) in which ranges for other parameters were unchanged.

Parameter	Range
Water depth (m)	0.5–3.5
Water temperature (°C)	1–25
Aerobic efficiency, η^*	$\eta \pm 0.07$
Dry mass/bud (g)	0.030–0.18
Bud metabolizable energy (kJ/g dry mass)	$11.568 \pm 5\%$
Mean number of buds per m ²	111–366
Negative binomial k of bud dispersion	1–5, 1–10
Bout deficit fraction, BDF	$-0.5 \pm 5\%$, $\pm 20\%$
Handling time coefficient, a^\dagger	$0.1926 \pm 5\%$, $\pm 20\%$
Search time coefficient, b^\dagger	$29.473 \pm 5\%$, $\pm 20\%$

* η = mechanical power output \div aerobic power input, calculated for different temperatures from the data of Bevan and Butler (1992).

† From the functional response equation for intake rate (Fig. 2).

the large prey grids we used (Fig. 5) minimized instances in which model choices of new loci fell outside the grid (see Haefner et al. 1991). In such cases, another locus at the appropriate distance was selected by the model.

In the model, the duck continued foraging until it (a) filled its esophagus, or (b) accumulated an energy deficit that exceeded one-half the fraction of daily energy requirement that on average must be met during a foraging bout [i.e., bout deficit fraction (BDF) = -0.5]. Durations of entire foraging bouts were not measured in the field, but it appeared that Canvasbacks generally engaged in only one bout per half hour. Canvasbacks at Lake Mattamuskeet spent 45% of their time foraging (Lovvorn 1989b), so we estimated the mean duration of foraging bouts as 13.5 min, or 2.02% of daily foraging time (24 h minus time spent in other activities = 11.16 h). Nagy's (1987) allometric equation, based on doubly-labeled water measurements of free-ranging birds, estimates a field metabolic rate of 1120 kJ/d for an average adult male Canvasback on Lake Mattamuskeet in November (Lovvorn 1994b). Thus, a Canvasback must achieve an average profit per foraging bout of 22.62 kJ (0.0202×1120 kJ) to meet its daily energy requirements. When cumulative profit during a bout falls to less than half that value (11.31 kJ), it is unlikely that the duck can achieve positive energy balance by continuing for the average bout duration; hence the choice of BDF = -0.5 . The duck should then stop feeding and move to another foraging site, i.e., to another 40×40 grid with a different food regime.

By this scheme, a Canvasback continued feeding in a locus until its energy balance in that locus became negative, regardless of potential for higher net gain at other loci. This decision rule differs from marginal value formulations (Tome 1988, Houston and Carbone 1992), in which an omniscient animal leaves a patch when the net profitability in that patch falls below the average for all patches. However, core samples of winter buds indicated that Canvasbacks sometimes de-

pleted patches to below the habitat average, while higher-than-average densities remained in other patches (Lovvorn 1994a). These patterns probably resulted from high costs of searching for better patches (owing to high locomotor costs and tactile foraging of Canvasbacks), constant alteration of food densities by other flock members, and consequent lack of omniscience about the average for all food patches (see also Bernstein et al. 1991). Our decision rule allowed Canvasbacks to deplete foraging loci to below-average food densities, and to avoid costs of searching for better loci, as long as their energy balance (including daily overhead costs) remained positive.

Our selection of new loci did not explicitly consider effects of foraging aggression, or of predation risk and related flocking behavior (Thompson et al. 1974, Lovvorn 1989b, Hyman et al. 1990). Such factors might influence the direction or distance moved, although the negative binomial expectation of food density was independent of direction or distance. Such effects on search costs were accounted for implicitly by sampling from the frequencies of distances moved in the field (Fig. 4).

Uncertainty analyses

We evaluated effects of variation in selected parameters (Table 1) on model estimates of mean profit per dive. In some recent literature (e.g., Madenjian et al. 1993), "sensitivity analyses" are simulations that evaluate variability within a coefficient of variation (CV) of 2% for parameters assumed to be normally distributed, whereas "error analyses" are such simulations for a CV of 20%. We use the term "uncertainty analyses" to avoid these connotations. We considered ranges of values likely to occur in areas where Canvasbacks forage on winter buds of *Vallisneria*, such as Lake Mattamuskeet, the Chesapeake Bay region, Long Point Bay of Lake Erie, and the upper Mississippi River. Values for the parameters examined can vary appreciably among these areas. Consequently, we were concerned not with sampling from normal or similar dis-

tributions around particular means, but rather with variation between observed endpoints (Table 1). All parameters were considered uniformly distributed within these ranges.

At the above-mentioned areas, Canvasbacks generally feed on *Vallisneria* buds at depths from 0.5 to 3.5 m. During observations at foraging sites (see Lovvorn 1989b), water temperatures varied from 1°C at all areas to 25° at Lake Mattamuskeet in early November. We wished to examine variations in aerobic efficiency (η = mechanical power output ÷ aerobic power input) independently of effects of water temperature on η . Thus, for each randomly selected temperature, we varied η by ± 0.07 (i.e., $\pm 7\%$ efficiency) around the value calculated for that temperature from the data of Bevan and Butler (1992), which ranged from 23.37% at 7.4°C to 14.38% at 22.9°. [See Stephenson et al. (1989) for a review of η values for different studies of swimming endotherms.]

Mean dry mass per bud ranged from 0.0296 to 0.0451 g during late and early periods, respectively, at Lake Mattamuskeet, but was 0.18 ± 0.07 g (mean ± 1 SE, $n = 100$) during autumn at the upper Mississippi River (Takekawa 1987:167). Takekawa reported a coefficient of variation of 4% for the metabolizable energy (ME) of *Vallisneria* winter buds fed to Canvasbacks; we varied bud ME by $\pm 5\%$ around the value calculated in Lovvorn (1987:33). We had no data on the range of variability in the handling time coefficient a and search time coefficient b of the functional response equation of bud intake rate [$I = ax / (b + x)$, where I = buds ingested/s and x = buds/m²]. We therefore did two sets of simulations (Simulations 1 and 2), one in which these coefficients were varied by $\pm 5\%$ around the values fitted to Takekawa's (1987) data (Table 1), and another in which these parameters were varied by $\pm 20\%$. In the model, the bout deficit fraction (BDF) is the negative fraction of the average profit per bout needed for energy balance that a Canvasback will incur before quitting a foraging bout. In Simulations 1 and 2, we varied BDF by ± 5 and $\pm 10\%$, respectively, around -0.5 , which was the value used in all other simulations in this paper.

At Lake Mattamuskeet, mean number of buds per square metre varied from 149 in the early period and 111 after the late period in autumn 1983, to 366 in mid-October 1993. Takekawa (1987:130) reported that *Vallisneria* buds at the upper Mississippi River "reached densities of 350 buds/m²." In uncertainty analyses, we varied bud density from 111 to 366 buds/m². For bud dispersion as measured by negative binomial parameter k (35×35 m grids), we had no data to indicate the possible range of variation: at Lake Mattamuskeet in autumn 1983, values ranged from 1.504 in the early period to 0.930 after the late period. In Simulations 1 and 2, we varied k from 1 to 5 and from 1 to 10, respectively.

Uncertainty Simulations 1 and 2 each included 150

foraging bouts. In a Latin hypercube design (Swartzman and Kaluzny 1987), the uniform distributions (Table 1) were divided into 150 equal intervals, and for each bout, values for each parameter were randomly selected from intervals chosen randomly without replacement. After simulations, all variables were ranked and the dependent variable (mean profit per dive) was regressed against the independent variables (randomly chosen parameter values) for each bout. Relative partial sums of squares (RPSS) for ranked data indicated the variance in mean profit per dive (in joules) explained by variation of individual parameters, with effects of the other parameters statistically removed (see Bartell et al. 1986, Swartzman and Kaluzny 1987). This method revealed which parameters should be measured more accurately and precisely to improve estimates of mean profit per dive. For ease of comprehension, we also report partial coefficients of determination (partial r^2); however, parameters can show high correlation (partial r^2) but account for small residual variances as indicated by RPSS (Bartell et al. 1986).

RESULTS

Model estimates vs. field observations

Giving-up frequencies.—Proportions of dives followed by swimming > 1 m on the water surface (changing foraging loci) differed between model simulations and field observations. We generated five foraging grids each for early and late periods, based on negative binomial distributions fitted to field data from Lake Mattamuskeet. In model simulations, percentages of dives followed by moving to different loci (mean ± 1 SE) were $31.5 \pm 1.5\%$ for the early period and $78.0 \pm 1.8\%$ for the late period. In field observations, the values were 3.4% for the early period (7–13 November 1983) and 17.5% for the late period (4–6 December 1983, see Lovvorn 1994a).

Patterns of winter bud depletion.—Ten prey grids (20×20 m) were generated from core data in the early period, and then depleted by successive, simulated foraging bouts until the mean bud densities resembled that in the late sampling period. In the model, reduction of the mean number of buds per square metre had no significant effect on bud dispersion as measured by negative binomial k (Fig. 6). In the field, similar levels of depletion lowered k from 1.504 to 0.930. Because lower k means greater clumping, the latter pattern indicates that *Vallisneria* buds were more clumped after the waterfowl feeding period, i.e., that loci with initially intermediate bud densities were depleted more frequently than were loci with initially high bud densities (see Fig. 3). Thus, waterfowl in the field did not find high-density loci (or second-order clusters of loci) and deplete them disproportionately, but appeared to feed in all loci encountered with profitable food densities (see Lovvorn 1994a). This pattern is logically consistent with our model algorithm, although the mod-

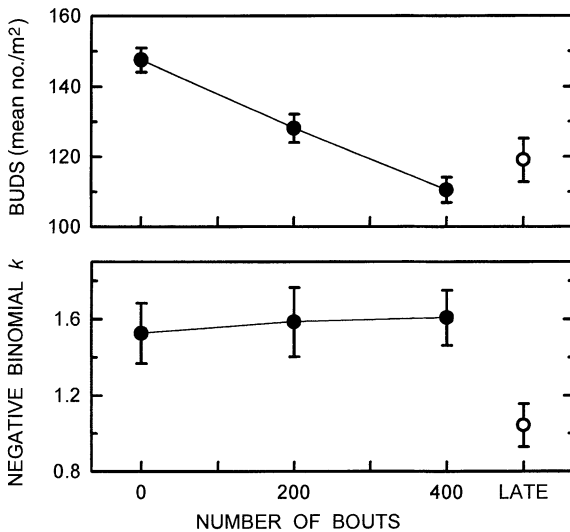


FIG. 6. Mean density and dispersion of *Vallisneria* winter buds at Lake Mattamuskeet, as described by the mean and parameter k for negative binomial frequencies of bud densities. Solid symbols are the means and standard deviations for five 20×20 m model food grids after 200 and 400 simulated foraging bouts by Canvasbacks. Initial values (zero bouts) are the mean and k from field samples before waterfowl arrived (early period), and show variation of the grid generation algorithm. Open symbols are values from field samples after waterfowl departed (late period), with variation among model grids generated from these values.

el did not predict the observed change in k at measured levels of depletion.

Abandonment of Lake Mattamuskeet

Canvasbacks began arriving at Lake Mattamuskeet in early November, and fed there until they abandoned the

lake and moved to nearby Pamlico Sound in December (Lovvorn 1989a). In 1983, this habitat shift corresponded to a significant decrease in overall densities of winter buds (Lovvorn 1994a). However, it was previously not certain that the habitat shift resulted from the Canvasbacks' inability to maintain energy balance, or that the decrease in bud density was the main factor affecting their energetics. Model simulations based on grids generated from core samples before and after Canvasbacks abandoned the lake show clearly that the ducks could not forage profitably after December (Table 2). With increased water depth and decreased bud mass and density, bottom time and food intake decreased, and the work of diving and recovering from dives during pauses increased; these changes resulted in negative profit per dive cycle. In the late-period grid, Canvasbacks averaged only 1.5 dives in a foraging locus before moving to another locus, which increased their time spent traveling (surface-swimming) from 3.2 to 8.4% of total foraging time. The model indicates that by the time Canvasbacks abandoned the lake, the proportion of total habitat area that was viable foraging habitat (proportion of profitable loci) had decreased from 64 to 26%. However, as noted below, the model suggests that the decrease in number of buds per square metre was not the major factor in the Canvasback energy deficit.

Uncertainty analyses

Uncertainty analyses indicated that among the 10 parameters examined, only dry mass per bud and water depth explained appreciable variation in mean profit per dive (Table 3). rPSS (Relative Partial Sums of Squares) indicate the fraction of total variance in the dependent variable (mean profit/dive) explained by

TABLE 2. Selected output from model simulations of Canvasbacks foraging at Lake Mattamuskeet. Five different food grids each for early and late periods were generated from negative binomial distributions with mean μ and parameter k that had been fitted to field samples. Means in the table are averages of five means, each based on 200 simulated foraging bouts in each of the five food grids for either early or late periods. A bout includes foraging at a sequence of loci (0.8 m^2 areas) in which Canvasbacks dive one or more times before moving ≥ 1 m to a different locus. For the early period, $\mu = 149$ *Vallisneria* buds/ m^2 , $k = 1.504$, dry mass/bud = 0.045 g, and water depth = 0.39 m; for the late period, $\mu = 111$ buds/ m^2 , $k = 0.930$, dry mass/bud = 0.030 g, and water depth = 0.68 m. Water temperature was 11.4°C for both periods.

Variable	Early		Late	
	Mean	1 SE	Mean	1 SE
Energy balance per dive cycle*				
Dive work (J)	111.8	2.4	147.4	4.2
Pause work (J)	93.1	0.7	115.1	1.1
Travel work (J)	6.6	0.8	10.8	1.3
Overhead work (J)	184.4	3.6	246.2	5.9
Energy intake (J)	535.4	10.3	375.0	21.6
Profit (J)	139.4	7.5	-144.4	17.0
Search and success rates				
Dives per locus	11.1	0.5	1.5	<0.1
Dives per bout	60.3	1.2	6.7	0.9
Travel time per total time (%)	3.2	0.3	8.4	0.4
Profitable loci per total loci (%)	64.1	1.1	26.0	2.2
Profitable bouts per total bouts (%)	73.2	1.6	1.2	0.4

* Dive cycle includes dive and subsequent pause. Work of traveling (surface-swimming) to a locus is prorated among dives in that locus. Overhead includes work per second of all daily nonforaging activities prorated to the time required for diving, pausing, and traveling between loci.

TABLE 3. Relative partial sums of squares (RPSS) and partial coefficients of determination (r^2) for rank-transformed results of uncertainty analyses of the foraging model for diving ducks. In Simulation 1, negative binomial k varied from 1 to 5, and the bout deficit fraction (BDF) and coefficients for handling time (a) and search time (b) varied by $\pm 5\%$; in Simulation 2, k varied from 1 to 10, and BDF and coefficients a and b varied by $\pm 20\%$ (see Table 1). Simulations 1 and 2 each included 150 foraging bouts, each bout with parameter values randomly selected from ranges in Table 1 by the Latin hypercube method. RPSS indicate the variance in mean profit per dive (joules) explained by variation in each parameter, with effects of the other parameters statistically removed. Multiple $R^2 = 0.64$ for Simulation 1 and 0.74 for Simulation 2, $P < 0.001$.

Simulation 1			Simulation 2		
Parameter	RPSS	Partial r^2	Parameter	RPSS	Partial r^2
Dry mass/bud	23 599 354	0.505†	Dry mass/bud	32 697 699	0.641†
Water depth	15 941 592	0.408†	Water depth	12 130 613	0.398†
Bout deficit fraction	293 896	0.013	Handling time coefficient*	1 518 088	0.077†
Buds (mean no./m ²)	290 535	0.012	Buds (mean no./m ²)	1 272 378	0.065†
Search time coefficient*	179 322	0.008	Water temperature	428 314	0.023
Handling time coefficient*	159 036	0.007	Search time coefficient*	250 062	0.013
Water temperature	27 853	0.001	Aerobic efficiency	111 557	0.006
Aerobic efficiency	21 804	0.001	Negative binomial k	79 081	0.004
Negative binomial k	17 762	0.001	Bout deficit fraction	39 923	0.002
Bud metabolizable energy	140	<0.001	Bud metabolizable energy	4522	<0.001

* From the functional response equation for intake rate (Fig. 2).

† $P < 0.05$.

each independent variable (parameter value), with effects of the other independent variables statistically removed. RPSS are very sensitive to the magnitude of variation (the range of values) in the parameters (Table 1). Except for the last four parameters in Table 1, the range of variation was based on empirical data, and for those last four parameters we did simulations with both conservative and liberal ranges. In neither case did these parameters explain over 8% (and usually much less) of total variance in mean profit per dive, so their influence is likely negligible relative to mass per bud and water depth. The range of dry mass per bud was greatly expanded by including a sample mean (0.18 g) from the upper Mississippi River (Takekawa 1987), which was 4–6 times higher than means from Lake Mattamuskeet during early (0.045 g) and late (0.030

g) periods in 1983–1984. Important effects of water depth result from the high locomotor costs of descent relative to foraging at the bottom in diving ducks (Lovvorn and Jones 1991, 1994, Lovvorn 1994a).

For the two critical variables of dry mass per bud and water depth, we performed individual-parameter perturbations to examine the form of their effects, and their implications for the amount of habitat needed to sustain Canvasback populations. Although including *Vallisneria* buds from the upper Mississippi River greatly extended the range of variation in mass/bud, effects of changes in mass/bud occurred over only half the maximum range (Fig. 7). The influence of water depth was essentially linear over the range examined (Fig. 8). Percentage of profitable loci is equivalent to the proportion of total habitat area that is viable foraging habitat; thus, we can evaluate effects of these

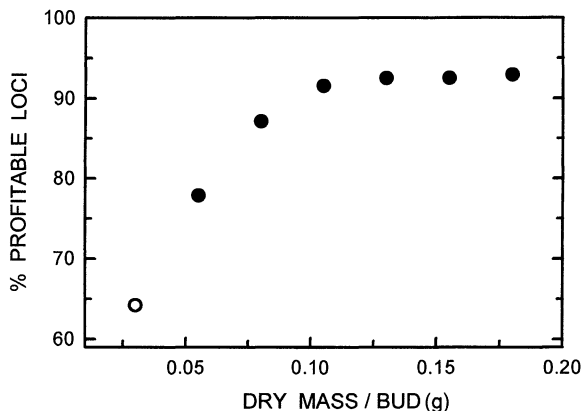


FIG. 7. Effects of individual-parameter perturbation of dry mass per bud on model estimates of the percentage of profitable foraging loci. The open symbol is for simulations based on dry mass per bud during the late period on Lake Mattamuskeet.

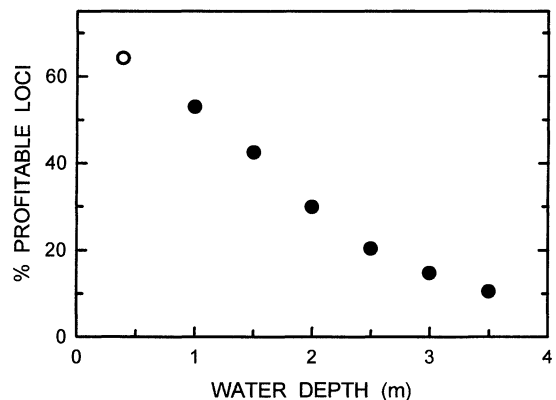


FIG. 8. Effects of individual-parameter perturbation of water depth on model estimates of the percentage of profitable foraging loci. The open symbol is for water depth during the early period on Lake Mattamuskeet.

variables on the total amount of habitat required to sustain Canvasbacks. For example, an increase in water depth from 0.5 to 2 m, with no other change in the mass, density, or dispersion of *Vallisneria* buds, would decrease the fraction of viable foraging habitat from 64 to 30% (Fig. 8). Therefore, maintaining the same amount of viable foraging habitat would require a 2.1-fold increase in total habitat area if the water were this much deeper. Similarly, a decrease in dry mass per bud from 0.10 g to 0.03 g (Fig. 7) would require a 1.4-fold increase in total habitat area to provide the same foraging benefits. Measuring the number of buds per m² without measuring mass per bud is obviously insufficient in this context. Moreover, although variation in mass per bud explains a greater proportion of variance in mean profit per dive in the RPSS analysis (Table 3), changes in water depth have a greater effect on percentage of viable habitat (10–64%, range 54%) than do changes in mass/bud (64–95%, range 31%) if other parameters do not vary appreciably (Figs. 7 and 8).

DISCUSSION

Our model simulations suggest that the energetics of Canvasbacks foraging on belowground plant tubers were driven mainly by food-item size and the locomotor costs of descent. In our model formulation, several parameters often examined in habitat studies proved relatively unimportant when placed in quantitative perspective with other factors, namely, metabolizable energy of food, water temperature (thermoregulation), food dispersion on the scale examined, and search and handling time coefficients as they affect intake rates (Table 3). Variation in mean number of food items per square metre also explained negligible variance in mean profit/dive, suggesting that it was the combination of increased water depth and decreased mass per bud, beyond the decrease in buds per m², that prompted Canvasbacks to stop feeding in Lake Mattamuskeet in early winter.

Model estimates vs. field observations

Giving-up frequencies and patterns of bud depletion.—The percentage of dives followed by moving to a different foraging locus was greater in model simulations than in field observations (31.5 vs. 3.4%, and 78.0 vs. 17.5% in early and late periods, respectively). The very high model estimate for the late period probably resulted in part from the fact that Canvasback behavior was observed before they abandoned Lake Mattamuskeet, whereas bud sampling was done after waterfowl had stopped feeding there. However, the overall discrepancy suggests several possible shortcomings in our model formulation.

The difference between observed and simulated giving-up frequencies might result if there was second-order patchiness, detected and exploited by Canvasbacks in fall 1983, that was not present or that we did not detect in fall 1993. Along the transect sampled in

both years, mean buds per square metre was 87% higher in 1993 (366) than in 1983 (196). Second-order patchiness present at the lower density might not be present at the higher density, but we were unable to evaluate such effects. Cain (1985) concluded that if clumping is a plant strategy to avoid herbivory, it should occur at high rather than low densities. Anderson and Low (1976) found that herbivory by Canvasbacks and other waterfowl on belowground buds of *Potamogeton pectinatus* reduced its biomass in the subsequent growing season; thus, effects of herbivory are significant, and if clumping should consequently occur at high densities then we should have detected it in 1993. Also, the reduction in negative binomial k (relative decrease in loci of intermediate densities) observed in the field (Figs. 3 and 6) indicates that waterfowl did not focus on higher density loci, but rather depleted all loci encountered above some profitability threshold. Otherwise, the relative frequency of higher density loci would have decreased rather than increased.

Less frequent moves between loci in the field than in model simulations might also indicate that Canvasbacks were more effective at extracting winter buds from the sediment at a given bud density than is indicated by Takekawa's (1987) measurements. Takekawa's data covered a low range (0–110 buds/m²) of bud densities relative to means observed in the field (111–366) and examined in our uncertainty analyses (Table 1). However, the asymptotic shape of the curve in Fig. 2 suggests that intake rates are strongly limited by handling time at higher bud densities, and would not change much from intake rates extrapolated from lower density ranges. Probably more importantly, the trays of sand in which buds were buried during Takekawa's foraging trials might not have mimicked adequately the sediment characteristics, dispersion and depth of buds in the sediments, and consequent search and extraction effort experienced by Canvasbacks in the field. Further work should evaluate effects of such variables on the functional response, and include a larger range of bud densities.

In simulating the percentage of dives followed by moving to another locus, we used a bout deficit fraction (BDF) of -0.5 . The bout deficit fraction is the negative fraction of the mean profit per bout needed for daily energy balance that a duck will incur before ending a foraging bout. We reasoned that once a Canvasback incurred that energy debt, it was unlikely that continuing to forage in the same location would yield a positive energy balance. As discussed below, we do not know the time scale over which Canvasbacks balance their energy budget, i.e., on the scale of individual bouts, some multiple of bouts, daily, or even weekly. Uncertainty analyses indicated that variation in BDF had negligible effects on mean profit per dive (Table 3), suggesting that Canvasbacks balance their energy budgets over longer periods than individual bouts. Empirical studies of the time scale of energy balance will be

difficult in species that characteristically undergo large changes in fat and other stored nutrients (see Lovvorn 1994b), and thus have large and variable lags in balancing their energy budgets. However, such information may be critical to better model predictions of giving-up frequencies, and of patterns of depletion as affected by giving-up food densities.

In our model, Canvasbacks left a locus only when profitability in that locus became negative. This decision rule differs from marginal value criteria, in which an omniscient animal remains in a patch only until its profitability in that patch falls below the average profitability for all possible patches (Tome 1988, Houston and Carbone 1992). At some temporal and spatial scale, there probably is a marginal value-type optimization scheme employed by the ducks. In applying the marginal value approach to field situations, the problem is identifying over what period of time and over what spatial region ducks assess the "average" profitability. In model simulations, Bernstein et al. (1991) based the optimization on the animal's experience within a particular foraging bout. Their approach would reasonably apply to diving ducks foraging by touch, which cannot visually assess food availability beyond their direct experience in probing the sediments. However, in the field as opposed to models, it is usually not practical or possible to evaluate the past experience of highly mobile individuals at a particular foraging site, especially since they might use multiple sites repeatedly during a season and several sites more than once in a day.

If the daily or even hourly experience of different individuals is not knowable, one might simply assume omniscience as in many marginal value analyses. However, assuming omniscience about the average for all foraging loci seems appropriate only for species with low search costs and few competitors to modify prey distributions. In contrast, Canvasbacks must dive at appreciable energy cost and forage by touch in searching for profitable loci, and often feed in large flocks that constantly alter information gained by sampling. In dive tank experiments, Ruddy Ducks (*Oxyura jamaicensis*) did not leave patches on the basis of expectation rules for time spent in a patch or for number of prey consumed from the patch (Tome 1989b). Although foraging behavior of Ruddy Ducks was often consistent with marginal value predictions, when it was not they stayed in patches longer and consumed more prey than the model predicted, and this extra time in the patch caused only a small deviation from the maximum rate of energy intake achievable if the birds were omniscient (Tome 1988). Unfortunately, it is unclear how costs of searching for grains of wheat in a 2 × 4 m array of trays filled with 6 cm of sand compares to search costs of diving ducks in the field. At any rate, our rule for when to leave a patch excluded issues of risk sensitivity (e.g., Guillemette et al. 1992), because expectation of relative profitabilities in different foraging loci had no effect on the decision.

Finally, the simulated patterns of depletion did not include effects of other species that probably eat winter buds at Lake Mattamuskeet, mainly scaup (*Aythya affinis*, *A. marila*), Ring-necked Ducks (*A. collaris*), and Tundra Swans (*Cygnus columbianus*). Depletion by other *Aythya* spp. should resemble patterns for Canvasbacks, but effects of 20–30 000 swans that fed in the same areas might differ appreciably.

Effects of different parameters

Mass, density, and metabolizable energy of Vallisneria buds.—Of all parameters examined, variation in dry mass per bud had greatest influence on the variance in mean profit per dive (Table 3). Although food-item size is often not measured in field sampling of food abundance, a variety of studies in both laboratory and field have shown distinct size selection by benthivorous diving ducks and shorebirds. Zwarts and Blomert (1992) evaluated factors affecting size selection of molluscs by benthic-probing Knots (*Calidris canutus*), including maximum size swallowable, depth in the sediments, probability of being detected by touch, shell thickness, and profitability relative to search and handling costs. Common Eiders (*Somateria mollissima*), Tufted Ducks, and Common Pochards (*Aythya ferina*) chose mussels (*Mytilus edulis*, *Dreissena polymorpha*) of intermediate size both in the field and in laboratory experiments, to minimize the mass fraction of shell, avoid taking items too large to be swallowed, reduce variations in profitability, or decrease competition with other diving duck species (Draulans 1982, 1984, 1987, Bustnes and Erikstad 1990). In field experiments with Tufted Ducks, both higher mussel density and lower water depth (range 2–6 m) resulted in increased size selectivity (Draulans 1982).

All sizes of *Vallisneria* winter buds can be swallowed by Canvasbacks, and digestibility and ash fraction do not vary appreciably with bud size. We examined Canvasback esophagus contents only in 1982 and 1983 when mean mass per bud (0.030–0.045 g dry mass) was far lower than that observed at the upper Mississippi River (0.18 g, Takekawa 1987), so evaluation of size selection at Lake Mattamuskeet alone might be misleading. Regarding search and handling parameters, effects of varying the functional response coefficients were relatively negligible in *Vallisneria* habitats (Table 3); however, RPSS and partial r^2 specifically exclude interactions between parameters, such as between mass per bud and functional response coefficients, water depth, and buds per m². Given the importance of food-item size revealed by our simulations, such interactions need to be empirically evaluated and incorporated into the model. In dive-tank experiments on selection by Canvasbacks among *Potamogeton pectinatus* winter buds, *Tenebrio* spp. (beetle) larvae, wheat, and corn, Ball (1994) found that Canvasbacks did not select corn although it had the highest true metabolizable energy. Based on these and additional studies using pelletized

foods varying in energy and protein content, Ball suggested that Canvasbacks use simple "rules of thumb" to select among foods: (1) if taste cues are available, select the most profitable food; (2) if taste cannot be used to evaluate nutrient content, select larger over smaller food items; and (3) if foods vary in texture, select softer ones that will digest more rapidly. These rules are consistent with results of our model, in which selection of larger buds resulted in higher profitability.

Water depth, locomotion, and thermoregulation.—Our model identified water depth as having critical influence on foraging profitability (Table 3, Fig. 8). Several field studies have noted the importance of water depth in feeding site selection by diving ducks (Phillips 1991, Guillemette et al. 1992, Mitchell 1992). Effects of water depth on foraging profitability (Table 3, Fig. 8) result from high costs of descent in diving ducks, which appear to have high buoyancies relative to other foot-propelled divers such as grebes, loons, and cormorants (Lovvorn and Jones 1994). Biomechanical analyses indicate that because of hydrostatic changes in buoyancy with depth, and high costs of accelerating the body with each stroke during descent, effects of variations in water depth on dive costs must be accounted for in foraging analyses (Lovvorn and Jones 1991, 1994, Lovvorn 1994a). Moreover, given that changes in food dispersion are expected to affect foraging energetics mainly through locomotor costs of searching, such costs must be well-quantified to evaluate accurately the significance of food dispersion to foragers. Unlike respirometry alone, our complementary use of biomechanics allows quantification of energy costs for dives to different depths for varying durations, thereby filling a critical need identified in previous studies (Beauchamp et al. 1992, Ball 1994). However, aerobic efficiencies (η) at various temperatures used in our model are based on a single species (Tufted Ducks) diving to a single depth (0.6 m) (Bevan and Butler 1992). Because η (which subsumes costs of transport and thermoregulation) likely varies with body size and water depth (see Lovvorn and Jones 1991, Lovvorn et al. 1991, Lovvorn 1994a), respirometry is needed for different body sizes, water depths, and water temperatures to refine general models.

Food dispersion.—Foraging site selection occurs at a variety of scales, e.g., at levels of regional systems, landscape systems, habitat associations, and "feeding stations" (e.g., foraging loci, Senft et al. 1987). Our model simulated the energetics of Canvasbacks once they had selected a habitat and were foraging among different loci. The effectiveness of hunting decoys reveals the importance to ducks of watching other birds in order to locate suitable foraging sites; and within sites, foraging Canvasbacks are often displaced from profitable loci by other individuals that observe their success (Lovvorn 1989b). Despite this use of visual cues, we envision the process as one in which ducks are attracted to a foraging site, but then must sample

as individuals among available loci (cf. Gotceitas and Colgan 1991). This scenario seems realistic, given the lack of second-order patchiness at scales we examined, and the fact that negative binomial frequencies of first-order patchiness do not vary spatially (all loci have the same probabilities of different bud densities, regardless of densities in neighboring loci). Aside from aggressively displacing other individuals perceived as successful, there was no alternative to individual sampling once a generally suitable area was located (i.e., with acceptable mean and negative binomial frequencies of bud densities).

In field-sampling foods as a basis for simulating prey grids, quadrat size is critical to negative binomial frequencies (cf. Pielou 1974:143–150), and must correspond to the grain of patch structure, i.e., the smallest scale at which the organism differentiates among patches (Kotliar and Wiens 1990). Whether foraging loci are sampled along transects, at points on a uniform grid, or randomly throughout the area has no effect on negative binomial frequencies as long as the sample is representative. The spatial pattern of samples has great influence, however, on measures of second-order patchiness, and samples must be systematically arranged (Pielou 1974:173–174) at distances corresponding to the movement patterns and perceptions of the organism in question (e.g., Fig. 4). For example, animals that can visually survey the surrounding area for potential food (Gillingham and Bunnell 1989) might respond to patchiness on larger scales than Canvasbacks, which search mainly by touch.

A critical problem in spatial analyses is that detection of pattern (such as second-order patchiness) depends strongly on the scales examined. One can probably always find significant pattern at some scale, while analyses at many other scales reveal no patterns. When relating foraging behavior to food dispersion, this situation allows categorical acceptance of any prediction, or categorical dismissal of any result, by claiming that data were not collected at the proper scale. As with implementing marginal value principles, the difficulty is determining at what scale the animal assesses food density. We feel that defining a foraging locus 1 m wide as a first-order patch is functionally valid, so that our method of measuring second-order patchiness by replicate cores at 1-m intervals was also appropriate.

Although we detected no second-order patchiness in *Vallisneria* habitats, it is likely that such patchiness does exist in other foods of avian benthivores. With available computer software (see Legendre 1993), the patch structure of foods can be mapped as continuous patterns by spatial interpolation among field samples, and model food grids can be generated according to specified levels of autocorrelation at given scales (Lam 1983, Legendre and Fortin 1989; see also Press et al. 1989 for probabilistic approaches). However, in applying these methods to spatial foraging models, it is critical that the grain of the environment from the forager's

perspective be accurately identified. Patchiness at scales smaller or larger than those perceived or used by the forager will not be meaningful to the animal, except perhaps to infer why that animal's search strategy is appropriate or inappropriate for the patch structure in particular environments. Because detailed mapping is not feasible for benthic foods of highly mobile birds, it is important to identify the scales at which they search, and to incorporate this knowledge into relevant, parsimonious sampling.

Environmental applications

Habitat needed to sustain populations.—As human pressures on existing habitats intensify, there are increasing needs to estimate how much habitat, of what quality, is required to sustain animal populations. In varying environments, such estimates should consider combinations of relevant variables over their natural range, and perhaps the probability of extreme combinations (Lovvorn 1994b). Our modeling approach can provide such estimates for diving ducks, and as noted below can be adapted for other avian and mammalian benthivores. Estimates of changes in the amount of viable foraging habitat with variations in different parameters, as shown for single parameters in Figs. 7 and 8, can be readily calculated for multivariate combinations. Although food dispersion and water temperature proved relatively unimportant for Canvasbacks foraging on *Vallisneria* buds (Table 3), our model allows direct consideration of local conditions. In addition to modeling effects of varying environments on diving ducks, the model holds promise for predicting the magnitude, pattern, and limits of prey depletion, thereby linking the physiology and biomechanics of predators to community and ecosystem processes.

Contaminant uptake in varying environments.—Among aquatic vertebrates, benthivores are often the most affected by chronic pollution that accumulates in nearshore sediments and foods (Vermeer and Peakall 1979, Di Giulio and Scanlon 1985, Smith et al. 1985). For example, in Commencement Bay, Washington, Surf Scoters (*Melanitta perspicillata*) with a sediment-associated diet contained 50 times more cadmium in their kidneys than did fish-eating Western Grebes (*Aechmophorus occidentalis*). Because the toxicity of given contaminant burdens can vary with an animal's energy balance (Porter et al. 1984, Lemly 1993), models of ecotoxicology (e.g., DuBowy 1989, Madenjian et al. 1993) would be much enhanced by relating energy costs and intake rates to varying field conditions such as weather, water depth, and food dispersion (Lovvorn and Gillingham 1996). Cleanup and restoration of nearshore systems are often focused on relatively small areas at great expense (Mallins et al. 1984), so that models based on intensive food sampling and behavior observations might often be justified for predicting results of various cleanup scenarios. In such cases, our approach can be adapted for use with other divers feed-

ing benthically, such as cormorants (*Phalacrocorax* spp., Birt et al. 1987) and sea otters (*Enhydra lutris*, Kvitek and Oliver 1992).

In summary, our simulations suggest that the energetics of diving ducks foraging on benthic foods are determined mainly by locomotor costs of descent and food-item size. For belowground winter buds of *Vallisneria*, metabolizable energy, water temperature, functional response coefficients, and bud dispersion have relatively minor influence. Within generally suitable habitat, water depth and food-item size appear more important than food density in limiting sustainable populations of diving ducks. Our modeling results should be viewed not as conclusions, but as thoroughly and specifically formulated hypotheses. The model does not substitute for detailed data, but rather integrates data mechanistically to indicate the relative importance of different factors. Empirical studies under controlled field and laboratory conditions should focus on refining critical data and testing the model's predictions. In particular, better understanding of the time scale over which ducks balance their energy budgets is needed for more accurate prediction of giving-up times and giving-up food densities observed in the field.

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