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Biomechanics and foraging profitability: an approach to assessing trophic needs and impacts of diving ducks

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Abstract

A biomechanical model of underwater locomotion is described, and data required by the model presented for 3 species of diving duck (*Aythya* spp.). Based on field observations of behavior and foods consumed, the model is used to estimate energy costs of foraging and minimum food intake rates of canvasbacks (*Aythya valisineria*) in two habitats in North Carolina. Increased water depth from 0.5 m in Lake Mattamuskeet to 1.5 m in Pamlico Sound increased the net cost of time spent foraging at the bottom by 43%. Biomechanical calculations are combined with data on intake rates at different food densities (Takekawa, 1987) to determine minimum food densities for profitable foraging in Lake Mattamuskeet. Field observations of behavior are used to adjust minimum intake per dive for unsuccessful dives spent locating food patches. Density and dispersion of plant tuber foods in Lake Mattamuskeet, before and after the fall staging period, suggest that the fraction of habitat with tuber densities above a profitability threshold is more critical to canvasbacks than average tuber density. Such factors are important in relating bird energy requirements and benthic sampling data to carrying capacity and total area of usable habitat. The proportion of foods that can be fed upon profitably also determines the fraction of food organisms subject to depletion as components of trophic pathways.

Introduction

As habitats of aquatic birds are increasingly impacted by human activities, there is a need for estimates of food densities required by the birds. Such estimates would aid in establishing habitat protection priorities, acceptable levels of impact, and standards for restoration (Goss-Custard, 1977; Korschgen *et al.*, 1988).

Diving ducks inhabit inland or inshore marine environments where effects of development and the likelihood of contaminant spills tend to be gretaer than offshore. Many diving ducks forage benthically in sandy or muddy substrates, where spilled oil and its effects on food organisms often persist (National Research Council, 1985). Where diving ducks eat mostly submerged vegetation, their foods are often reduced by eutrophication, suspended sediments, or other factors affecting plant growth (Kemp *et al.*, 1983; Schloesser & Manny, 1990).

Diving ducks are good subjects for developing models of food base requirements. On many lakes and estuaries, the most common diving ducks are in the genus *Aythya*, primarily benthic feeders that dive without much lateral movement underwater (Alexander, 1980; Lovvorn, 1989a). Thus, their locomotor patterns while foraging are more easily modeled than those of pursuit predators such as mergansers or loons (Lovvorn, 1991). Density and dispersion of benthic foods (e.g., Anderson & Low, 1976; Smith *et al.*, 1986; Korschgen *et al.*, 1988; Lovvorn, 1989b) can be quantified more accurately in the field than for nektonic prey, and can be manipulated both in the field (Draulans, 1982) and in the laboratory (Tome, 1988; Ball, 1990). *Aythya* spp. also tend to stay in open water during the day, so they can be counted accurately to document distributional responses to weather and habitat conditions (Lovvorn, 1989b).

Oxygen consumption ($\dot{V}_{O_2}$) during dives to single depths has been measured in tufted ducks (*Aythya fuligula*) and canvasbacks (*A. valisineria*) (Woakes & Butler, 1983; Takekawa, 1987). However, recent studies (Lovvorn *et al.*, 1991; Lovvorn & Jones, 1991a) have shown that mechanical energy costs of descent are at least 3–4 times the costs of bottom foraging, so power requirements measured as $\dot{V}_{O_2}$ between dives depend strongly on the relative time spent descending versus at the bottom. Consequently, changes in water depth or time spent seeking or manipulating prey at the bottom have important effects on intake rates and food densities required for profitable foraging. Biomechanical models of locomotor costs, when combined with values of aerobic efficiency (mechanical power output/$\dot{V}_{O_2}$), allow consideration of water depth and bottom time in analyses of foraging energetics.

The issue of minimum food densities required for profitable foraging is important in relating food biomass to carrying capacity and total area of suitable habitat. Past studies have calculated population energy requirements of birds, and then compared these estimates to total food biomass present to assess adequacy of the food base (e.g., Korschgen *et al.*, 1988; Schloesser & Manny, 1990). A similar approach has been taken in estimating the impact of birds on food organisms, other predators, nutrient cycling, and the trophic web in general (Wolff *et al.*, 1975; Bedard *et al.*, 1980; Eadie & Keast, 1982; Howard & Lowe, 1984; Nienhuis & Groenendijk, 1986). However, food dispersion affects the proportion of food biomass that can be fed upon profitably, and thus the fraction of food organisms subject to depletion. Quantifying foraging profitability (food intake per unit effort) relative to food density and dispersion is therefore critical in relating bird energy requirements to the food base.

To this end, I here outline a biomechanical model of underwater locomotion in *Aythya*, and present data required by this model for different species. I then use the model to investigate food base relations of canvasbacks in two habitats. Finally, I identify additional information needed to fully implement this mechanistic approach.

Methods

Study animals

Eggs of wild canvasbacks, redheads (*Aythya americana*), and lesser scaup (*A. affinis*) were collected from nests near Minnedosa, Manitoba, hatched in an incubator, and shipped to holding facilities at the University of British Columbia. Ducks were kept outdoors in concrete ponds 0.5–1 m deep, where they were fed mixed grain and poultry ration *ad libitum* on platforms. I regularly encouraged ducks to dive by throwing grain into the water.

Model of locomotion in Aythya

Lovvorn *et al.* (1991) and Lovvorn & Jones (1991a) developed a model of underwater locomotion based on data for canvasbacks, redheads, and lesser scaup. 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 in a water-filled cylinder. In model calculations, buoyancy was adjusted for compression of respiratory and plumage air spaces with depth (Lovvorn & Jones, 1991a). Ducks descending in a tank 2 m deep were filmed at 100 frames s^{-1} to determine linear displacement at 0.01-s intervals during 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 required to reach the bottom and remain there (from video films, see below) allowed calculation of total work during dives.

Vertical speeds and stroke rates

Vertical speeds and stroke rates were determined from video recordings. Ducks were filmed in a tank 2.5 m high, 0.8 m from front to back, and 1.2 m wide. The back and sides of the tank were made of plywood painted white, and the front was of clear plexiglas. Water depth was kept at either 1.2 or 2 m by standpipes that drained continuously flowing water. A platform (21 × 61 cm) hanging from the side of the tank allowed ducks to leave the water to rest and preen.

Ducks were trained to feed on mixed grain placed in an iron pan lowered to the bottom of the tank. The birds began feeding regularly from the pan in 1–6 days. Because individuals varied in the time they took to begin feeding, some birds initially lost more mass than others. The body mass of a sample of ducks was measured when they were placed in the tank, and again when they were removed after filming. Rate of change in body mass in this sample (in g per 24 h) ranged from −13.0 to −36.7 for 8 canvasbacks, + 8.2 to −37.2 for 9 redheads, and −5.5 to −19.9 for 9 scaup. Thus, there was a minor and variable difference between body mass when birds were removed from the tank and body mass when filming was done. This variation was minimized by removing ducks from the tank immediately after the last films were made, and no longer than four days after filming began. Body mass and volume measured upon removing the birds from the tank were used in all calculations. For all filming, two ducks of the same species were put in the tank together, and were distinguished in films either by sex (plumage) or by white plastic leg bands.

Video recordings were made with a JVC GX-N4 color video camera with an f1.2, 8.5–51 mm zoom lens. With the video cassette recorder in extended play mode, films lasted 8 hours. Most filming was done between 18:00 and 06:00 hours, but a few recordings were made during the day. Recordings were viewed on a video monitor, when vertical speeds were timed with a stopwatch, stroke rates counted with the film in slow motion, and dive trajectories to the bottom sketched. Some individuals, especially redheads, consistently took very linear, vertical paths to the bottom, whereas others, particularly scaup, tended to dive in an arc or at an angle across the tank. Dives in which ducks took unusually nonlinear paths or hesitated on the way to the bottom were excluded from analyses. Thirty to 40 dives per individual at each of two depths (1.2 and 2 m) were analyzed. These data were not normally distributed, so medians and 15-85% quantiles are reported. These quantiles include about the same proportion of the distribution as ± 1 S.D. (68%). Differences in dive parameters between depths were tested with nested (by individual duck) analyses of variance on rank-transformed data (PROC GLM, SAS Institute, Cary, NC).

Dive costs and required food intake of canvasbacks in North Carolina

Energy costs of diving and required food intake were calculated for canvasbacks at two sites in North Carolina: Lake Mattamuskeet and Pamlico Sound. Lake Mattamuskeet is about 300 km^2 in area and < 1 m deep throughout, with abundant stands of the submerged plants *Vallisneria americana* and *Potamogeton perfoliatus* (Lovvorn, 1989b). Pamlico Sound is a shallow estuarine lagoon. Canvasbacks arriving in early November concentrate on Lake Mattamuskeet, where they eat exclusively the subterranean tubers (winter buds) of *Vallisneria*. In early December, they move 5–45 km away to Pamlico Sound, where they eat clams, mostly *Macoma* spp., until departing north beginning in late February (Lovvorn, 1987).

Procedures for behavioral observations of canvasbacks on Lake Mattamuskeet and Pamlico Sound are described in detail by Lovvorn (1989a). Five-min, focal-individual samples of equal numbers of males and females were taken throughout daylight hours in fall and winter 1983–84. During the prewinter fattening period on Lake Mattamuskeet (Lovvorn, 1993), canvasbacks foraged continuously and did not leave the area at night (Lovvorn, 1989a); thus, daytime dive frequencies are assumed to extend through the night. Canvasbacks in both habitats almost always dived and surfaced without significant lateral movement underwater, allowing continuous observation of individuals. Distances moved on the water surface were estimated by assuming three body lengths per meter.

Costs of diving at the two sites were calculated with the biomechanical model described above. For Lake Mattamuskeet (water depth about 0.5 m), stroke rates and speeds of descent and ascent were assumed to be the same as for canvasbacks diving to 1.2 m in a tank (Table 1). For Pamlico Sound, dive parameters for 1.2 and 2 m (Table 1) were linearly interpolated to a depth of 1.5 m (descent: 0.90 m s^{-1}, 4.1 strokes m^{-1}; at the bottom: 2.8 strokes s^{-1}; ascent: 0.83 m s^{-1}). 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 (Lovvorn & Jones, 1991a). These two work values were then averaged for dives to given depths. Variations in water salinity were ignored in calculations, as salinity has negligible effects on the net buoyancy of diving ducks (Lovvorn & Jones, 1991a).

Densities of Vallisneria *tubers*

In fall 1983, transects for tuber sampling were established in four areas of Lake Mattamuskeet heavily used by canvasbacks the previous fall (see Fig. 2 in Lovvorn, 1989b). Substrate cores were taken from 20 September to 5 October before canvasbacks arrived, and again from 7 January to 2 February after they moved to Pamlico Sound.

Sampling stations were marked with stakes at 50-m intervals along transects, and three cores per station were taken during each sampling period. The sampler was a hand-held plunger device

Table 1. Dive parameters (medians and 15–85% quantiles) of ducks in a tank as determined from video recordings. Within species, all parameters differ between depths (nested ANOVA on rank-transformed data, $P < 0.001$).

Species	N	Depth (m)	N of dives	Descent			Bottom	Ascent	Dive duration (s)
				Vertical speed (m s^{-1})	Stroke rate (Hz)	Strokes m^{-1}	Stroke rate (Hz)	Vertical speed (m s^{-1})	
Canvasback	8	1.2	320	0.93	3.6	4.1	2.8	0.88	8.2
				0.81–1.11	3.4–3.8	3.3–4.9	2.6–3.0	0.66–1.10	4.8–13.8
		2.0	323	0.86	3.7	4.1	2.7	0.75	13.3
				0.75–1.01	3.4–4.0	3.6–4.6	2.6–2.9	0.64–0.89	7.9–17.8
Redhead	9	1.2	360	0.91	4.2	4.9	3.3	0.75	6.2
				0.81–1.04	3.9–4.4	4.1–4.9	3.1–3.4	0.59–0.91	4.4–10.7
		2.0	363	0.87	4.2	4.6	3.2	0.67	8.6
				0.78–0.98	3.9–4.4	4.1–5.1	3.0–3.4	0.57–0.79	6.6–12.8
Lesser scaup	8	1.2	305	0.68	4.5	6.5	3.6	0.78	8.3
				0.58–0.80	4.3–4.8	5.7–7.3	3.4–3.7	0.63–1.02	5.6–12.9
		2.0	313	0.66	4.4	6.6	3.5	0.67	11.2
				0.59–0.74	4.1–4.8	6.1–7.6	3.3–3.6	0.58–0.91	8.5–15.1

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 deeply into the substrate as possible. Tubers >10 cm deep in the firm sediments of Lake Mattamuskeet apparently were not utilized by canvasbacks (Lovvorn, 1989b). Cores from the early sampling period were divided into upper (top 10 cm) and lower sections only at Transect 4, whereas all cores from the second sample were divided. For analyses in this paper, numbers of tubers in the upper 10 cm of cores from Transects 1–3 in the first sample were estimated by multiplying total tubers in each core by the average proportion of tubers in the upper 10 cm of cores from Transect 4 (93%).

Results

Dive parameters

Within species, all dive parameters differed between depths of 1.2 versus 2 m (Table 1). Even when medians were the same, tests on ranked data were significant. Descent speed was greater at shallower depths, probably owing to momentum developed by springing upward before submergence. Speed of passive ascent decreased with increasing depth (Table 1) because of reduced buoyancy from compression of respiratory and plumage air spaces at higher pressures. Dive duration increased with water depth.

Among species, vertical speed during both descent and ascent generally decreased with decreasing body size, whereas stroke rates and strokes per meter increased with decreasing body size. No trends in dive duration with body size were apparent. Within species, regression of all dive parameters on body mass and on buoyancy yielded no significant trends ($p > 0.05$). Therefore, effects on dive parameters of individual variations in locomotor behavior were greater than any intraspecific effects of body mass or buoyancy.

Dive costs in Lake Mattamuskeet and Pamlico Sound

Calculations of the energy costs of descent and bottom foraging for canvasbacks at sites in Lake Mattamuskeet and Pamlico Sound are in Tables 2–4. Although dive duration increased by 22% at the greater depth in Pamlico Sound (Table 4), foraging time at the bottom was nearly the same (Table 3). Reduced buoyancy at the greater depth decreased the mechanical power required for bottom foraging by almost 15% (2.75 to 2.34 W). Because of higher buoyancy and descent speed, the power cost of descent was 4% higher at the shallower depth (14.14 versus 13.56 W). Despite lower power requirements of both descent and bottom foraging, the greater time spent descending and ascending resulted in a 41% increase in aerobic cost per dive at the deeper depth (Table 4), while time spent at the bottom decreased by 5% (Table 3). Thus, increased depth of only 1 m, still far less than depths of 2–5 m at some foraging sites in Pamlico Sound, increased the net cost of time spent at the bottom by 43%. This important effect of depth would not be ap-

Table 2. Calculations of mechanical work during descent by a 1238-g canvasback at foraging sites in Lake Mattamuskeet and Pamlico Sound. Accounting for effects of pressure with depth on body volume and density, buoyancy and virtual mass were 5.15 N and 1.591 kg at the surface, 4.93 N and 1.586 kg at 0.5 m, and 4.56 N and 1.579 kg at 1.5 m.

Site	Water depth (m)	Speed ($m\ s^{-1}$)	Duration (s)	Strokes m^{-1}	N of strokes	Work $stroke^{-1}$ (J)[a]	Work $dive^{-1}$ (J)
Lake Mattamuskeet	0.5	0.93	0.54	4.1	2.05	3.726	7.64
Pamlico Sound	1.5	0.90	1.67	4.1	6.15	3.682	22.64

[a] Average of (1) work/stroke calculated assuming no change in buoyancy or added mass with depth (3.752 J) and (2) work/stroke considering change with depth at either 0.5 m (3.700 J) or 1.5 m (3.611 J).

Table 3. Calculations of mechanical work at the bottom by a 1238-g canvasback at foraging sites in Lake Mattamuskeet and Pamlico Sound. Buoyancy and virtual mass at 0.5 and 1.5 m are as in Table 2.

Site	Water depth (m)	Duration (s)[a]	Stroke rate (Hz)	Distance stroke^{-1} (m)	Work stroke^{-1} (J)	N of strokes	Work dive^{-1} (J)
Lake Mattamuskeet	0.5	7.89	2.8	0.198	0.980	22.1	21.66
Pamlico Sound	1.5	7.52	2.8	0.184	0.834	21.1	17.60

[a] Based on dive durations in Table 4, and speeds of descent and ascent in Table 1.

parent or estimable from oxygen consumption measurements at any single depth, illustrating the value of the biomechanical approach.

Higher cost of foraging at greater depths requires higher energy intake per dive. Minimum mass intake of clams in Pamlico Sound is 3.5 times higher than of tubers in Lake Mattamuskeet (Table 4). However, clams, being larger, have a higher energy content per food item, so that 55% fewer clams than tubers per dive are required. Without knowing intake rates of clams versus tubers, foraging profitability (energy gain per unit effort) in the two habitats cannot be compared.

Intake rates of tubers and changes in tuber density

Intake per dive for canvasbacks to meet daily energy requirements is about 1.32 tubers (Table 5). Over half of food intake is required to meet costs of diving. Extrapolation of data for captive canvasbacks diving in 1 m of water for *Vallisneria* tubers buried in trays of sand (Takekawa, 1987; Fig. 1) suggests that this intake rate is possible at densities greater than about 190 tubers m^{-2}. However, in Takekawa's study, tubers were spread evenly over an area of only 4.9 m^{2}. This situation eliminated or greatly reduced unsuccessful dives spent searching for food patches, which can appreciably decrease intake per dive (Tome, 1988).

To evaluate the effects of unsuccessful dives during searches, I examined the proportion of dives by canvasbacks on Lake Mattamuskeet that were followed by surface swimming ≥ 1 m to another site where diving was resumed. Canvasbacks appeared to dive repeatedly in a food patch until profitability became inadequate, at which time they began searching for a new patch. As a minimum estimate, I assumed that no tubers were acquired during only the last dive before traveling to a new patch. The proportion of dives followed

Table 4. Locomotor costs of diving, and minimum food intake to meet those costs, for canvasbacks at two foraging sites.

Site	Water depth (m)	Dive duration[a] (s)	Mechanical cost/dive (J)	Aerobic cost/dive[b] (J)	Minimum intake/dive[c]	
					Fresh mass (g)	N of items
Lake Mattamuskeet	0.5	9 (5–15)	29.3	176.2	0.046	0.74
Pamlico Sound	1.5	11 (7–15)	40.2	249.0	0.159	0.33

[a] Median (and 15–85% quantiles) for 6,070 dives by 1,559 focal individuals on Lake Mattamuskeet, and 935 dives by 332 focal individuals on Pamlico Sound.

[b] Assuming aerobic efficiency (mechanical power output/$\dot{V}_{O_2}$) = 0.17 (Lovvorn *et al.* 1991), and resting metabolic rate during passive ascent = 5.49 W kg^{-1} (Woakes & Butler, 1983).

[c] Accounting for efficiency of assimilation and intermediary metabolism, *Vallisneria americana* tubers on Lake Mattamuskeet yield 3.846 kJ g^{-1} fresh mass and 0.239 kJ/tuber; *Macoma* spp. clams (including shell) on Pamlico Sound yield 1.562 kJ g^{-1} fresh mass and 0.752 kJ/clam (Lovvorn, 1987: 38).

Table 5. Observed dive frequencies and calculated food intake per dive needed to meet daily energy expenditure (DEE) for canvasbacks on Lake Mattamuskeet.

Dives (5 min)$^{-1}$	Intake/dive to meet DEE[a]			% of intake to meet costs of diving
	Energy (kJ)	Mass (g)	N of items	
7.5 ± 8.4 (0–42)[b]	0.315	0.082	1.32	56.1

[a] Based on DEE for black ducks (*Anas rubripes*) of 680 kJ day^{-1} (Morton *et al.*, 1989).

[b] Mean ± S.D. (range) for 1,560 5-min, focal-individual samples.

by traveling to a different site increased linearly over the period canvasbacks used the lake (Fig. 2), reflecting gradual depletion of tubers. If these unsuccessful dives are included, minimum intake increased from 1.02 × 1.32 = 1.35 to 1.18 × 1.32 = 1.56 tubers per dive during this time (fractions of unsuccessful dives, 0.02 and 0.18, are minimum and maximum predicted values from regression of data in Fig. 2, and 1.32 is from Table 5). These minimum intake rates could be achieved at tuber densities exceeding about 200 m^{-2} in early November and 260 m^{-2} in early December (extrapolating from the equation in Fig. 1).

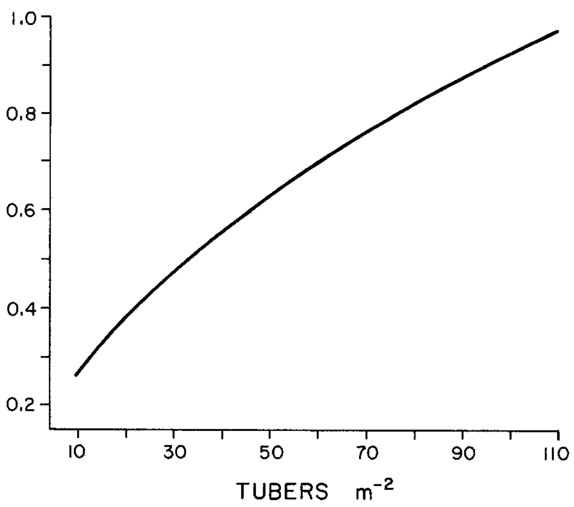

Fig. 1. Intake of *Vallisneria americana* tubers per dive *N* versus tuber density *D* for canvasbacks in a tank 3 × 3 × 1 m deep (based on data from Takekawa, 1987). Tubers (winter buds) were buried in sand at depths of 2.54 to 6.35 cm in 6 trays, each 0.82 m^2 in area. ($N = 0.0727\ D^{0.552}$, $r^2 = 0.83$, $p = 0.004$)

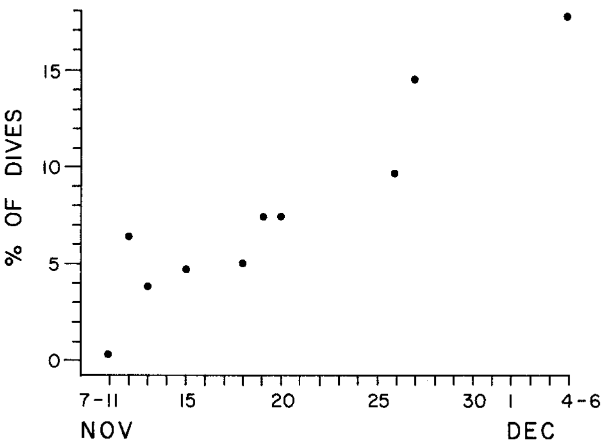

Fig. 2. Percentage of dives by canvasbacks on Lake Mattamuskeet that were followed by surface swimming a distance ≥ 1 m, whereupon diving was resumed. Mean number of dives per point = 747 (range 375–1,195).

The proportion of 70 sampling stations in Lake Mattamuskeet with tuber densities above these minima decreased from 40% in early November to about 20% when canvasbacks left the lake (Fig. 3). Note that in samples taken after the lake was abandoned, severe tuber depletion begins above the threshold density of about 260 tubers m^{-2} (Fig. 3). In contrast to the 50% decline in stations above profitability thresholds, the average density of tubers for all stations declined by only 20.5% ($p < 0.001$, nested ANOVA on rank-transformed data). A few stations with extremely high tuber densities remained after canvasbacks abandoned the lake (Fig. 3). These patterns suggest that average food densities, or continued high densities at a few sites, are less critical than the fraction of all sites with densities above profitability thresholds. However, many stations were depleted to densities far below profitability thresholds (Fig. 3), indicating that the birds continued to exploit foods at subprofitable densities. The latter result probably reflects the increasing cost of finding new patches with higher tuber densities (cf. Fig. 2). The decision of canvasbacks to leave the lake appears to have depended mainly on depletion of areas with densities that allow profitable foraging.

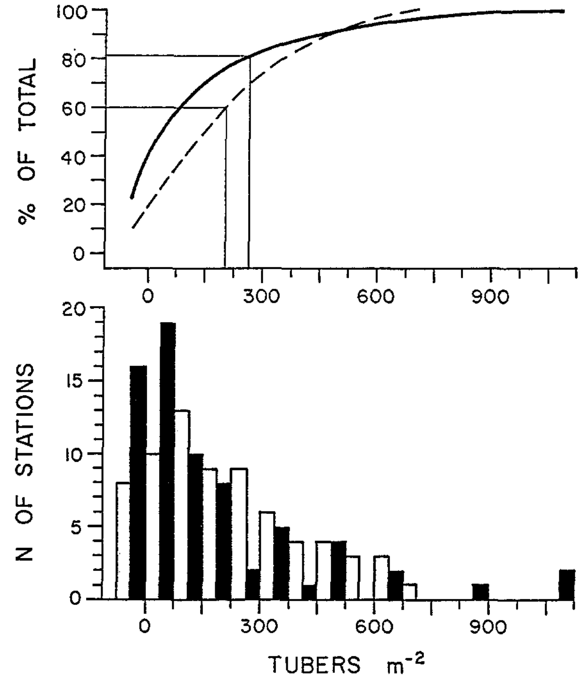

Fig. 3. Number and percentage of sampling stations in Lake Mattamuskeet with different densities of *Vallisneria americana* tubers in the upper 10 cm of substrate cores ($N = 70$ stations, 3 cores/station). Open bars and dashed line are for densities before canvasbacks arrived; solid bars and solid line are for densities after canvasbacks moved from the lake to Pamlico Sound. Vertical lines in the upper figure indicate threshold densities of 200 and 260 tubers m^{-2} (see text).

Discussion

Biomechanical calculations, together with data on food dispersion, food density, and intake rates at different food densities, yield important insights into the quality and extent of foraging habitat. Water depth and time spent seeking and manipulating foods at the bottom have strong effects on dive costs, and thus required intake rates and food densities. These relations determine effects of water depth and food dispersion on how much of total food biomass and habitat area are actually usable. The biomechanical model can be applied to different *Aythya* spp. (Table 1; Lovvorn & Jones, 1991a), and further developed for similar foot-propelled divers (Lovvorn, 1991; Lovvorn & Jones, 1991b; Lovvorn & Jones, 1993). Although difficult to apply over large areas, this method would be valuable in smaller areas of critical habitat or intensive study.

Full implementation and accuracy of this approach require investigation and refinement of several components. These include (1) better measurements of aerobic efficiency and factors affecting it, such as use of 'waste' heat from exercising muscles for thermoregulation; (2) measurement and modeling of the microclimate of floating birds, and the interaction of thermoregulation during dives and at the surface; (3) measurement of intake rates at different food densities under conditions that mimic natural substrates and extraction costs; and (4) studies of search patterns relative to food dispersion, and development of habitat sampling schemes based on scales of food dispersion that are relevant to search strategies.

Aerobic efficiency and thermal substitution

To translate biomechanical calculations into total energy costs and required intake rates, it is necessary to know aerobic efficiency (mechanical power output/$\dot{V}_{O_2}$). Aerobic efficiency varies not only with body size (cost of transport in J kg^{-1} m^{-1} decreases with increasing body size; Schmidt-Nielsen, 1972; Lovvorn *et al.*, 1991), but also with the level of work performed (Hill, 1950). Consequently, differences in power output between descent and bottom foraging, and changes in buoyancy with water depth, probably correspond to variations in aerobic efficiency. However, $\dot{V}_{O_2}$ can be measured only between dives, requiring that such effects be partitioned by regression analyses of $\dot{V}_{O_2}$ values for dives of varying depth and duration. An example is the approach of Woakes & Butler (1983) in partitioning $\dot{V}_{O_2}$ during dives versus pauses between dives.

Another potentially important effect on aerobic efficiency is use of 'waste' heat from digestion and exercising muscles for thermoregulation (Webster & Weathers, 1990). For example, in white-crowned sparrows (*Zonotrichia leucophrys*) at −10 °C, the energy cost of hopping on a treadmill is no greater than for shivering while inactive

(Paladino & King, 1984). Thus, under conditions of high heat loss, foraging has effectively no energy cost. Water has a thermal conductivity 23 times and specific heat 4 times that of air, so thermoregulation is especially important in aquatic birds (Jenssen *et al.*, 1989) and is probably critical to foraging energetics. Use of the heat increment of digestion ('specific dynamic action' or SDA) for thermoregulation is appreciable in sea otters (*Enhydra lutris*) (Costa & Kooyman, 1984) and little penguins (*Eudyptula minor*) (Baudinette *et al.*, 1986), but has not been investigated in other aquatic birds and mammals.

Regarding both exercise and SDA, the appearance of incomplete thermogenic substitution might result from a regulated increase in body temperature during exercise (Walsberg, 1983), or a regulated decrease in body temperature during fasting (Chaplin *et al.*, 1984). Body temperature must be measured in investigating these effects.

Microclimate at the water surface

Captive diving ducks fed *ad libitum* often reduce food intake during very cold weather (Perry *et al.*, 1986); Lovvorn 1993). The birds may be genetically programmed to avoid negative energy balance incurred by foraging at low temperatures or at deeper, less productive feeding sites left uncovered by ice. Because water temperatures in the above captive holding ponds did not change appreciably during the cold periods, any direct temperature effects on food intake probably involve microclimate at the water surface. In tufted ducks diving in water at 7.4 °C and air at 5.8 °C, body temperature dropped 1° during dive bouts (periods of repeated diving) and returned to normal during subsequent resting periods (Bevan & Butler, 1992). Muskrats also allow their body temperature to drop while diving in cold water, followed by rewarming after leaving the water (MacArthur, 1979). These studies suggest that in diving ducks, foraging in the wild becomes unprofitable when surface microclimate prevents efficient rewarming after dive bouts.

Models must be developed and tested for above-water microclimate, including effects of wave action on convective regime. Interactions between surface microclimate and thermoregulation during diving and resting probably have important effects on profitability thresholds of food density and dispersion. These relations under different weather conditions need to be explored.

Relating intake rate to food density

Limitations of the curve in Fig. 1 are that (1) the range of tuber densities spans only the very low end of that occurring in nature (Fig. 3); (2) tubers were spaced evenly in unconsolidated sand, perhaps reducing search and extraction costs; and (3) the data apply only to intake rates once a bird has located a patch with given food density, and do not include unsuccessful dives while searching for such patches. In a similar experiment with an array of 16 0.5-m^2 trays, ruddy ducks (*Oxyura jamaicensis*) averaged 5 unsuccessful dives before locating the one tray containing food (Tome, 1988). Diving ducks might locate good feeding areas by joining existing flocks, but finding profitable food patches within those areas can require substantial searching (Fig. 2). Methods for estimating the number of dives spent locating patches in the field need to be developed.

Search patterns and habitat sampling

How can benthic samples be designed and analyzed in a way that is relevant to the foraging energetics of diving ducks? Random or systematic sampling will indicate what fraction of stations, and thus what fraction of overall habitat, contains food densities above a profitability threshold. However, the profitability threshold for food patches depends on the number of dives spent searching for those patches, which changes with food dispersion (Fig. 2; Tome, 1988). For example, if 25% of the habitat has food densities above a certain level, is this 25% in one continuous patch easily found by joining feeding flocks, or is that 25% scattered in small patches? Spatial autocorrelation analysis of properly-spaced benthic samples (Thrush *et al.*, 1989) will indicate the size, density, and spatial arrangement of benthic organisms. These factors might then be related to search costs and profitability thresholds under experimental conditions, e.g., with captive birds in enclosed natural habitat in which food dispersion has been described.

In conclusion, combined use of biomechanics, respirometry, assimilation and conversion efficiencies of foods, food intake measurements, and studies of search patterns can potentially improve our ability to relate energy requirements of birds to the food base. Profitability relations will affect how much of the total food biomass and habitat area are functionally usable, as well as the potential of birds to impact food organisms and the trophic web in general.

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