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Predicting Resource Partitioning and Community Organization of Filter-Feeding Dabbling Ducks from Functional Morphology

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ABSTRACT: Resource partitioning due to interspecific differences in phenotype is a key component of ecological and evolutionary theory, but the relationship between morphology and resource use is poorly understood for most species. In addition, ecologists often assume that morphological differences cause distinct resource preferences between species. Using mechanistic models that combine bill morphology and kinetics, I show that filter-feeding dabbling ducks face a morphology-mediated trade-off between particle size selection and water filtration rate. When detritus is absent, mallards (*Anas platyrhynchos*) and northern shovelers (*Anas clypeata*) should maximize their intake rates and exhibit high overlap in prey size. When prey and detritus co-occur, species should separate prey from detritus by size, leading to reduced intake rates and size-based prey partitioning. Models for both species correctly predicted variation in water filtration rates, particle retention probabilities, and prey ingestion rates due to variation in prey size, the presence of detritus, and experimental modification of bill morphology. Because species have both shared and distinct resource preferences, duck communities should exhibit strong density-dependent niche shifts (i.e., centrifugal dynamics), a finding that contradicts previous studies that assumed that ducks have distinct resource preferences only. Centrifugal dynamics may be widespread among filter feeders because of the common cost of separating prey from detritus.

Keywords: filter feeding, resource partitioning, ecomorphology, *Anas*, bill morphology, centrifugal community organization.

The constraints phenotype imposes on resource use play a central role in ecological (Morris 2003; Kneitel and Chase 2004) and evolutionary (Arnold 2003) theory. Of particular interest is whether these constraints result in a performance trade-off, such that each phenotype is more efficient than all others at using certain resources. Performance trade-offs promote the evolution of ecological diversity through adaptive radiation (Schluter 2000) and allow species to coexist by permitting resources to be partitioned (Chesson 2000). In spite of the potential for trade-offs to predict how resource availability and interspecific interactions determine community composition (Chase and Leibold 2003), few studies have mechanistically linked morphological variation to variation in performance exploiting different resources (Wainwright 1991; Wake 1992; Rubega 2000; Irschick 2002) or shown that morphological variation permits resource partitioning (Dayan and Simberloff 2005).

This knowledge gap is due, in part, to the difficulty of identifying performance trade-offs. If species profit most from exploiting different resources (i.e., species have distinct resource preferences), trade-offs can be inferred from the association between morphology and resource use, which will be relatively independent of the density of competitors or resources (Rosenzweig 1981). Alternatively, species may profit most from exploiting the same resources, leading to shared preferences for these primary resources, but have distinct preferences for less profitable, secondary resources (Rosenzweig and Abramsky 1986). If primary resources are abundant or competitors are scarce, species with shared preferences may exhibit extensive overlap in primary resource use even though phenotypic differences allow them to partition secondary resources (Rosenzweig and Abramsky 1986; Robinson and Wilson 1998; Krivan and Sirot 2002), masking performance trade-offs. Rosenzweig and Abramsky (1986) called these communities centrifugally organized because all species use the same easily exploited primary resources when they are abundant but spin out to use different, less profitable secondary resources that can be partitioned when primary resources are rare. For example, even Galapagos finches (*Geospiza*) have shared preferences. In the early dry season, they all consume soft, easy-to-handle fruits and seeds (the profitable primary resource), but as these seeds deplete,

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their diets diverge to include hard, difficult-to-handle seeds (the less profitable secondary resource; Grant 1986). These distinct preferences reflect interspecific differences in beak morphology. It is the costs associated with cracking hard seeds that allow these secondary resources to be partitioned.

In addition to these difficulties, many ecologists' views on the role of morphology in determining resource preferences appear biased. In the absence of experimental data, ecologists presume that species have distinct preferences twice as often as shared preferences, although experiments indicate the opposite frequency (Wisheu 1998). Distinct preferences are twice as likely to be attributed to differences in morphology or physiology, while shared preferences are seven times more likely to be (tautologically) attributed to other factors, such as competition or behavior (Wisheu 1998). Consequently, the role of morphological variation in determining shared resource preferences is unknown for many communities that appear to be organized centrifugally.

Communities of filter-feeding organisms provide an opportunity to mechanistically link morphology, resource preferences, and community organization. A common problem facing filter feeders is the separation of prey from detritus particles, which have low energetic value. Because detritus imposes foraging costs due to increased handling time, reduced filtration rates, or imperfect separation of prey and detritus, centrifugal dynamics may be typical of communities of filter-feeding organisms. When detritus is rare relative to prey, foragers should filter many different prey types. If detritus becomes more abundant relative to prey, perhaps because of depletion of prey, foragers should specialize on prey types they can efficiently separate from detritus.

There are a few examples in which detritus is known, or suspected, to mediate competition among filter-feeding organisms. The presence of suspended clay can reverse the outcome of competition between cladocerans and rotifers (Kirk and Gilbert 1990) because rotifers feed more selectively than do cladocerans (Kirk 1991). Bivalves exhibit an array of mechanisms that allow separation of prey and detritus on the basis of physical and chemical characteristics of particles (Ward and Shumway 2004). Repeated divergence of freshwater fishes into benthic and limnetic forms is associated with differences in the morphology of gill rakers (Schluter and McPhail 1993; Robinson and Wilson 1994; Schluter 1996), which are involved in retaining prey and excluding detritus (Day et al. 1994; Sanderson et al. 2001; Callan and Sanderson 2003).

The ecological consequences of interspecific differences in bill morphology between filter-feeding dabbling ducks (*Anas* spp.) is controversial (Nudds et al. 2000). Dabbling ducks filter feed by creating a flow of prey and water that enters the oral cavity through the anterior opening between the maxilla and mandible (the gape) and is expelled laterally at the caudal end of the cavity (Zweers 1974; Zweers et al. 1977; Kooloos et al. 1989). Prey are retained by lamellae along the lateral edges of the maxilla and mandible at the caudal end of the oral cavity (Kooloos et al. 1989). Interspecific variation in interlamellar distance (fig. 1) was thought to allow ducks to partition prey by size (Nudds and Bowlby 1984), but interlamellar distance does not cause a trade-off in foraging performance. Ducks with fine lamellar spacing (small interlamellar distance) have higher prey ingestion rates than do species with coarse spacing (large interlamellar distance) and can retain both large and small prey (Crome 1985; Kooloos et al. 1989; Mott 1994), leaving the advantage of coarse spacing open to question. Coarse spacing may allow ducks to avoid

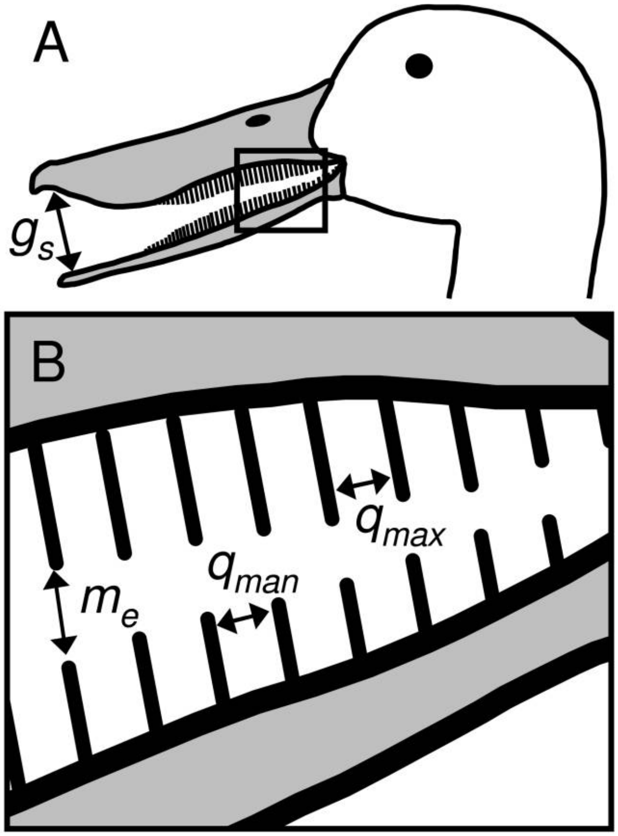

Figure 1: Detail of the lamellar filter of a dabbling duck. *A*, Profile of the head of a northern shoveler showing the gape (g_s). The rectangle indicates the region of the bill in which particles are retained by the lamellae. *B*, Magnification of the lamellar filter indicated in *A*. Lamellar separation (m_e) is the distance between the dorsal tips of the mandibular lamellae and the nearest surface of the maxilla. Interlamellar distance is the distance between adjacent lamellae on the mandible (q_{man}) or the maxilla (q_{max}).

ingesting small detritus particles (R. Bethke and T. D. Nudds, unpublished manuscript), but ducks do not ingest detritus, even when particles are larger than a duck's interlamellar distance (Tolkamp 1993). Although detritus does cause a greater decline in the ingestion rate of species with fine spacing, they ingest prey at the same rate as do species with coarse spacing (Tolkamp 1993).

Separation of prey from detritus must be dependent on other traits in addition to interlamellar spacing in order to avoid the injestion of detritus particles larger than the interlamellar distance (Gurd 2006). Ducks elevate and depress the maxilla and mandible during foraging (Zweers et al. 1977; Kooloos et al. 1989), which may allow them to separate prey from detritus in two ways. First, movement of the maxilla and mandible allows lamellar separation (fig. 1) to be greater than interlamellar distance (Kooloos et al. 1989), allowing small detritus particles to be expelled while large prey are retained (Gurd 2006). Second, reducing gape may prevent large detritus particles from entering the oral cavity (van Eerden and Munsterman 1997). However, because movement of the maxilla and mandible helps to pump water through the bill (Zweers et al. 1977), reducing gape or increasing lamellar separation will reduce water filtration rates (Kooloos et al. 1989), leading to a trade-off between detritus avoidance and ingestion rate. Species with long lamellae (and fine spacing) should face a more severe trade-off than species with short lamellae (and coarse spacing; fig. 2), potentially explaining Tolkamp's (1993) results.

To quantify this trade-off, I created quantitative models that predict the foraging performance of mallards (*Anas platyrhynchos*) and northern shovelers (*Anas clypeata*) directly from bill morphology and kinetics. The predictions of the models are consistent with the results of foraging experiments reported in the literature and predict that dabbling duck communities should be centrifugally organized.

Methods

Modeling Foraging Performance

The particle ingestion rate (I) of a filter-feeding duck can be estimated by

$$I = \sum_{i=1}^{z} C_i V_{s,e} Z R_{s,e,i}, \tag{1}$$

where C_i is the concentration of particles in size class $i = 1, 2, 3, \ldots, z$ in the environment, $V_{s,e}$ is the volume of water filtered per cycle of the pumping mechanism, Z is the rate of the pumping cycle, and $R_{s,e,i}$ is the probability a particle in size class i will be retained and ingested. The model allows the position of the maxilla and mandible at the start (s) and end (e) of the filtration cycle to vary, with consequences for $V_{s,e}$ and $R_{s,e,i}$.

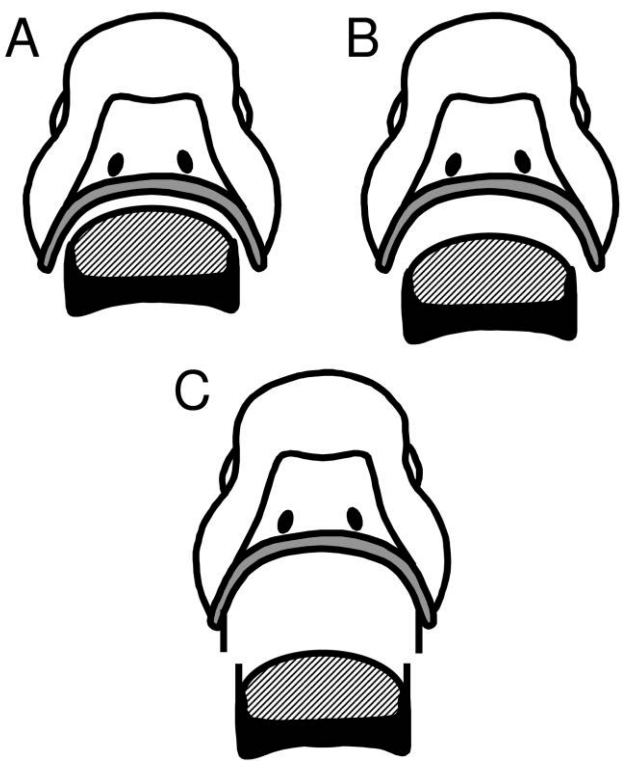

Figure 2: Dependence among water filtration rate, lamellar separation, and lamellar length. Diagrams show posterior views of transverse cross sections of the bill, indicating the end position of the maxilla (*shaded area*), mandible (*black area*), and tongue (*hatched area*). The cross-sectional area of the space between the maxilla and the tongue is smaller, and therefore more water can be expelled from the oral cavity, when lamellar separation is small (*A*) than when it is large (*B*). Lamellar separation is equal in *B* and *C*, but the maxillary and mandibular lamellae are longer in *C* than in *B*, causing less water to be expelled in *C* compared to *B*. Lamellar separation is defined in figure 1.

Cycle rate (Z) gives the time required to move the maxilla, mandible, and tongue through one filtration cycle from position s to position e and back to position s. Water filtration rate (F) is the product of $V_{s,e}$ and Z. Cycle volume is given by $V_{s,e} = V_s - V_e - T_s - T_e$ where V_s and V_e are the volume of the posterior cavity at the start and end of the filtration cycle, respectively, and T_s and T_e give the volume of the posterior cavity occupied by the tongue at the start and end of the cycle, respectively (see fig. A1 in the appendix in the online edition of the *American Naturalist*).

Changing gape or lamellar separation to avoid detritus will lead to a decline in F; F is maximized when V_s is maximized and V_e is minimized, which occurs when n_s and d_e are minimized and n_e and d_s are maximized (see fig. A1). When n_s is minimized and d_s is maximized, gape will be intermediate. As gape size decreases from this intermediate value, d_s must decrease, decreasing V_s. As gape increases from an intermediate value, d_s cannot increase, so n_s must increase, decreasing V_s. As lamellar separation increases, d_e will increase, and eventually n_e will have to decrease to keep $d \leq l + h$, causing V_e to increase.

If we assume that particles are retained by sieving (Rubenstein and Koehl 1977), the probability that a particle will be retained ($R_{s,e,i}$) is given by $R_{s,e,i} = G_{s,i}M_{e,i}$, where $G_{s,i}$ is the probability a particle of size i will enter the oral cavity given start position s and $M_{e,i}$ is the probability a particle of size i will not pass through the lamellar filter given end position e. Gape (g_s) and lamellar separation (m_e) vary with distance along the mandible (x; measured from the mandible tip). I expressed these functions as a cubic polynomial such that $g_s = v_s + w_s x + y_s x^2 + z_s x^3$, where $0 \leq x \leq n_s$, and $m_e = v_e + w_e x + y_e x^2 + z_e x^3$, where $k \leq x \leq j$. Given a particle of size class i of minimum size a and maximum size b, such that $g_s \geq a$ between x_1 and x_2, $g_s \geq b$ between x_3 and x_4, $m_e \leq a$ between x_5 and x_6, and $m_e \leq b$ between x_7 and x_8, then

$$G_{s,i} = \frac{\int_{x_1}^{x_2} g_s(x) + \int_{x_3}^{x_4} g_s(x)}{2\int_0^{n_s} g_s(x)}, \tag{2}$$

$$M_{e,i} = \frac{\int_{x_5}^{x_6} m_e(x) + \int_{x_7}^{x_8} m_e(x)}{2\int_k^j m_e(x)}. \tag{3}$$

Equations (2) and (3) assume that, for any combination of s and e, the water flow rate through g_s and m_e is constant for all values of x.

If retention is dependent on interlamellar distance alone, then equation (3) is irrelevant and $M_{e,i} = 0$ if $b \leq q$ and $M_{e,i} = 1$ if $b > q$, where q is the mean interlamellar distance measured between j and k on either the maxilla (q_{max}) or the mandible (q_{man}). If $M_{e,i}$ is determined by lamellar separation and interlamellar distance, then $M_{e,i} = 0$ if $b \leq q$ and is given by equation (3) if $b > q$. To predict the relative influence of lamellar separation and interlamellar distance on foraging performance, models were created that assumed different retention mechanisms: lamellar separation alone (LS model), lamellar separation and maxillary interlamellar distance (MAX model), and lamellar separation and mandibular interlamellar distance (MAN model). Only two models (LS and MAN) were created for shovelers because their maxillary and mandibular interlamellar distances are the same (Kooloos et al. 1989).

The model makes four implicit assumptions: particles retained during one filtration cycle are not expelled during subsequent cycles; the retention of particles does not affect the probability of other particles being retained or the water filtration rate; the retention probability of particles does not change during the filtration cycle; and cycle rate is constant and independent of the starting and ending positions of the maxilla, mandible, and tongue. The first two assumptions are reasonable. The lingual scrapers transfer retained particles from the lamellae to a position caudal of the lingual cushion during each cycle (Zweers et al. 1977; Kooloos et al. 1989), reducing subsequent loss of retained particles and obstruction of water flow. The third assumption is likely false but greatly simplifies the model. Lamellar separation decreases during the filtration cycle, causing retention probability to increase. Consequently, the model will tend to overestimate particle retention probabilities, particularly for small particles. This bias will be stronger for mallards than for shovelers because the short lamellae of mallards allow retention probability to vary more over a filtration cycle compared to shovelers. The fourth assumption may not be true. Cycle rate may increase with decreasing cycle volume because the amplitude of the maxilla, mandible, and tongue are reduced, potentially compensating for some of the decrease in $V_{s,e}$. If so, the model will overestimate the severity of the trade-off between filtration rate and particle size selection.

Estimating Model Parameters

To estimate the relationship among $V_{s,e}$, $G_{s,i}$, and $M_{e,i}$, three-dimensional, computer-generated scale replicas of real skulls of a male mallard and northern shoveler were created (see fig. A2 in the appendix in the online edition of the *American Naturalist*). The computer software allowed me to replicate individual components of the foraging apparatus, assemble these components so they could be articulated realistically, and measure g_s, m_e, n_e, n_s, d_s, d_e, x, V_e, and V_s for a range of start and end positions of the maxilla and mandible. (For additional details on the construction of the replica skulls and parameter measurement, see the appendix in the online edition of the *American Naturalist*.)

Testing the Models

Model predictions were compared to estimates of mallard and shoveler foraging performance from three studies reported in the literature. Kooloos et al. (1989) measured cycle volume and prey retention probabilities of mallards and shovelers foraging for 5 s on 1 g of prey in each of four size classes: shrimp pulp (≤0.5 mm), poppy seeds (0.7–1.2 mm), millet (1.2–2.4 mm), and red milo (2.6–4.4 mm). To determine the effect of lamellar length on cycle volume and prey retention, Kooloos et al. (1989) shortened the maxillary and dorsal mandibular lamellae of shovelers by 3 and 2 mm, respectively, and those of the mallards by 1.5 and 0.5 mm, respectively. I duplicated their manipulation by shortening the lamellae of the replica skulls, remeasuring m_e, and recalculating $R_{s,e,i}$. Mott (1994) estimated the relationship between prey intake rate and prey density for mallards and shovelers foraging on small (0.4–0.6 mm) and medium (0.8–1.0 mm) *Daphnia magna*. Using the same methods, Tolkamp (1993) estimated the functional response of the same ducks foraging on large *D. magna* (1.2–1.4 mm) alone and mixed with detritus particles 0.25–1 mm in size.

To generate the model predictions for these studies, foraging performance was assessed assuming two strategies: maximize net energy intake rate and minimize the percent volume of detritus in the ingesta. Ducks should use the former strategy in the absence of detritus (assuming the cost of foraging is negligible) and the latter when detritus is present (assuming gut capacity is a greater constraint on daily energy intake rate than the time available to forage). Further, I assumed that all particles were spherical, that the net metabolizable energy content of prey was proportional to their volume, that detritus contained no metabolizable energy, and that particles were distributed equally among each size class over each particle's size range. I accounted for the effect of particle depletion on intake rate, although this effect was small.

To determine whether the ducks should exhibit shared or distinct resource preferences, I used the LS version of equation (1) to predict the performance of both species foraging on each prey size class in the absence of detritus and when detritus was present in all size classes. The foraging medium was composed of 1% prey and 26% detritus (when present) by total volume. Prey and detritus were distributed equally, by volume, among size classes by varying the number of particles in each size class. Particles ranged from 0 to 4.4 mm in diameter.

Results

The relationship among filtration rate, gape, and lamellar separation predicted by the models shows a number of similarities and differences between species (fig. 3). Shovelers are expected to achieve a greater range of gape values, while mallards should achieve a greater range of lamellar separation values. The greater gape of the shoveler is due to its thicker tongue (h) and larger minimum value of n_s, while the low lamellar separation values are due to its long, overlapping maxillary and mandibular lamellae. Wherever the two species can achieve the same values of maximum gape and minimum lamellar separation, shovelers are expected to attain filtration rates greater than those of mallards. The shoveler's larger, spatulate bill, thicker tongue, and greater lingual amplitude allow greater cycle volumes, despite a

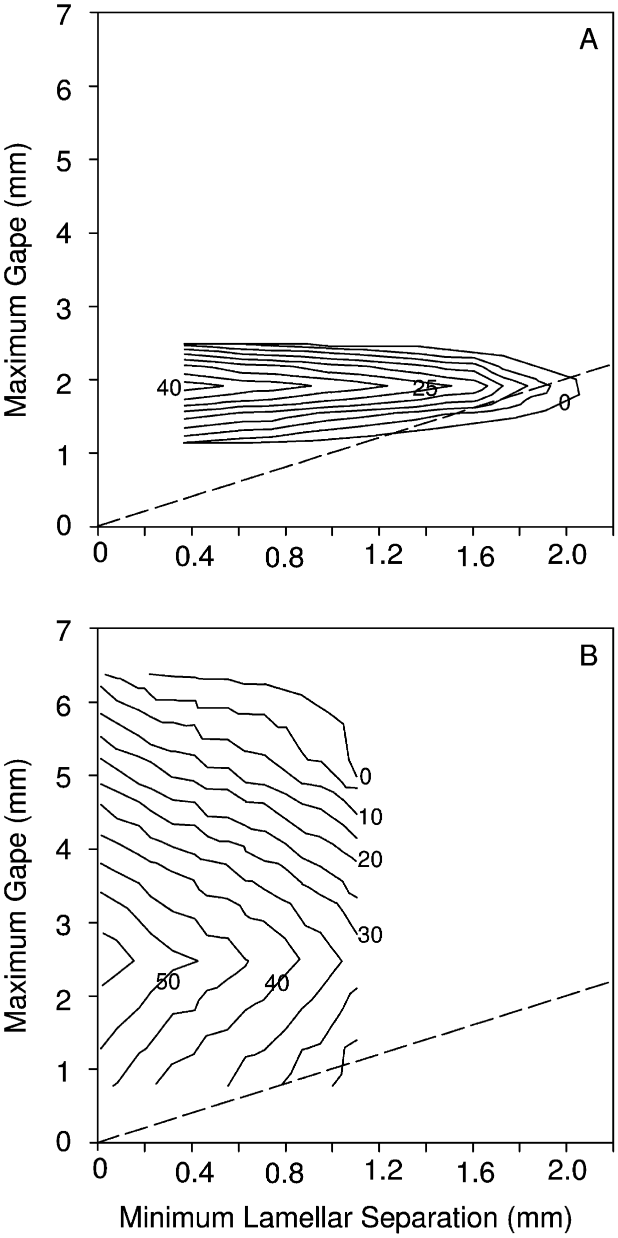

Figure 3: Relationship between lamellar separation, gape, and filtration rate (numerals and contour lines in mL/s) for mallards (*A*) and shovelers (*B*). The maximum value of gape (g_s) and minimum value of lamellar separation (m_s) for each bill position are plotted. As the difference between these two values declines, the size range of particles ingested declines and particle size selectivity increases. For both species, filtration rate is greatest when minimum lamellar separation is small and maximum gape is intermediate. Increasing selectivity requires maximum gape to decline, minimum lamellar separation to increase, or both, causing a decline in filtration rate. The dashed lines indicate bill positions for which size selectivity is maximized (i.e., maximum gape is equal to minimum lamellar separation). Mallards and shovelers are predicted to optimize selectivity and filtration rate when foraging on prey 1.7 and 0.8 mm in size, respectively.

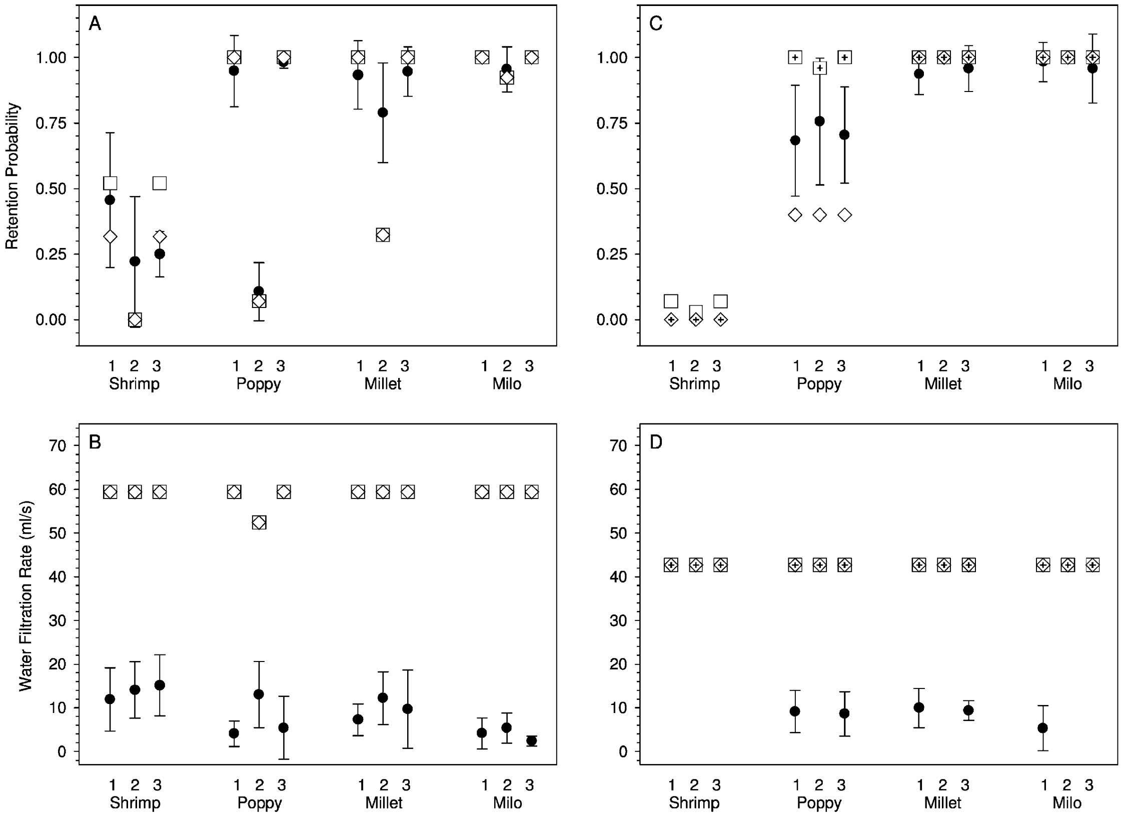

Figure 4: Comparison of predicted and observed (*filled circles*) performance of shovelers (*A*, *B*) and mallards (*C*, *D*) filter feeding on pulverized shrimp, poppy seed, millet seed, and milo seed (prey size increases from left to right). Error bars indicate 95% confidence intervals. Model predictions depend on which traits determine particle retention: lamellar separation alone (*squares*), lamellar separation and maxillary interlamellar distance (*diamonds*), or lamellar separation and mandibular interlamellar distance (*plus signs*). The maxillary and mandibular interlamellar distances of shovelers are equal, so these predictions are indicated by a single symbol (*diamonds*). Observed and expected performance are indicated following no change in lamellar length (*1*), shortening of the mandibular lamellae (*2*), and shortening of the maxillary lamellae (*3*). Mallards would not feed on shrimp. Data on water filtration rates were not reported for mallards with shortened mandibular lamellae foraging on any prey type or with shortened maxillary lamellae foraging on milo. Observed data are from Kooloos et al. (1989).

cycle rate lower than that of mallards. Both species will maximize their filtration rate when gape is at an intermediate value (2.5 mm for the shoveler and 1.9 mm for the mallard) at the start of the filtration cycle and lamellar separation is minimized at the end of the cycle. If gape is kept at these intermediate values, increasing lamellar separation from each species' minimum to 1.1 mm should reduce the filtration rate of shovelers by 43% (from 58.5 to 33.3 mL s^{-1}) compared to 25% (from 42.7 to 32.2 mL s^{-1}) for mallards. Shovelers should be unable to filter feed when their gape is larger than 2.5 mm because $l + h < d_s$ and when lamellar separation exceeds about 1.1 mm because $l + h < d_e$. Similarly, lamellar separation by mallards is limited to values below about 2.1 mm and gape to values below 6.5 mm. Both species should experience a decline in filtration rate with increasing particle size selectivity, but this decline should be greater for shovelers than for mallards. The net effect of these constraints is that mallards should be better at separating large prey from detritus, while shovelers should be better at separating small prey.

The particle retention probabilities predicted by the models were in good agreement with those measured by Kooloos et al. (1989; fig. 4*A*, 4*C*). Predictions of the LS and MAN models differed from those of the MAX model only when ducks were feeding on shrimp or poppy seeds, but the observed retention probabilities did not favor a specific model. However, as expected, the models tended to overestimate retention of small prey by shovelers (shrimp) and mallards (shrimp and poppy seeds) when prey were larger than the duck's interlamellar distance.

The shoveler model correctly predicted a large reduction in retention of poppy seeds with shortening of the mandibular lamellae and no change in retention with manipulation of the maxillary lamellae. The mallard model correctly predicted that retention should be insensitive to changes in length of either the mandibular or the maxillary lamellae. Although the models correctly predicted little variation in water filtration rate with variation in prey size or lamellar length, the predicted rates for both species were four to 24 times greater than the observed rates (fig. 4*B*, 4*D*).

The slope of the functional response predicted by both species' LS and MAN models rarely differed and closely tracked variation in the slope even though the predictions consistently underestimated the observed values for all species and treatment combinations (fig. 5). In contrast, the MAX mallard model performed poorly and incorrectly predicted that mallards would be unable to retain small or medium prey. The LS and MAN models predicted that both species could ingest large prey and avoid detritus if they accepted a reduction in both cycle volume and prey retention. Both mallard models predicted a decline in cycle volume from 2.26 to 1.77 mL and a decline in retention probability of large prey from 1 to 0.85. Both shoveler models predicted a decline in cycle volume from 4.57 to 2.68 mL and a decline in retention probability of large prey from 1 to 0.63. Both models accurately predicted the relative change in the slopes of the functional response for both species. The predicted declines were 31% and 60% for the mallard and shoveler, respectively, while Tolkamp (1993) measured mean declines of 27% and 51%. When ducks were assumed to maximize energy intake rate, the models predicted no change in cycle volume or prey retention and ingestion of 49% (MAN) or 92% (LS) of the detritus that entered the ducks' bills. The MAX mallard model incorrectly predicted no change in cycle volume or prey retention and no retention of detritus because detritus particles were smaller than the maxillary interlamellar distance.

In the absence of detritus, the models predicted that shovelers can achieve greater prey intake rates than mallards, regardless of prey size (fig. 6*A*). For both species, prey intake rate was predicted to increase sharply with increasing prey size until $M_{e,i} = 1$. Above this threshold, interspecific differences in intake rate are due to differences in cycle rate and cycle volume only. The presence of detritus had a strong effect on each species' predicted foraging performance. Avoidance of detritus should cause shovelers to ingest smaller prey than mallards (fig. 6*B*), reflecting the ability of each species to selectively ingest prey of different sizes (fig. 3).

Discussion

The mechanistic relationship between bill morphology and kinetics predicts that dabbling ducks must trade off prey size selection and water filtration rate because increasing lamellar separation to avoid small detritus particles, or decreasing gape to avoid large detritus particles, causes cycle volume to decline. The form of this trade-off is dependent on bill morphology, particularly lamellar length, allowing species to partition prey by size when prey co-occur with detritus. To the extent that the duck skulls used to parameterize the models are representative of the mean morphological state of each species, mallards should be more effective at selecting large prey from detritus because their short lamellae allow them to achieve bill positions in which gape and lamellar separation are similar when both are large. In contrast, shovelers should be more ef-

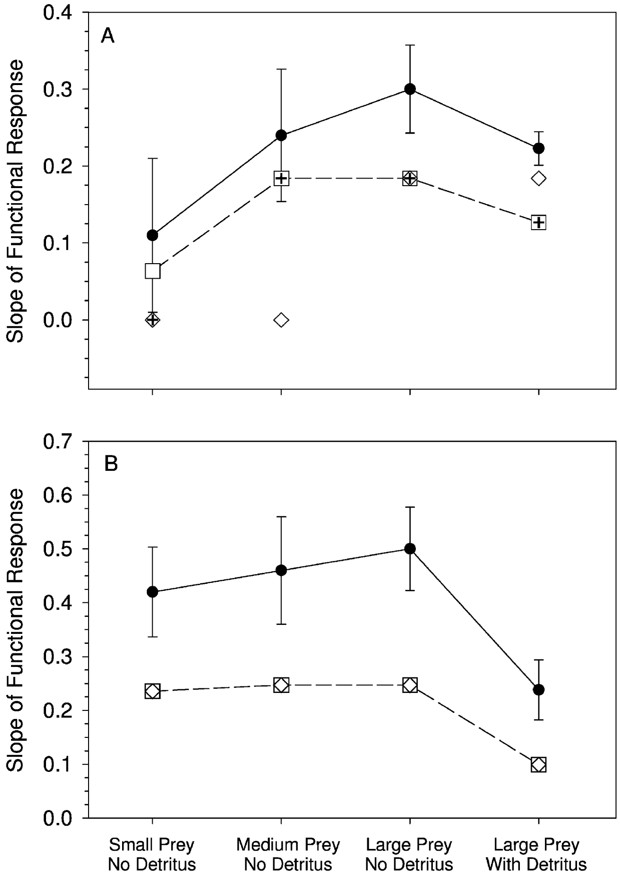

Figure 5: Comparisons of predicted and observed (*filled circles, solid line*) slopes of Type I functional responses of mallards (*A*) and shovelers (*B*) filtering *Daphnia* of three different sizes with or without detritus. Error bars indicate 95% confidence intervals. Model predictions depend on which traits determine particle retention: lamellar separation alone (*squares, dashed line*), lamellar separation and maxillary interlamellar distance (*diamonds*), or lamellar separation and mandibular interlamellar distance (*plus signs*). The maxillary and mandibular interlamellar distances of shovelers are equal, so these model predictions are given by a single symbol (*diamonds*). All model predictions assume that ducks forage to avoid ingesting detritus. Observed data are from Mott (1994) and Tolkamp (1993).

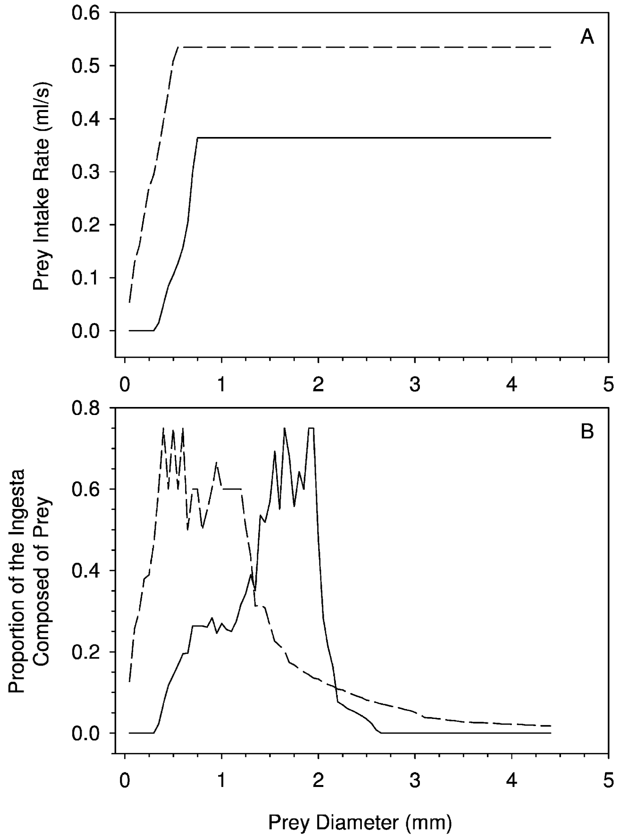

Figure 6: Foraging performance of mallards (*solid line*) and shovelers (*dashed line*) on prey of different sizes in the absence (*A*) and the presence (*B*) of detritus.

fective at selecting small prey because they can achieve values of gape and lamellar separation that are similar when both are small.

The ability of the models to predict the effect of detritus on the foraging performance of ducks provides strong support for the model. Avoiding detritus was the only foraging strategy that correctly predicted the reduction in prey intake rates. Tolkamp (1993) found that shovelers and blue-winged teal (*Anas discors*) avoided ingesting detritus, but he did not test whether mallards did as well. However, both mallards and shovelers are capable of selecting particles by size (Gurd 2006). Detritus caused the foraging rates of green-winged teal (*Anas crecca*) to decline, and the rates were lowest when prey and detritus were most similar in size, regardless of which was larger (van Eerden and Munsterman 1997). These results support the predictions that ducks can also increase particle selectivity by decreasing gape and that selectivity is based on differences in the size of prey and detritus.

The models were further supported by variation in the ducks' foraging performance following manipulation of the lamellae, but the models did not predict a decrease in retention by both species under all treatment and prey size combinations. Close inspection of the replica skulls revealed that both species likely used starting and ending bill positions in which minimum lamellar separation was defined by the distance between the tips of the mandibular lamellae and the base of the maxillary lamellae or the ventral surface of the maxilla. Neither of these distances was increased by shortening the maxillary lamellae. Lamellar separation of both species increased after the mandibular lamellae were shortened, but the amount they were shortened was much greater for shovelers (2 mm) than for mallards (0.5 mm). The manipulation was large enough to affect retention of shrimp pulp (<0.5 mm) and poppy seeds (0.7–1.2 mm) by shovelers but not retention of poppy seeds by mallards (i.e., retention is determined by the interaction between particle size and lamellar separation). Kooloos et al. (1989) rejected sieving as the mechanism of particle retention by mallards in favor of inertial impaction (Rubenstein and Koehl 1977) because shortening the lamellae did not reduce particle retention, as they had expected. Given that the model, which assumes a sieving mechanism, did not predict a reduction in retention by the mallards, Kooloos et al.'s (1989) rejection of sieving appears premature. In addition, Kooloos et al. (1989) showed that poppy seeds are retained medial to the mandibular lamellae in mallards, not in the interlamellar spaces of the maxilla, which is consistent with sieving by the mandibular lamellae and inconsistent with inertial impaction.

The models overestimated the water filtration rates measured by Kooloos et al. (1989) but underestimated the slope of the functional responses measured by Mott (1994) and Tolkamp (1993), even when large particles with high retention probabilities were being filtered. Flaws in the models or morphological differences between the ducks used in the foraging studies and the replica skulls may account for these differences, but the former seems unlikely, at least for the difference in water filtration rates. To account for the minimum fourfold difference, the linear dimensions of the bills of the replica skulls would have to be 1.6 times larger than those of the ducks used by Kooloos et al. (1989), which was not the case (table A1 in the appendix in the online edition of the *American Naturalist*).

Alternatively, three observations suggest that the foraging conditions experienced by the ducks differed between studies and from the model assumptions. First and most important, the observed data do not agree. Given the water filtration rates and particle retention probabilities measured by Kooloos et al. (1989), both mallards and shovelers foraging on poppy, millet, or milo seed would have exhibited functional responses with a slope of about

0.06 (Tolkamp 1993). This slope is five (mallard) and eight (shoveler) times smaller than the slope measured by Mott (1994) and Tolkamp (1993) for ducks feeding on *Daphnia magna* of similar size. Second, the absolute differences between the predicted slopes and those measured by Mott (1994) and Tolkamp (1993) were consistent across all treatment and species combinations, suggesting a systematic bias between the model predictions and the data. Third, the predicted relative change in the slopes due to the addition of detritus closely matched the data. Relative comparisons remove the contribution of C_i to the observed and predicted ingestion rates, suggesting that the ducks may have exploited prey concentrations greater than the mean densities reported in the studies. I duplicated the methods used by Mott (1994) and Tolkamp (1993) and found that prey and detritus became trapped in the current created by the air stones they used to keep prey and detritus mixed, creating local prey concentrations that exceeded the mean concentration in the bowl. Currents could have easily doubled the duck's prey encounter rate, accounting for the differences in slopes between the observed and predicted functional responses.

I suspect that the filtration rates reported by Kooloos et al. (1989) were low because they forced the ducks to feed with only their bill tips submerged. This would have forced the ducks to reduce their gape, and thus cycle volume, in order to create enough suction to move water into the oral cavity (Zweers et al. 1977). Kooloos et al. (1989) predicted filtration rates by estimating the change in volume of the posterior cavity, but they observed the bill positions of the foraging ducks and predicted filtration rates given these positions. Their model performed well when ducks were foraging on small prey but poorly when ducks foraged on large prey, which would have required larger gapes than small prey and decreased the ducks' ability to generate suction. Equation (1) assumes that gape is not constrained, which is more likely to be the case in Mott (1994) and Tolkamp's (1993) studies.

The models predict that prey size alone provides no opportunities for resource partitioning between mallards and shovelers, regardless of whether interlamellar distance or lamellar separation determines prey retention. Only when detritus is present are mallards and shovelers predicted to partition prey by size. Consequently, ducks should prefer prey of the same size when detritus is absent but have distinct prey size preferences when detritus is present. This may explain why some field studies indicate that ducks partition prey by size (Nudds and Bowlby 1984; Nummi 1993; Nudds et al. 1994; Guillemain et al. 2002) while other studies do not (Elmberg et al. 1993, 1994; Pöysä et al. 1994, 1996; Nummi and Väänänen 2001). Unfortunately, none of these studies quantified the size-frequency distribution of detritus. However, when partitioning was evident, almost all of the variation in prey size between species was due to prey larger than the interlamellar distance of any species, suggesting that ducks were avoiding detritus particles.

If dabbling ducks have shared prey size preferences, duck communities should exhibit centrifugal organization. Consistent with this prediction, interspecific overlap in the size of seeds consumed by wintering ducks declined with seed density (Guillemain et al. 2002). When seed density was lowest, mallards most frequently consumed seeds in a 1.6–3.0-mm size class, which corresponds well with the size of prey that mallards are predicted to select most efficiently (fig. 3). Shared preferences will make testing the implications of bill morphology for duck community structure more difficult. Future field studies will have to infer the expected distribution of species among habitats and resource use within habitats by predicting the foraging performance of each species given the size-frequency distribution of prey and detritus in each habitat.

Ecologists tend to assume that interspecific morphological differences cause distinct resource preferences rather than shared preferences (Wisheu 1998). I have shown that morphological differences can lead to shared preferences if the performance of all species is reduced by a common factor. This scenario should be widespread, perhaps explaining why shared preferences appear to be more frequent than distinct preferences (Wisheu 1998). In particular, shared preferences, and thus centrifugal community organization, may be common among filter feeders in which detritus imposes a common foraging cost.

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