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

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}).

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 (

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 he mia,4-mall.

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.

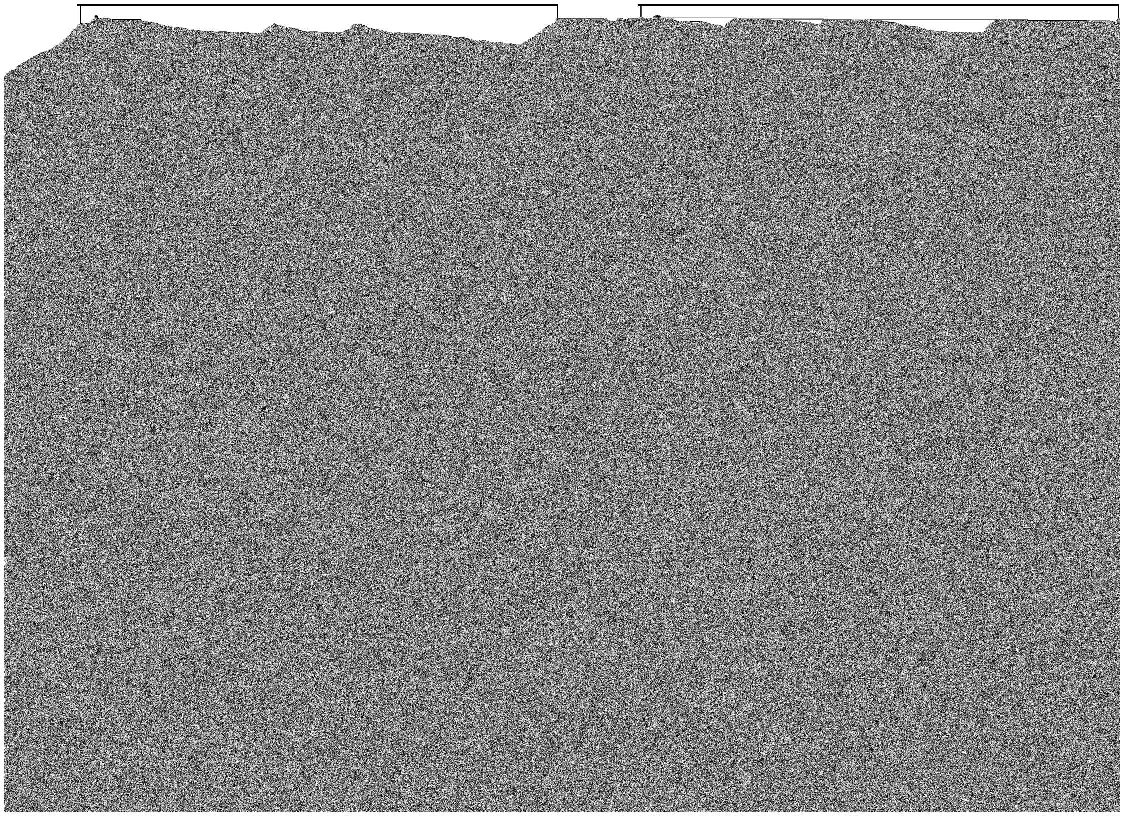

Figure 4: Comparison of predicted and observed (*filled circles*) performance of shovelers (*A*, *B*) and mallards (*C*, *D*) filter feeding on pulverized shrimp, poppy seed, millet seed, and milo seed (prey size increases from left to right). Error bars indicate 95% confidence intervals. Model predictions 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 cor-

Figure 5: Comparisons of predicted and observed (*filled circles, solid line*) slopes of Type I functional responses of mallards (*A*) and shovelers (*B*

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 par-